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New remains and new insights on the Gondwanan meiolaniform turtle *Chubutemys copelloi* from the Lower Cretaceous of Patagonia, Argentina ☆

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ABSTRACT

New cranial and postcranial remains of the Gondwanan meiolaniform turtle *Chubutemys copelloi* Gaffney, Rich, Vickers-Rich, Constantine, Vacca and Kool 2007 from the Lower Cretaceous Puesto La Paloma Member of the Cerro Barcino Formation (Chubut province, Patagonia, Argentina) are presented, described, and compared in this contribution. Carapace and plastral remains, pectoral and pelvic girdle, cervical and thoracic vertebrae, and the left maxilla and jugal are the new recovered elements from *C. copelloi*. These new remains were found in 2008 in Turtle Town locality, the same site where the holotype and referred specimens of *C. copelloi* had been found in 1997. The facies analysis of the sedimentary succession in Turtle Town and surrounding areas suggests a paleoenvironment constituted by a broad alluvial plain with influx of volcanic ash-falls, whose deposits were disturbed by pedogenesis or reworked by current flows that supplied water and sediment in ponded areas. The presence of a very thin shell, broad vertebrals (broader than pleurals), the presence of a shallow nuchal notch with the vertebral 1 almost reaching the anterior border of the carapace, the presence of costo-peripheral fontanelles, and the presence of an ectepicondylar canal in the humerus, are the most notable features provided by the new remains. A cladistic analysis has been performed to test the phylogenetic position of *C. copelloi*. This phylogeny corroborates the basal position of *C. copelloi* among Meiolaniformes. The plausible phylogenetic relationships of the clade Meiolaniidae with other Gondwanan (e.g., *Otwayemys cunicularius* Gaffney, Kool, Brinkman, Rich, and Vickers-Rich 1998) or Laurasian Lower Cretaceous taxa (e.g., sinochelyids) are also discussed in this contribution. Taxa included in Meiolaniformes have been mainly found in Gondwana and as the most basal taxon was found in Patagonia, paleobiogeographic studies suggest this clade originated in South America. Due to the basal position of *C. copelloi* among Meiolaniformes the discovery of more and previously unknown remains of this species sheds light on the origin and early evolution of this curious clade.

1. Introduction

Chubutemys copelloi Gaffney, Rich, Vickers-Rich, Constantine, Vacca and Kool 2007 was originally named and described by Gaffney et al. (2007). The description was based on an almost complete skull (holotype, MPEF-PV 1236), a fragment of a carapace with a cervical vertebra, thoracic vertebrae, scapula and humerus (MPEF-PV 1940), and three peripherals (MPEF-PV 1941, 1942, and 1943) recovered in field trips led by Dr. Rich and the Museo Egidio Feruglio (Trelew, Argentina) during 1997. *Chubutemys copelloi* and chelid turtle remains (Gaffney et al., 2007) were found in "Turtle Town" locality, Chubut Province, Argentina. "Turtle Town" is located on outcrops of the Puesto La Paloma Member of the Cerro Barcino Formation, Chubut Group, which would be Albian in age (J.M. Krause, pers. comm.). The phylogenetic position of *C. copelloi* seems to be consistent in different cladistic analyses. Gaffney et al. (2007) recovered *C. copelloi* as the basal most member of a Gondwanan clade also formed by *Otwayemys cunicularius* Gaffney, Kool, Brinkman, Rich, and Vickers-Rich 1998 and Meiolaniidae. This position was also recovered in Sterli and de la Fuente (in press) after the inclusion of characters and taxa to Sterli and de la Fuente's (2011a) paper. Recently, Sterli and de la Fuente (in press) named the clade formed by taxa more related to *Meiolania platyceps* Owen, 1886 than to Cryptodira and/or Pleurodira as Meiolaniformes. The most basal member of this clade is *C. copelloi*. This is also congruent with the stratigraphic distribution of the taxa because *C. copelloi* (Aptian–Albian), together with *O. cunicularius* (Aptian–Albian, Otway Group, Australia), is one of the oldest members of the clade.

Fieldwork conducted in 2008 to the Puesto La Paloma Member of the Cerro Barcino Formation leaded by Dr. de la Fuente resulted in the discovery of more cranial and postcranial remains of *C. copelloi* in "Turtle Town" locality. The objectives of the present contribution are to describe in detail the new remains, compare them with other meiolaniforms, and complete the character scoring of *C. copelloi* in a cladistic analysis of Meiolaniformes. Due to the basal position recovered

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for *C. copelloi* in previous analysis regarding the clade Meiolaniformes (Gaffney et al., 2007; Sterli and de la Fuente, 2011a; Sterli et al., 2013a, b; Sterli and de la Fuente, 2014) the discovery of more and unknown remains sheds light on the origin and early evolution of the group. The plausible relationships of other Early Cretaceous taxa with Meiolaniidae and the paleobiogeography of Meiolaniformes are also discussed in this contribution.

Institutional abbreviations: MPEF-PV, Colección Paleontología de Vertebrados, Museo Paleontológico Egidio Feruglio, Trelew, Argentina.

2. Geological setting and paleoenvironment

The study area, including the locality referred herein as Turtle Town, is located about 290 km westward from the Trelew city, Chubut province, Argentina (Fig. 1a). Extensive outcrops belonging to the Cretaceous Chubut Group occur in the area, which are part of the postrift deposits of the Somuncurá-Cañadón Asfalto Basin (Fig. 1a; Figari and Courtade, 1993; Cortiñas, 1996; Ranalli et al., 2011). The Chubut Group overlies Mesozoic synrift deposits including the Middle Jurassic

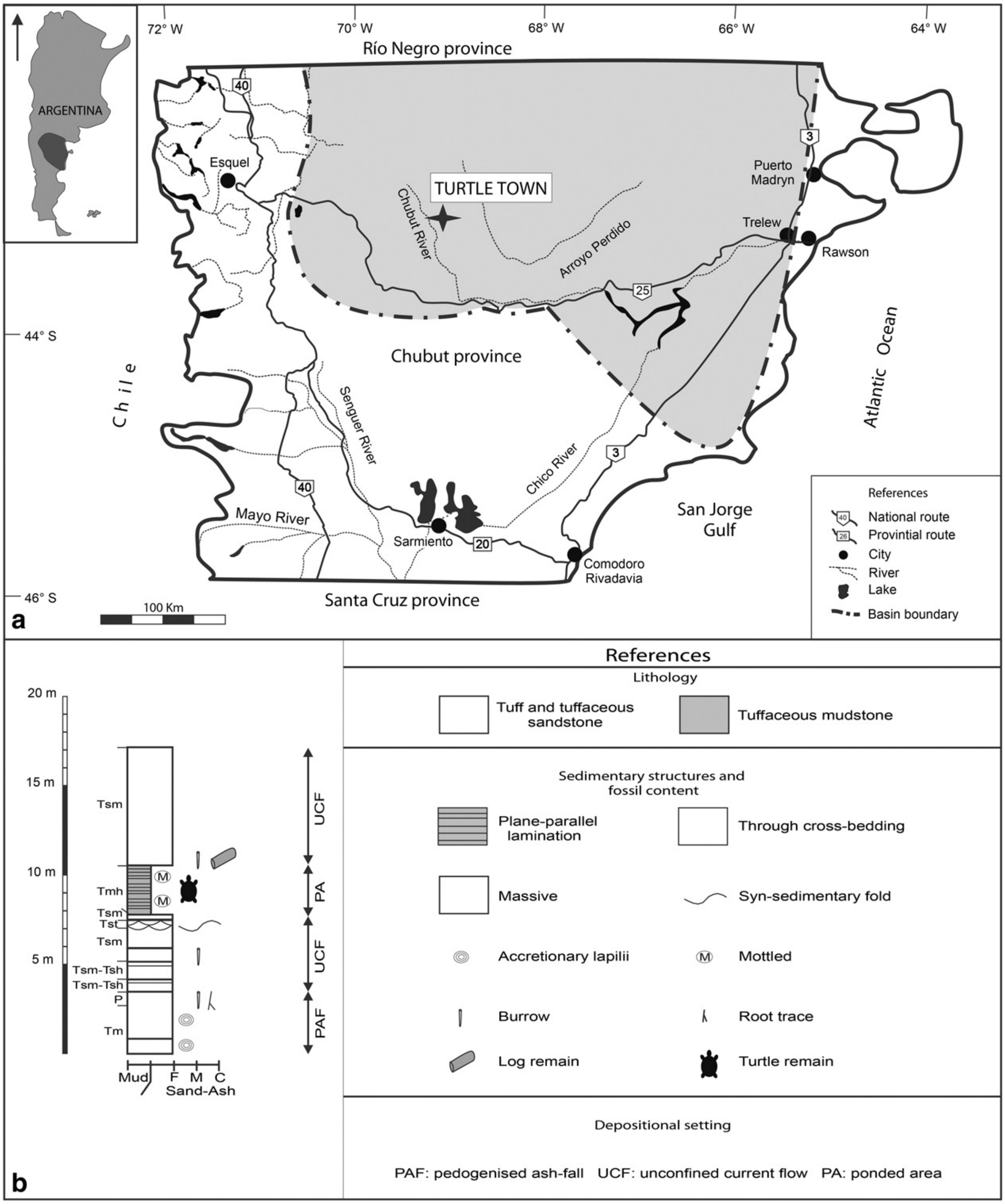

Fig. 1. a, Location map of the Somuncurá-Cañadón Asfalto Basin, including "Turtle Town" Locality, within the Chubut Province (Patagonia, Argentina). b, Measured sedimentary log, which shows the turtle remains and the inferred sedimentary paleoenvironments.

Lonco Trapial Group, a volcano-sedimentary sequence (Lesta and Ferello, 1972; Lizuain and Silva Nieto, 2005), as well as Middle Jurassic to Lower Cretaceous lacustrine and fluvio-lacustrine sediments with volcanic intercalations assigned to Cañadón Asfalto and Cañadón Calcáreo formations (Proserpio, 1987; Cabaleri and Armella, 1999, 2005; Cabaleri et al., 2005; Volkheimer et al., 2008, 2009; Gallego et al., 2011). The recently proposed Sierra de la Manea Formation is approximately equivalent to the Cañadón Calcáreo Formation (Figari, 2011). On the other hand, the Chubut Group is locally covered by Upper Cretaceous to Quaternary, marine and continental deposits (Malumián, 1999), or Cenozoic basalts (Ardolino and Franchi, 1993).

Two stratigraphic schemes have been proposed for the Chubut Group in the studied area. According to one of these, the Chubut Group is composed of the Los Adobes and Cerro Barcino formations (Codignotto et al., 1978). Los Adobes Formation is characterized by conglomerates and sandstones, both with channel-like geometry, interbedded with tabular, finer grained, mostly siliciclastic sediments. This succession records a fluvial environment composed by different types of channels that crossed a vegetated floodplain (Codignotto et al., 1978; Allard et al., 2009, 2010a,b). The overlying Cerro Barcino Formation is an alluvial, pyroclastic-rich succession, which can be divided in four members using the dominant coloration of the strata. From base to top, they are: Puesto La Paloma (green), Cerro Castaño (reddish), Las Plumas (pinkish and reddish), and Puesto Manuel Arce (gray). In some parts of the basin, the Puesto Manuel Arce Member is replaced by greenish yellow tuffs denominated Bayo Overo Member. The lower part of the Cerro Barcino Formation (Puesto La Paloma Member) is essentially composed of strata with sheet to lobe morphology; it mainly records unconfined alluvial sedimentation with high pyroclastic sediment supply (Allard et al., 2010c; Umazano, 2010; de la Fuente et al., 2011; Umazano and Krause, 2013). The remaining members are mostly constituted by channeled sandstones interbedded with sheet-like, thicker and finer grained tuffaceous sediments. These members represent a fluvial paleoenvironment (Manassero et al., 2000; Cladera et al., 2004; Foix et al., 2012; Umazano et al., 2012; Umazano and Krause, 2013), in which the spatial and temporal changes in the channel configuration were highly influenced by the differential influx of pyroclastic detritus (Manassero et al., 2000; Cladera et al., 2004).

The turtle remains were collected in Turtle Town from a level assigned to Puesto La Paloma Member (Fig. 1a). An Aptian–Albian (?) age is assigned to this unit according with the biostratigraphic data from Cañadón Calcáreo, Los Adobes and Cerro Barcino formations (Musacchio, 1972; Musacchio and Chebli, 1975; Llorens and Marveggio, 2009; Volkheimer et al., 2009); this criteria was also used by de la Fuente et al. (2011). Accordingly, the recent radiometric ages obtained from tuffaceous strata of the lower and upper parts of the Puesto La Paloma Member suggest an Albian age (J.M. Krause, pers. comm.). At Turtle Town the sedimentary section is poorly exposed and vertically limited; therefore, a thicker sedimentary log was measured at the adjacent Estancia La Madrugada locality, in which the turtle-bearing strata have been positioned (Fig. 1b). The measured sedimentary section underlies to the Cerro Castaño Member, whereas the contact with Los Adobes Formation is covered.

The studied section has 17 m of thickness and is composed of sheet-like tuffaceous sandstones with subordinated participation of tuffs and tuffaceous mudstones (Fig. 1b). Commonly, the tuffaceous sandstone beds show scarce intraclasts and scour and fill structures in their bases. The lowermost 3.5 m of the succession includes massive tuffs with accretionary lapilli disposed in bodies with mantle bedding and non-erosive base (facies Tm); the top of this stratigraphic interval shows vertical burrows and root traces (facies P). The remaining 13.5 m of the succession is mostly composed of massive tuffaceous sandstones (facies Tsm) which occasionally bear transported log remains and vertical burrows; involvement of tuffaceous sandstones with plane parallel lamination (facies Tsl) or through cross-bedding and syn-sedimentary folds (facies Tst) is rare. Approximately 7 m below the contact with the Cerro Castaño Member, there is an intercalation (3.90 m thick) of laminated and occasionally mottled tuffaceous mudstones (facies Tmh) in which the turtle remains occur. The facial description of the unit suggests a broad alluvial plain with influx of volcanic ash via atmospheric settling (facies Tm); these primary pyroclastic detritus were pedogenised (facies P) or reworked by unconfined current flows (facies Tsm, Tsh and Tst) that supplied water and sediment in ponded areas (facies Tmh).

Regarding the paleontological content of the unit, the Cerro Barcino Formation has yielded a rich fauna of tetrapods. Among them eilenodontin sphenodontians, peirosaurid crocodylomorphs, theropod (e.g., Abelisauridae, Carcharodontosauridae, Coelurosauria, Ceratosauridae) and sauropod (titanosauriforms) dinosaurs, and chelid turtles have been collected in the same lithostratigraphic unit as *C. copelloi* (Rauhut et al., 2003; Rauhut, 2004; Novas et al., 2005; Leardi and Pol, 2009; Carballido et al., 2011; de la Fuente et al., 2011; Apesteguía and Carballido, 2014).

3. Materials and methods

Chubutemys copelloi was included in the cladistic analysis of Sterli and de la Fuente (in press) and by then 78 of 240 characters have been scored based on the skull (MPEF-PV 1236) and few postcranial remains (MPEF-PV 1940). The discovery of new remains of *C. copelloi* (attributed to MPEF-PV 1940) allowed us scoring 12% more characters (106 of 240) in the data set. The resulting data set has 240 characters and 101 taxa (4 outgroups and 97 in the ingroup) (Appendices A, B, C). The ingroup is formed by extant and extinct species of turtles. The cladistic analysis was performed using TNT (Goloboff et al., 2008a,b). All characters were equally weighted and all the characters showing a clear morphocline have been ordered (21 in total, Appendix B). One thousand replicates starting from Wagner trees were perturbed using Tree Bisection Reconnection (TBR) algorithm to find the most parsimonious trees (MPTs). In the following step, all the MTPs were subject of a second round of TBR to find all the possible MPTs. Consistency and retention indexes (CI and RI) were also calculated using TNT. Bremer support and Jackknife and bootstrap resamplings have been computed for branch support. Jackknife and bootstrap values have been calculated using 1000 replicates and both absolute and difference of frequencies (GC of Goloboff et al., 2003). If more than one MPT was found, a strict consensus tree was calculated. Furthermore, if the strict consensus tree had big polytomies in the region where we are interested in, the script written by Pol and Escapa (2009) has been run. This script iteratively looks for the most unstable taxa (wildcard taxa), prunes them from the strict consensus and shows why the/these taxon/taxa is/are unstable (due to contradicted characters or missing data) (Pol and Escapa, 2009).

4. Systematic paleontology

Testudinata Klein, 1760

Meiolaniformes Sterli and de la Fuente, in press

Chubutemys copelloi Gaffney, Rich, Vickers-Rich, Constantine, Vacca and Kool, 2007

Figs. 2–8

Holotype: MEPF-PV 1236, almost complete skull. In the field trip of December 2008, the left maxilla and the left jugal of MPEF-PV 1236 were found. Both bones are missing in the specimen described by Gaffney et al. (2007) and they fit in the preserved skull. Consequently, it is likely that they belong to that specimen.

Referred material: In the same spot (1 m^2) where the left maxilla and left jugal were found in 2008 (and where more than ten years before the skull MPEF-PV 1236 was found), the postcranial remains described here were also found which in turns fits with the postcranial remains described in Gaffney et al. (2007) under MPEF-PV 1940. The size of the skull and postcranial remains plus the proximity where they were found would suggest MPEF-PV 1236 and 1940 could belong

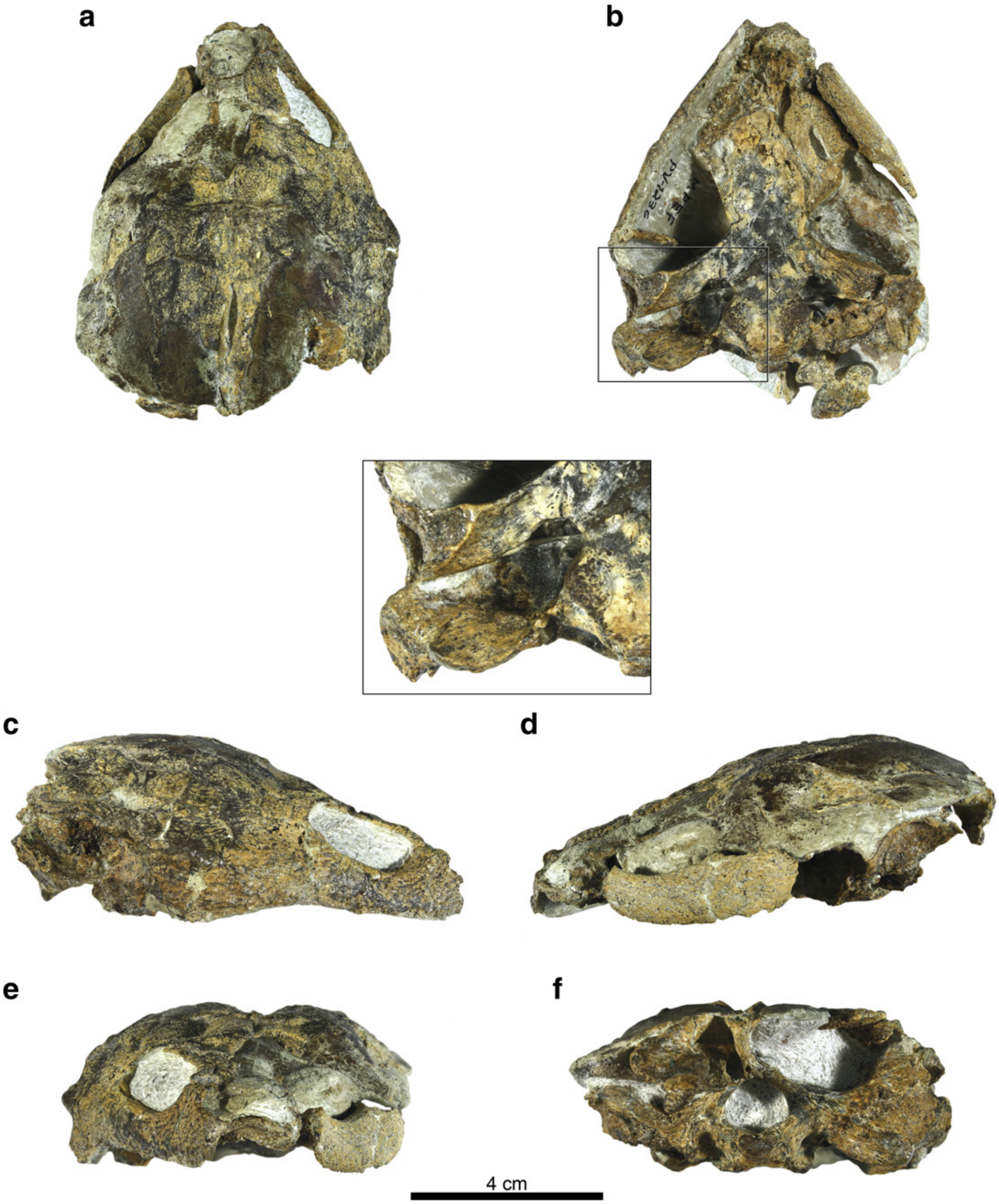

Fig. 2. Photographs of the skull of *Chubutemys copelloi* MPEF-PV 1236, Turtle Town, Chubut, Patagonia; Lower Cretaceous; a: dorsal; b: ventral (with a zoom in); c: left lateral, d: right lateral, e–f: anterior and posterior views.

to the same individual. However, as the skull and the shell remains have been published with two different collection numbers (MPEF-PV 1236 and 1940, respectively) by Gaffney et al. (2007), in the sake of clarity we decided to keep both numbers. MPEF-PV 1940, carapace remains (nuchal almost complete, peripherals 1–11 from the right side and peripherals 1–2 and 11 from the left side, costals 1–8 from the right side and 1–2, 5, 7, and 8 from the left side, preneural, neurals 1–2 and 4–6, suprapygal), entoplastron, both hyoplastra, both hypoplastra, cervical vertebra 8, thoracic vertebrae 1–3, ?5, and 10, both scapulae, both illia, and other fragments of pelvic remains, both humeri, and probably a distal end of the right femur and the proximal end of the right? tibia. MPEF-PV 1941, peripheral bone. MPEF-PV 1942, peripheral bone. MPEF-PV 1943, peripheral bone.

Type locality and horizon: “Turtle Town”, Paso de Indios Department, Chubut Province, Argentina. Puesto La Paloma Member (contrary to Gaffney et al., 2007), Cerro Barcino Formation, Chubut Group (Codignotto et al., 1978). In the abstract and in the horizon under Systematics Gaffney et al. (2007) pointed out *C. copelloi* was found in the Cerro Castaño Member of the Cerro Barcino Formation. However, under Geology in the same paper Gaffney et al. (2007) pointed out that ‘All of the vertebrate fossils recovered from “Turtle Town” were found lying on the upper surface of outcrops of the La Paloma Member.’ Fieldwork studies suggest the last option is the correct one. Aptian–Albian in age (Musacchio, 1972; Musacchio and Chebli, 1975; Llorens and Marveggio, 2009; Volkheimer et al., 2009) or Albian (J.M. Krause, pers. comm.).

Emended diagnosis: *Chubutemys copelloi* belongs to Testudinata because it has a complete shell (formed by interlocking neurals, nuchal, pygal, peripherals and costals) enclosing the pectoral girdle. *Chubutemys copelloi* is characterized by the unique combination of characters such as: frontal not entering the orbit; supratemporal emargination absent; cheek emargination absent; absence of an extensive supraoccipital–

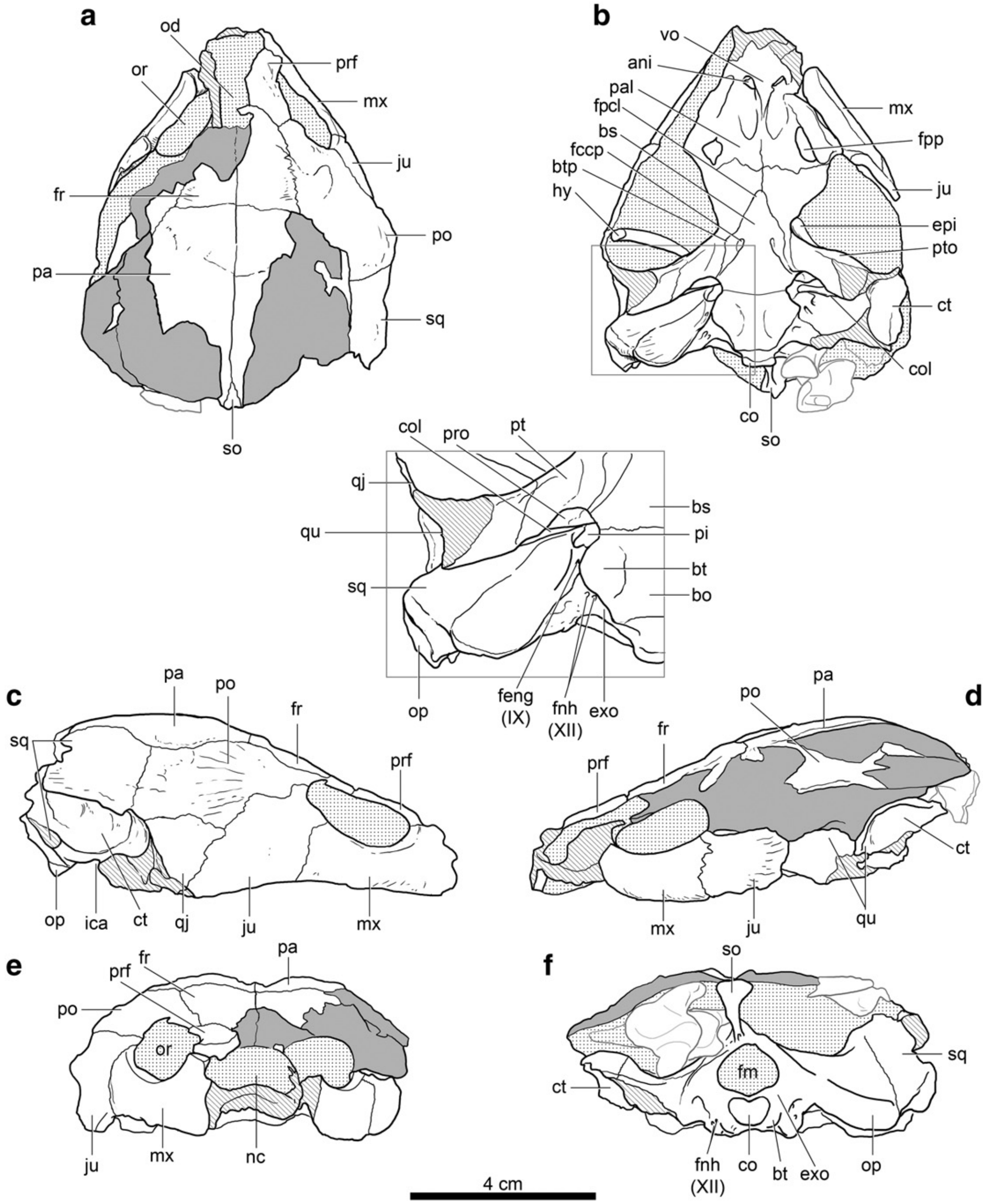

Fig. 3. Drawings of the skull of *Chubutemys copelloi* MPEF-PV 1236, Turtle Town, Chubut, Patagonia; Lower Cretaceous; a: dorsal; b: ventral (with a zoom in); c: left lateral; d: right lateral; e–f: anterior and posterior views. Abbreviations: ani, aperture nariun interna; bo, basioccipital; bs, basisphenoid; bt, tubera basioccipitalis; btp, basis tuberculus basalis; co, condylus occipitalis; col, columella; ct, cavum tympani, epi, epipterigoyd; exo, exoccipital; fccp, foramina carotici cerebralis posterior; feng, foramen externum nervi glosopharyngei; fm, foramen magnum; fnh, foramen nervi hypoglossi; fpcl, foramina posterior carotici lateralis; fpp, foramen palatinum posterius; fr, frontal; hy, hyoids; ica, incisura columella auris; ju, jugal; mx, maxilla; nc, nasal cavity; od, olfactory duct; op, opisthotic; or, orbit; pa, parietal; pal, palatine; pi, processus interfenestralis; po, postorbital; prf, prefrontal; pro, prootic; pt, pterygoid; pto, processus trochlearis oticum; qj, quadratojugal; qu, quadrate; so, supraoccipital; sq, squamosal; vo, vomer. In grey: mold. Spotted texture: sediment. Stripped texture: broken surfaces.

squamosal contact; jugal reaching the orbit; long contact between postorbital and squamosal; medial thick crest all along the vomer (which is wider in the anterior and posterior ends); absence of parasagittal choanal groves; large and elongated foramen palatinum posterius; foramina carotici cerebralis posterior located on the basisphenoid and foramina carotici lateralis located in between the basisphenoid and pterygoid; presence of only a tall labial ridge on palatal triturating surface; basipterygoid (=basitrabecular) process present; pterygoid not forming part of the foramen palatinum posterius; basisphenoid pentagonal in ventral view; basioccipital not contacting pterygoid; part of the prootic seen in ventral view; reduced processus interfenestralis and visible in ventral view; very thin shell; nuchal bone without nuchal notch; vertebral 1 almost reaching the anterior border of the carapace; cervical reduced or absent; plastron loosely articulated; entoplastron with a long posterior process and with two anterior concavities separated by a blunt crest in the anterior part; scapula with a thin lamina between the dorsal process and the acromion; costals with free ribs attached to peripheral bones through peg-and-socket structure; costo-peripheral small fontanelles; carapace–plastron attachment by ligaments and peg-and-socket structure. *Chubutemys copelloi* shares with basal turtles broad vertebrals, broader than pleurals. *Chubutemys copelloi* shares with other Meiolaniformes the presence of large exposure of the prefrontal and the exclusion of the frontal in the orbital rim; processus trochlearis oticum present; marginal sulci with an anterior marked inflection; the

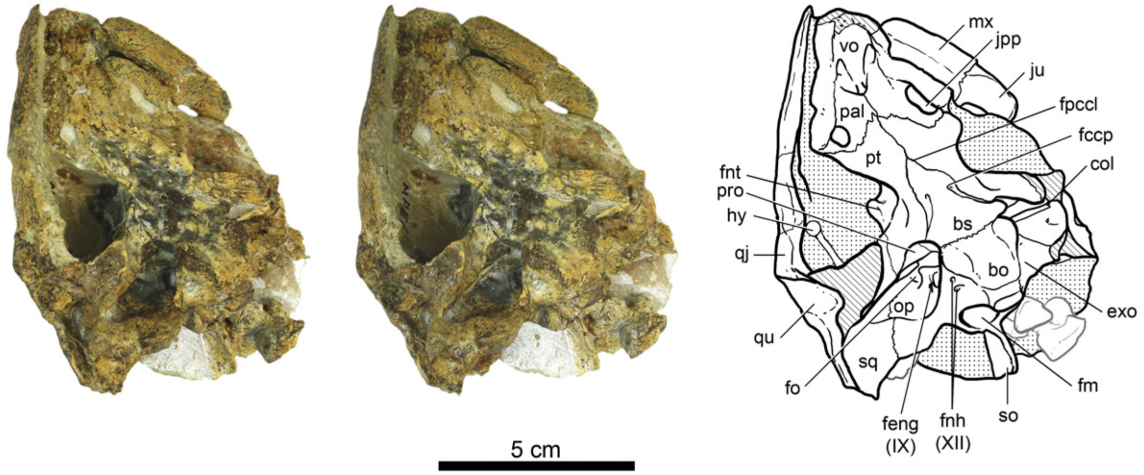

Fig. 4. Stereophotographs and schematic drawing of *Chubutemys copelloi* MPEF-PV 1236 (Turtle Town, Chubut, Patagonia; Lower Cretaceous) in posteroventrolateral view. Abbreviations: bo, basioccipital; bs, basisphenoid; col, columella; exo, exoccipital; fccp, foramina carotici cerebralis posterior; feng, foramen externum nervi glossopharyngei; fm, foramen magnum; fnh, foramen nervi hypoglossi; fnt, foramen nervi trigemini; fo, fenestra ovalis; fpcl, foramina posterior carotici lateralis; fpp, foramen palatinum posterius; hy, hyoid; ju, jugal; mx, maxilla; op, opisthotic; pal, palatine; pro, prootic; pt, pterygoid; qj, quadratojugal; qu, quadrate; so, supraoccipital; sq, squamosal; vo, vomer. Spotted texture: sediment. Stripped texture: broken surfaces.

socket for the reception of the rib is located in the rear part of the peripheral bone; bridge peripherals “C”-shaped, tall, flatten dorsally. It differs from *Mongolochelys efremovi* Khozatskii, 1997, *Niolamia argentina* Ameghino, 1899, and *Me. platyceps* by the absence of an extensive supraoccipital–squamosal contact. *Chubutemys copelloi* differs from other meiolaniforms by the presence of only a tall labial ridge on palatal triturating surface. The basisphenoid is triangular in ventral view, not rectangular as in *Kallokibotion bajazidi* Nopcsa, 1923 and *Mo. efremovi*. Shares with *Patagoniaemys gasparinae* Sterli and de la Fuente, 2011a a sulcus between vertebrals 3 and 4 mainly on costal 6, crossing to costal 5. Shares with *P. gasparinae* and *Mo. efremovi* in the presence of a wide and short, trapezoidal nuchal.

5. Description

5.1. Skull

The skull was previously described by Gaffney et al. (2007). During the field work of 2008, the left maxilla and left jugal of the holotype was found. The left maxilla and jugal fit perfectly in the holotype of *C. copelloi* (MPEF-PV 1236), and as they were found in the same quarry as the remaining parts of the postcranium (MPEF-PV 1940), it is likely that all of them belong to the same individual. Besides this new finding we re-prepared and re-studied *C. copelloi* holotype and found out some differences in the interpretation of several structures in the skull. In this regard a new interpretation of *C. copelloi* skull is given.

5.1.1. Dermal roofing elements

The dermal roofing elements are eroded, consequently we cannot assess whether the cranial scutes had been present or not.

5.1.1.1. Nasal. As Gaffney et al. (2007) noticed, the anterior region of the skull is badly damaged; consequently the presence or absence of nasal cannot be defined.

5.1.1.2. Prefrontal (Figs. 2–3a, c–e). As pointed out by Gaffney et al. (2007) both prefrontals are eroded. The most superficial layer of bone of the right prefrontal has been eroded, while all the horizontal process of the left prefrontal has been eroded as well which makes the ventral process visible. The general shape of the prefrontal recognized by us is very similar to that presented by Gaffney et al. (2007). The prefrontal contacted the maxilla anterolaterally, the vomer ventrally, the postorbital posterolaterally, the frontal posteromedially, and likely the nasal anteriorly. Although the medial part of prefrontals is missing it is highly probable they contacted each other in the midline (Gaffney et al., 2007). On the contrary, in *K. bajazidi* the prefrontals do not meet in midline because the maxilla is in between anteriorly and the frontal posteriorly. In *C. copelloi* and *Me. platyceps* the prefrontal together with the postorbital forms the dorsal margin of the orbit in equivalent proportions, precluding the frontal to reach the orbital margin, whereas in *K. bajazidi* the prefrontal forms 2/3 of the dorsal margin of the orbit, and only the postorbital the remaining 1/3.

5.1.1.3. Frontal (Figs. 2–3, a, c–e). Both frontals are eroded; however, the right frontal preserves much of its general shape. Our interpretation of the frontal bone is different from Gaffney et al.'s (2007) reconstruction. In our interpretation the frontal is triangular in shape and is larger, than in Gaffney et al.'s (2007) study, although the contacts are the same. The frontal contacts the prefrontal anteriorly, the postorbital laterally, the parietal posteriorly, and the other frontal medially. The frontal does not reach the orbital margin (Gaffney et al., 2007).

5.1.1.4. Parietal (Figs. 2–3a, c–e). As our interpretation of the frontal is different from that of Gaffney et al.'s (2007) reconstruction, the shape of the parietal is also affected. In this case the parietal is shorter than in Gaffney et al.'s (2007) reconstruction, but it is still longer than wide and the contacts are the same. Parietal contacts frontal anteriorly, postorbital anterolaterally, squamosal posterolaterally, the other parietal medially, and supraoccipital posteomedially. The ventral process of the parietal is present because the foramen trigemini is enclosed; however its extension cannot be established. Contrary to the generalized condition seen in other turtles (see Gaffney, 1979a), in meiolaniforms such as *Me. platyceps* the processus inferior parietalis is relatively short anteroposteriorly and barely forms the posterior margin of the foramen interorbitale. Most of the parietal bone is missing; however the mold of this bone is preserved. It is seen that *C. copelloi* has a complete skull roof which goes further back than the occipital condyle showing no dorsal emargination (Gaffney et al., 2007). This condition is recognized in other Meiolamiformes such as *K. bajazidi*, *Mo. efremovi*, and Meiolaniidae and in Chelonioidea.

5.1.1.5. Jugal (Figs. 2–3, a–e; Fig. 4). Contrary to Gaffney et al. (2007), this description is based on both jugals. The jugal contacted the maxilla anteriorly, the postorbital dorsally, and the quadratojugal posteriorly.

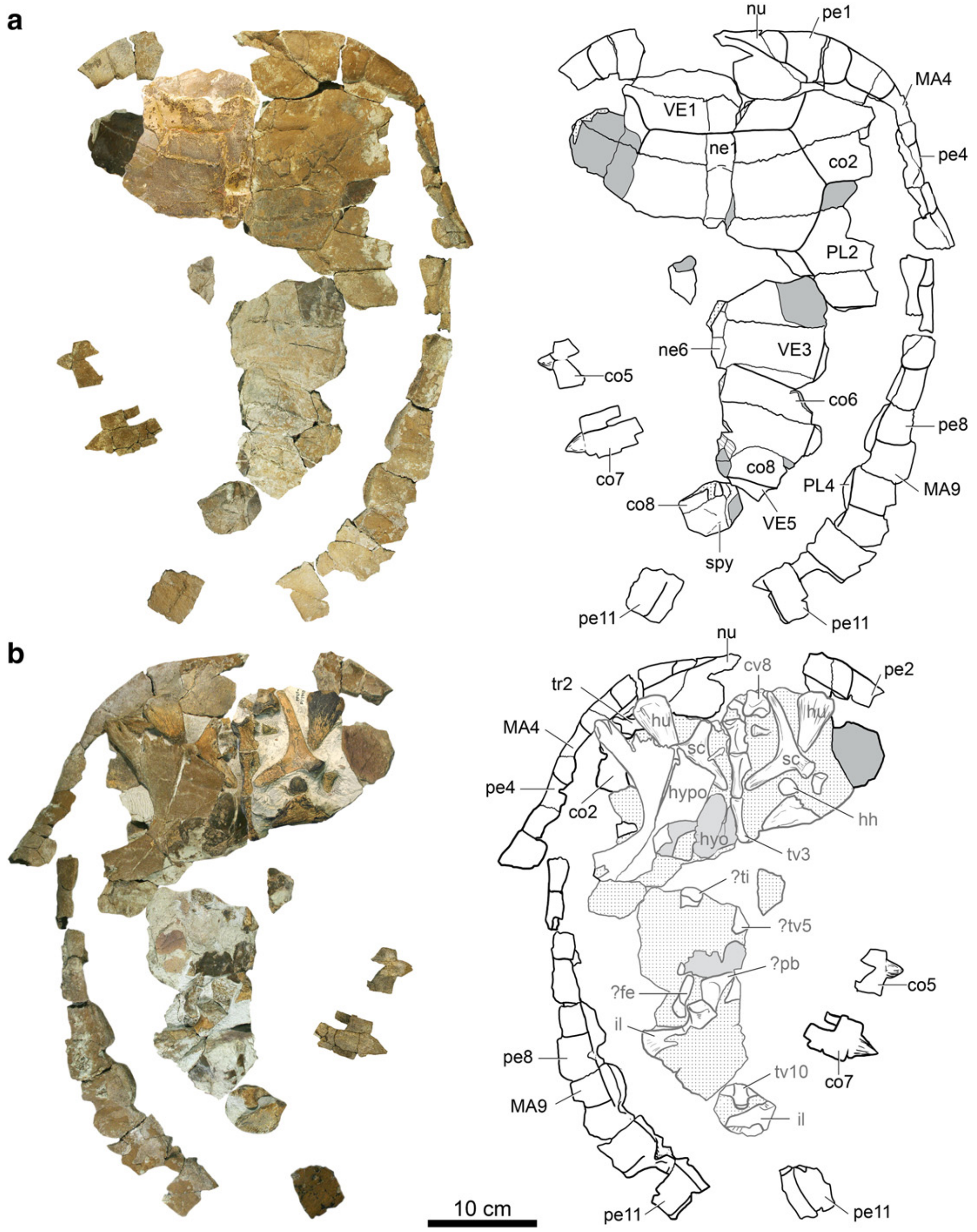

Fig. 5. Carapace of *Chubutemys copelloi* MPEF-PV 1940, Turtle Town, Chubut, Patagonia; Lower Cretaceous; a: dorsal view (photograph and drawing); b: ventral view (photograph and drawing). Abbreviations: co, costal; cv, cervical vertebra; ?fe, femur; hh, head of the humerus; hu, humerus; hyo, hyoplastron; hypo, hypoplastron; il, ilium; MA, marginal; ne, neural; nu, nuchal; ?pb, pubis; pe, peripheral; PL, pleural; sc, scapula; spy, suprapygal; ti, tibia; tv, thoracic vertebra; VE, vertebral. In grey: mold. Spotted texture: sediment.

The jugal is a flat bone with a minor contribution to the posterior margin of the orbital rim and with a major contribution to the cheek region. As it was pointed out by Gaffney et al. (2007) no cheek emargination is present in *C. copelloi*. A similar condition is seen in other Meiolaniformes (e.g., *K. bajazidi*, *Mo. efremovi*, *M. platyceps*, and *N. argentina*) and basal turtles (e.g., *Proganochelys quenstedti* Baur, 1887, *Palaeochersis talampayensis* Rougier et al., 1995, *Kayentachelys aprix* Gaffney et al., 1987).

5.1.1.6. Quadratojugal (Figs. 2–3, b–d; Fig. 4). Only the right quadratojugal is present in *C. copelloi*. The right quadratojugal is broken posteriorly avoiding any description of the posterior end. This bone contacts the jugal anteriorly, postorbital dorsally, and quadrate medially.

5.1.1.7. Squamosal (Figs. 2–3, a–c; Fig. 4). Only a small fragment of the right squamosal is preserved in *C. copelloi*'s holotype. The squamosal contacts opisthotic ventromedially, quadrate anteroventrally, postorbital anteriorly, and parietal medially. It is highly probable that the squamosal formed the lateral wall of the well-formed antrum postoticum.

5.1.1.8. Postorbital (Figs. 2–3, a, c–e). The postorbital, as most bones, is better preserved on the right side. The postorbital is a long bone forming the posterior rim of the orbit. This bone contacts the jugal anteroventrally, quadratojugal posteroventrally, squamosal posteriorly, parietal posteromedially, frontal anteromedially, and prefrontal anteriorly.

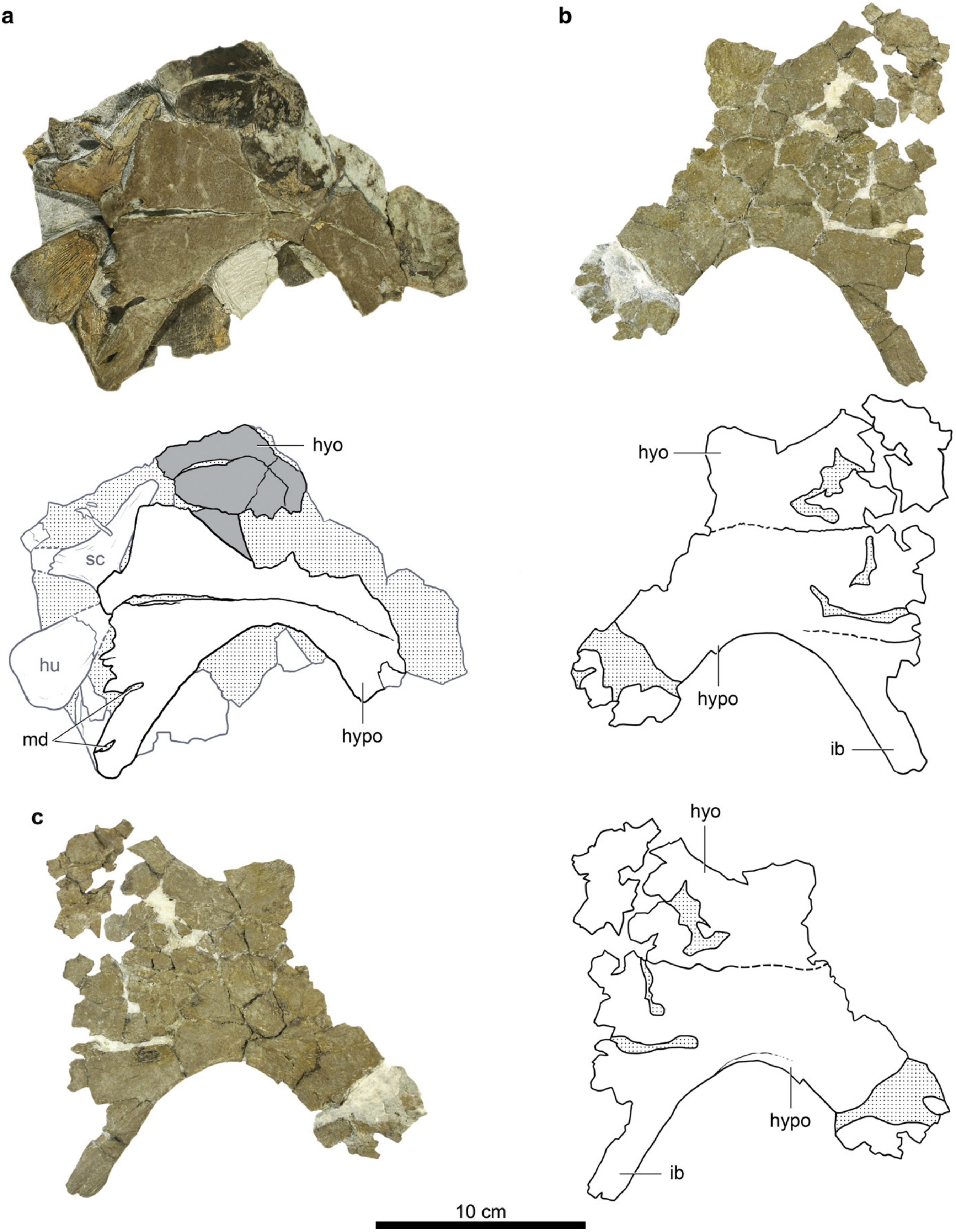

Fig. 6. Plastron of *Chubutemys copelloi* MPEF-PV 1940, Turtle Town, Chubut, Patagonia; Lower Cretaceous; a: right hyo–hypoplastron in ventral view: photograph and drawing; b: left hyo–hypoplastron in ventral view (photograph and drawing); c: left hyo–hypoplastron in visceral view (photograph and drawing). Abbreviations: hu, humerus; hyo, hyoplastron; hypo, hypoplastron; ib, inguinal buttress; md, musk duct; sc, scapula. In grey: mold. Spotted texture: sediment.

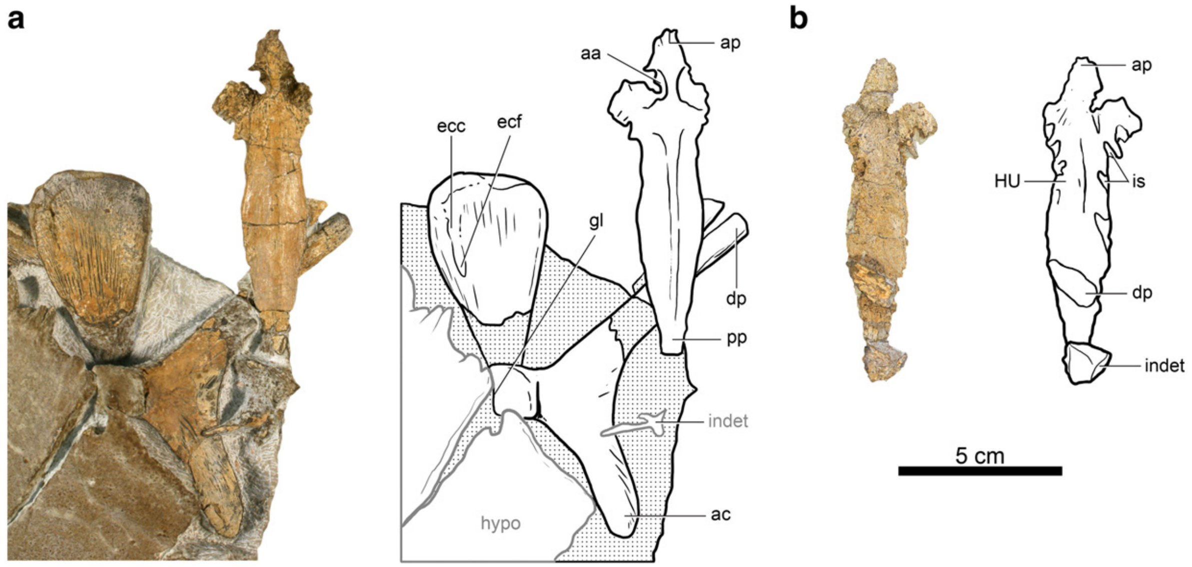

Fig. 7. Entoplastron of *Chubutemys copelloi* MPEF-PV 1940, Turtle Town, Chubut, Patagonia; Lower Cretaceous; a: visceral view: photograph and drawing; b: ventral view: photograph and drawing. Abbreviations: aa, articulation with the acromion; ac, acromion; ap, anterior process; dp, dorsal process; ecc, ectepicondylar canal; ecf, ectepicondylar foramen; gl, glenoid facet; HU, humeral scale; hypo, hypoplastron; indet, indeterminate; is, interfingered suture; pp, posterior process. Spotted texture: sediment.

5.1.2. *Palatal elements*

5.1.2.1. Premaxilla (Figs. 2–3, b). As was pointed out by Gaffney et al. (2007), the anterior region of the skull of *C. copelloi* is broken and it seems that both premaxillae are missing. The premaxilla likely contacted maxilla posteriorly, nasal dorsally, and vomer posteriorly.

5.1.2.2. Maxilla (Figs. 2–3, a–e; Fig. 4). After the new findings both maxillae are available for description. The maxilla contacted the premaxilla anteriorly, the jugal posteriorly, the palatine medially, the prefrontal anterodorsally, and probably the vomer anteromedially. The dorsal part of the maxilla forms the ventral rim of the orbit. In ventral view, the maxilla forms part of the triturating surface. It has only a tall labial ridge (contrary to Gaffney et al., 2007 where a lingual ridge was also described) and the triturating surface is very broad. Well-defined labial and lingual ridges are recognized in meiolaniids [e.g., *N. argentina*, *Me. platyceps* or *Ninjemys oweni* (Woodward, 1888)]. In these two Australasian meiolaniid species accessory ridges are seen between labial and lingual ridges (Gaffney, 1983). One accessory ridge is also recognized in *Mo. efremovi*.

5.1.2.3. Vomer (Figs. 2–3, b; Fig. 4). The vomer in *C. copelloi* is well preserved, however the sutures with other bones are not seen. The vomer likely contacts the premaxilla anteriorly, the maxilla laterally, the palatine posteriorly, and the prefrontal dorsally. It has a medial thick crest (Gaffney et al., 2007) all along the bone, which is wider in the anterior and posterior ends. The vomer palate forms the medial rim of the apertura narium interna. Both apertura narium interna are separated in *C. copelloi* by a relative narrow vomer in comparison to *Me. platyceps* (see Gaffney, 1983), *Nin. oweni* or *Nio. argentina* (see Gaffney, 1996; Sterli and de la Fuente, 2011b). The parasagittal choanal groves characteristic of *Me. platyceps* (Gaffney, 1983) are not recognized in *C. copelloi*. In *K. bajazidi* these parasagittal groves are mostly seen on the palatine bones (Gaffney and Meylan, 1992).

5.1.2.4. Palatine (Figs. 2–3, a; Fig. 4). Both palatines are well preserved in *C. copelloi*. The palatine contacts vomer medially, maxilla laterally, and pterygoid posteriorly. Its contact with prefrontal is not seen in this specimen. In contrast to *Me. platyceps*, the palatines in *C. copelloi* meet in the midline and they are larger (Gaffney et al., 2007). The palatine forms part of the foramen palatinum posterius, which seems to be better preserved in the left side of the skull. The foramen palatinum posterius in *C. copelloi* is large and elongated in comparison to the small foramen palatinum posterius characteristic of other meiolaniforms such as *Me. platyceps* or *K. bajazidi*.

5.1.3. *Palatoquadrate elements*

5.1.3.1. Quadrate (Figs. 2–3, b–f; Fig. 4). Both quadrates are preserved, however not complete (both mandibular condyles and the most lateral part of both quadrates are missing). The right quadrate is the most complete of the two. The quadrate contacts pterygoid ventromedially, prootic medially, quadratojugal anterolaterally, squamosal dorsally, and opisthotic posteriorly. The quadrate contributes to the processus trochlearis oticum, however as the suture with the prootic is not seen, the proportions are not clear. The quadrate also forms the well-developed cavum tympani (Gaffney et al., 2007), which is continuous posterodorsally with the antrum postoticum. The incisura columella auris is open posteroventrally; however as much of the lateral part of the quadrate is missing, we cannot discard it was closed laterally as in meiolaniids (Gaffney et al., 2007).

5.1.3.2. Epipterygoid (Figs. 2–3, b). In ventral view, through the left infratemporal fenestra the ventral part of the epipterygoid can be seen, however no sutures are recognized. Due to the preservation, the shape of the epipterygoid cannot be seen, not allowing recognizing whether it is like in basal or cryptodiran turtles. The epipterygoid is located above the pterygoid and forms the anterior rim of the enclosed foramen nervi trigemini. Its dorsal contact with the parietal cannot be seen. The epipterygoid likely contacts also the prootic.

5.1.3.3. Pterygoid (Figs. 2–3 b; Fig. 4). Both pterygoids are preserved in good shape. Pterygoid contacts palatine anteriorly, quadrate posterolaterally, basisphenoid posteromedially, epipterygoid and prootic dorsally, and the other pterygoid anteromedially. In *C. copelloi* as in other Meiolaniformes (e.g., *Mo. efremovi*, *Me. platyceps*) the medial contact of pterygoids between the basisphenoid and palatines is extensive, contrary to the short contact observed for *K. bajazidi*. The palatine–pterygoid suture is transverse medially as in *Mo. efremovi* and most turtles. It seems there is a small space between the pterygoids and the anterior tip of the basisphenoid (a slit-like opening as in *Dracochelys bicuspis* Gaffney and Ye, 1992) where the palatine artery may have entered the skull (space homologous with the foramen posterius canalis

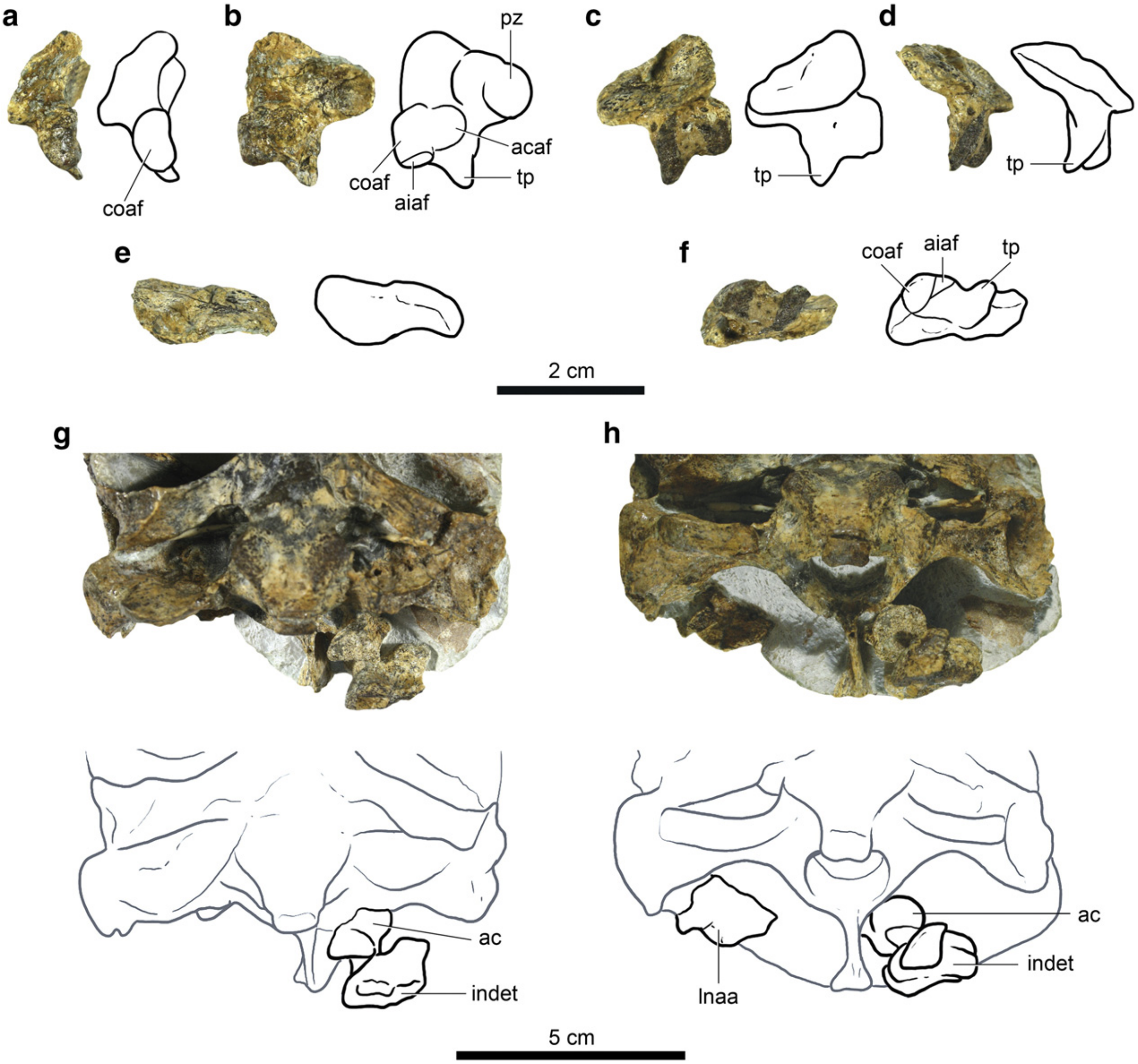

Fig. 8. Atlas of *Chubutemys copelloi* MPEF-PV 1236, Turtle Town, Chubut, Patagonia; Lower Cretaceous; a–f: Pictures and drawings of the right neural arch of the atlas; a: anterior; b: medial; c: lateral; d: posterior; e: dorsal; f: ventral views (photographs and drawings); g–h: Pictures and drawings of the posterior part of the skull in ventral view showing the atlas centrum, the left neural arch of the atlas, and an indeterminate element; g: ventral view; h: ventroposterior view. Abbreviations: ac, atlas centrum; acaf, atlas centrum articular facet; aiaf, atlas intercentrum articular facet; coaf, condylus articular facet; indet, indeterminate; lnaa, left neural arch of the atlas; pz, postzygapophysis; tp, transverse process.

caroticus laterale, Sukhanov, 2000). This interpretation agrees with Gaffney et al. (2007) and Brinkman et al. (2013). However, this interpretation differs from Smith's (2009) interpretation where the interpterygoid vacuity was reconstructed as a big space between pterygoids. Smith's (2009) interpretation could be biased because the anterior part of the basisphenoid is broken. The pterygoid has a processus pterygoideus externus protruding laterally similar in shape to *Pr. quenstedti*, with no posterior overhanging process. This process is very thin and has no vertical flange. Contrary to Gaffney et al. (2007), we interpret the pterygoid does not form part of the foramen palatinum posterius. Posteriorly, the pterygoid partially floors the canalis acustico-jugulare which is a segment of the canalis cavernosus; however part of the prootic is still seen in ventral view. The pterygoid is not broken posteriorly as was claimed by Gaffney et al. (2007). Further preparation of the holotype allowed us to reinterpret the carotid circulation pattern of *C. copelloi*. Our interpretation dismisses the presence of a foramen posterior canalis carotici interni formed by the pterygoid (contrary to Gaffney et al., 2007).

5.1.4. Braincase elements

5.1.4.1. Supraoccipital (Figs. 2–3, a–b, f; Fig. 4). Further preparation on the holotype allowed us recognizing new structures. The supraoccipital of *C. copelloi* is well preserved. Its preserved contacts are with the exoccipital ventrally and the parietal dorsally. It has a well-developed supraoccipital crest protruding the condylus occipitalis further back. The supraoccipital as in many turtles forms the dorsal border of the foramen magnum. In meiolaniforms the contribution of the supraoccipital to the skull roof is variable. As in *Mo. efremovi*, a small contribution of the supraoccipital to the skull roof is inferred for *C. copelloi*. In Meiolaniidae (i.e., *Nio. argentina*, *Nin. oweni*, *Me. platyceps*) the supraoccipital forms a large part of the skull roof, while in *K. bajazidi* it is apparent that there is no dorsal exposure of the supraoccipital (Gaffney and Meylan, 1992).

5.1.4.2. Exoccipital (Figs. 2–3, b, f; Fig. 4). Both exoccipitals are preserved in good shape in *C. copelloi*. Exoccipital contacts opisthotic laterally, basioccipital ventrally, and supraoccipital dorsally. It forms part of the rim of the foramen magnum, which has a triangular shape being slightly wider than tall. Its contribution to the condylus occipitalis cannot be ruled out, however no sutures are seen to corroborate this fact. Foramina nervi hypoglossi are present in the exoccipital (Gaffney et al., 2007).

5.1.4.3. Basioccipital (Figs. 2–3, b, f; Fig. 4). The basioccipital is well preserved in *C. copelloi*. It contacts the basisphenoid anteriorly and the exoccipitals dorsolaterally. In contrast to other Meiolaniformes like *K. bajazidi*, *Me. platyceps* or *Nio. argentina* (Gaffney, 1983; Gaffney and Meylan, 1992; Sterli and de la Fuente, 2011b) the basioccipital in *C. copelloi* does not contact the pterygoids. It forms the condylus occipitalis. The contribution of basioccipital to the condylus cannot be dismissed (see above). Two tubera basioccipitalis are present in *C. copelloi*.

5.1.4.4. Prootic (Figs. 2–3, b; Fig. 4). Both prootics are preserved in *C. copelloi*. Its contacts are ventrally with the pterygoid, posteriorly with the opisthotic, laterally with the quadrate, and probably anteromedially with the epipterygoid. The contact between prootic and parietal is not seen. The prootic forms, together with the quadrate, the processus trochlearis oticum, however the contribution of each bone to the process cannot be established. Besides, in ventral view, the prootic is exposed and the fenestra ovalis is seen. Most crown-Pleurodira (except *Podocnemis* and close relatives) have the cavum labyrinthicum open ventrally, whereas in many cryptodires this space is closed by the contact of the opistothic and prootic (Gaffney, 1979a). The fenestra ovalis is formed by the prootic anteriorly and the opisthotic posteriorly. As in most living turtles (Gaffney, 1979a), the fenestra ovalis in *C. copelloi* is not ossified ventrally. The prootic of *C. copelloi* might be also involved in the posterior closure of the foramen nervi trigemini.

5.1.4.5. Opisthotic (Figs. 2–3, b–c, f; Fig. 4). Left and right opisthotics are preserved in *C. copelloi*, however the right opisthotic is better preserved. The opisthotic has well developed paroccipital process, which is tightly sutured with the squamosal. In posterior view, the opisthotic barely encloses the middle ear region that results in a large space where the foramen jugulare posterius and fenestra postotica coalesce. The floor of the cavum acustico-jugulare in *C. copelloi* is widely open. The opisthotic has a small, ventral processus interfenestralis, which closes the fenestra ovalis from behind. The processus interfenestralis is pierced by the nervi glossopharyngei (IX) (Gaffney et al., 2007). Between the processus interfenestralis of opisthotic and the exoccipital, the foramen jugulare anterius is defined (Gaffney et al., 2007). Through this foramen the vagus nerve (X) and the accessory nerve (XI) exit the skull and the vena capitis lateralis enters the skull (Gaffney, 1979a).

5.1.4.6. Basisphenoid (Figs. 2–3, b; Fig. 4). The basisphenoid is nicely preserved in *C. copelloi*. This bone contacts pterygoids laterally, basioccipital posteriorly, and prootic dorsally. Ventrally the basisphenoid has a pentagonal shape with the anterolateral margins converging anteriorly rather than forming sub-parallel margins as in *K. bajazidi*. In *C. copelloi* two ventrolateral projected "wings" are present in the middle of the basisphenoid body. These "wings" have been interpreted by several authors as the basipterygoid processes (Evans and Kemp, 1975; Gaffney, 1979b; Brinkman et al., 2013). Medial and close to these wings, a pair of foramina pierces the basisphenoid. These foramina are interpreted as the foramen carotici cerebralis posterior (Sterli et al., 2010), through which the cerebral artery enters the skull. Posterolaterally to each foramen, there is a sulcus showing the course of the internal carotid artery. We interpreted that the internal carotid artery is not covered by bone posterior to the foramen carotici cerebralis posterior based on that the bone is intact along the sulcus of the internal carotid artery and the posterior end of the pterygoid is not broken in the specimen. Our interpretation differs from the enclosed internal carotid canal presented by Gaffney et al. (2007). In the anteriormost part of the basisphenoid, there is a small space (slit-like structure) between the basisphenoid and pterygoid. We interpret this space as the remnants of the interpterygoid vacuity (homologous to the foramina posterius canalis carotici laterale) where the palatine artery would enter the skull. No ventral pits are present in the basisphenoid of *C. copelloi*.

5.1.5. Columella auris (Figs. 2–3; Fig. 4)

Both medial sections of the columella auris are preserved in *C. copelloi*. The extracolumella is not preserved. The columella is a long element and the footplate is conical as described by Gaffney et al. (2007).

5.2. Carapace (Fig. 5, a–b)

5.2.1. Bones

A remarkable feature of the shell is that it is very thin. The shell of *C. copelloi* is thinner than the shells of the other well-known Meiolaniformes like *P. gasparinae*, *O. cunicularius*, *K. bajazidi*, *Mo. efremovi*, *Me. platyceps*, or *Nio. argentina*. Although a thin shell could be a sign of immaturity, the highly sutured shell and its size, suggest MPEF-PV 1940 is an adult specimen. Costal bones are 2 or 3 mm thick and they become thicker towards the margin of the carapace and in the peripherals. The plastron is also very thin, even thinner than the costal bones. The estimated total length of the shell is of 55 cm. Unfortunately, the shell is covered by a thin oxide patina which precluds any description of the shell surface (e.g., ornamentation).

5.2.1.1. Nuchal. The nuchal is trapezoidal in shape as in *P. gasparinae* and *Mo. efremovi*, being wider than long, but it has no anterior notch in contrast to *P. gasparinae* and *Mo. efremovi*. It contacts the peripheral 1 laterally, the costal 1 and the plausible preneural ventrally.

5.2.1.2. Neural series. Preneural, neural 1 and 2 were described in Gaffney et al. (2007). In the new recovered remains fragments of neural 2 and 4–6 are preserved. Unfortunately, the preservation of neural 4 does not allow any insightful description. On the contrary, neurals 5 and 6 are hexagonal-shaped with short sides facing anteriorly. In *K. bajazidi* (see Gaffney and Meylan, 1992) neural 6 is also hexagonal.

5.2.1.3. Suprapygal. In a small carapace fragment, a remnant of the suprapygal is recognized. Due to the nature of the preservation, only the contact with costal 8 is seen. Among the Meiolaniformes where the suprapygal area is well known, two suprapygal bones are recognized in *K. bajazidi* (see Gaffney and Meylan, 1992: fig. 17) and in *Mo. efremovi* (see Sukhanov, 2000: fig. 17.29). However, the proportions between both bones are different in these species: the largest suprapygal is the first in *K. bajazidi*, whereas is the second in *Mo. efremovi*.

5.2.1.4. Costal series. Costals 1 to 8 from the right side are preserved. The costal plates are very thin and their thickness is reduced from the midline (3 mm) towards the lateral side (1 mm). Costals 1–3 wave anteriorly, while costals 5–8 do posteriorly. Costal 1 contacts with nuchal (via a slightly concave suture), peripherals 1–3, costal 2, neural 1, and preneural. Costal 2 contacts costal 1 and 3, neurals 1 and 2, and peripherals 3 to 5. Costal 3 contacts costals 2 and 4, neural 2, probably neural 3, and peripherals 5 and 6. Costal 4 contacts costals 3 and 5, 2 neurals interpreted here as neurals 4 and 5, peripheral 6, and probably 7. Costal 5 contacts costal 4 and 6, 2 neurals (here interpreted as neural 5 and 6), peripheral 7, and probably peripheral 8. Costals 6 to 8 contacted peripherals through a "peg and socket" structure. The tip of the fused thoracic rib represents the peg, while the socket is located near the posterior border of the peripheral. The only two preserved contacts of costal 6 are with costals 5 and 7 and it probably contacted peripherals 8 and 9. The only preserved contacts of costal 7 are with costals 6 and 8 and it likely contacted peripherals 9 and 10. The only preserved contact of costal 8 is the anterior one with costal 7. In contrast to eight pairs of costal bones recognized in *C. copelloi* and *K. bajazidi*, nine pairs are illustrated by Sukhanov (2000: fig. 17.29) for *Mo. efremovi*.

5.2.1.5. Peripherals. Peripheral 1 contacts the nuchal medially, costal 1 ventrally, and peripheral 2 laterally. Peripheral 2 contacts costal 1 medially and peripherals 1 and 3. Peripheral 3 contacts costal 1, peripheral 2 and 4, and probably contacted costal 2. The contacts between the costals and the remaining peripherals are not preserved; consequently some of them are inferred. The only contacts preserved from peripherals 4–11 are the anterior and posterior contacts with the previous and the following peripherals. The bridge starts in peripheral 3 and ends in peripheral 7. There is no gutter in bridge peripherals. Peripherals 4–6 are C-shaped with the dorsal surface almost horizontal and the lateral surface is convex and almost vertically oriented. According to Sukhanov (2000: 348) a different bridge extension seems to be present in *M. efremovi*, where the anterior process of the axillary buttresses reached peripheral 2, whereas the posterior process of the inguinal buttresses reached peripheral 8. The relationship between the costals and peripherals is characterized by a peg and socket structure and it is likely that the carapace had pleuro-peripheral fontanelles, like in *Mo. efremovi* and *P. gasparinae*. The sockets in the peripherals 3–10 are located in the posterior end of each bone, near the suture with the following peripheral. The contact between the costals and the peripherals are inferred from the comparison with *Mo. efremovi* (Sukhanov, 2000; Suzuki and Chinzorig, 2010). The third rib (costal 2) penetrates in the socket of peripheral 4, the fourth rib (costal 3) penetrates in peripheral 5, the fifth rib (costal 4) in peripheral 6, the sixth rib (costal 5) in peripheral 7, the seventh rib (costal 6) in peripheral 8, the eighth rib (costal 7) in peripheral 9, the ninth rib (costal 8) in peripheral 10, and the tenth rib (costal 8) in peripheral 11.

5.2.2. Scales

The carapace scales are well preserved. The sulci are clearly seen and they are deep and broad.

5.2.2.1. Cervical scale. This region is not well preserved, consequently we cannot assure whether the cervical scale was present or absent. The cervical scale is present in *P. gasparinae*, *Mo. efremovi*, and *Me. platyceps*. The morphology of the anterior scales on the margin of the carapace in *K. bajazidi* is unclear (Gaffney and Meylan, 1992).

5.2.2.2. Vertebral scales. Vertebral scales are wider than pleural scales and they are wider than long. All vertebral scales can be seen in the specimen. Vertebral 1 is located on costal 1, preneural, nuchal, and peripheral 1. This scale contacts marginals 1 and 2 anteriorly, pleural 1 laterally, and vertebral 2 posteriorly. The sulcus between vertebrals 1 and 2 is located on costal 1 and in the suture of the preneural and neural 1. Vertebral 2 is located on costals 1–3 and neurals 1 and 2, and probably 3. Sulcus between vertebral 2 and 3 is located on costal 3 and maybe on neural 3. Vertebral 2 contacts vertebrals 1 and 3 anterior and posteriorly (respectively) and pleurals 1 and 2. Vertebral 3 is located on costals 3 to 6 and neurals 4 to 6, and probably neural 3 as well. It contacts vertebral 2 anteriorly and 4 posteriorly, and pleurals 2 and 3 laterally. The sulcus between vertebral 3 and 4 is located on costal 6 and probably crossed to costal 5 (as in *P. gasparinae*) and neural 6. Vertebral 4 is located on costals 6 to 8. It contacts vertebral 3 anteriorly and 5 posteriorly, and pleurals 3 and 4 laterally. A small fragment of vertebral 5 is recognized on costal 8 and suprapygal.

5.2.2.3. Pleural scales. All pleural scales are recognized in *C. copelloi*. Pleural 1 is located on costals 1 and 2, nuchal, and peripherals 1 to 3. The preserved contacts of pleural 1 are vertebrals 1 and 2 medially, marginals 2 to 5 laterally, and pleural 2 posteriorly. The sulcus between pleural 1 and 2 is located on costal 2. Pleural 2 is located on costals 2–4 and its preserved contacts are pleural 1 anteriorly, pleural 3 posteriorly, and vertebrals 2 and 3 medially. Inferred contacts of pleural 2 are with marginals 5 to 7. Small fragments of pleural 3 are located on costals 4 to 6 and peripheral 8. The sulcus between pleural 3 and 4 is located on costal 6. Also small fragments of pleural 4 are recognized on costal 7 and peripheral 9.

5.2.2.4. Marginal scales. As a consequence of the preservation of the specimen we cannot see if any of the marginal scales extended to the costal bones, but we are sure in that pleural scales 1, 3, and 4 reached peripherals. Marginal 1 is located on the nuchal and peripheral 1. The sulcus between marginal 1 and the cervical scale, if it was present, is not seen, while the sulcus with the marginal 2 is located on peripheral 1. Marginal 1 contacts vertebral 1 and marginal 2. Marginal 2 is located on peripherals 1 and 2 and contacts marginal 1 and 3, vertebral 1 medially and pleural 1 ventrally. Marginal 3 is located on peripherals 2 and 3. The preserved contacts of marginal 3 are marginals 2 and 4 and pleural 1. Marginal scales 6 and 7 are not seen. The posterior part of the marginal 8 is present on peripheral 8. Marginal 9 is located on peripherals 8 and 9 and contacts marginals 8 and 10. Marginal 10 is located on peripherals 9 and 10 and contacts marginals 9 and 11. Marginal 11 is located on peripherals 10 and 11 and contacts marginals 10 and 12.

5.3. Plastron (Fig. 5, b; Fig. 6; Fig. 7)

5.3.1. Bones

As it is shown by the interdigitated suture of the entoplastron, hyoplastron, and hypoplastron, and by the morphology of those elements, the relationships among plastral elements and their connection with the carapace are weak.

5.3.1.1. Entoplastron. Most of the entoplastron is present, missing only the anteriormost part. It is cross-shaped, with a short and tiny anterior process and a long posterior medial process. A different entoplastral shape is recognized in *K. bajazidi* (see Gaffney and Meylan, 1992: fig. 18). As the medial parts of the hyoplastra are broken, we cannot determine whether the entoplastron separated completely or partially their medial contact. Besides, as the anterior process is also broken, we cannot confirm whether there was a medial contact of the epiplastra either. The anterior region of the visceral side of the entoplastron has two concavities interpreted as the articular facets for the scapula. The posterior process of the entoplastron broadens slightly in the mid part and it narrows again towards posteriorly. In ventral view, the highly interdigitated suture with the hyoplastra is seen.

5.3.1.2. Hyoplastron and hypoplastron. The hyoplastron and the hypoplastron are very thin elements, the major thickness being at the base of the axillar process (5.3 mm) and the thinner in the medial part (around 1 mm). As the thickness decreases towards the central region of the plastron it is likely that there was a central fontanelle. The connection between the plastron and the carapace in *C. copelloi* is through ligaments as it is shown by the interdigitated contact area of the hyoplastron and hypoplastron and the sockets in the peripheral bones of the carapace. It is also likely that *C. copelloi* had fontanelles between the hyoplastron–hypoplastron and the peripherals. A hyo–hypoplastral central fontanella is also present in *O. cunicularius* and in *Mo. efremovi* (see Gaffney et al., 1998: fig. 9; Sukhanov, 2000: fig. 17.29). Additionally, in this last species a smaller hypo–xiphiplastral fontanella is recognized. On the contrary neither hyo–hypoplastral nor hypo–xiphiplastral fontanelles are seen in *K. bajazidi*.

The only preserved contact of the plastron is between the left hyoplastron–hypoplastron. Both hypoplastra are almost complete. In the lateral side of the right hypoplastron there are two incisions for musk ducts. There was no mesoplastron in *C. copelloi* as in *O. cunicularius* or *Me. platyceps* (see Gaffney, 1996: figs. 27–29; Gaffney et al., 1998: fig. 9). On the contrary in *K. bajazidi* (see Gaffney and Meylan, 1992) and in *Mo. efremovi* (see Sukhanov, 2000) one pair of mesoplastra appears to be present.

5.3.2. Scales

Unfortunately, as an oxide patina covers the plastron, almost no sulci are preserved. The only seen sulcus is the medial sulcus separating pectoral scales which is present in the entoplastron.

5.4. Vertebrae

5.4.1. Atlas (Fig. 8)

Both neural arches of the atlas, the atlas intercentrum, and the atlas centrum are preserved in *C. copelloi*. The right neural arch has been removed from the matrix, while the left neural arch and the atlas centrum are still in the matrix near the posterior margin of the skull. Few atlases of extinct turtles have been described so far, limiting comparisons within extant turtles. As in all turtles, the neural arch of *C. copelloi* has two portions (one dorsal and the other ventral). The dorsal portion is anteroposteriorly elongated and mediolaterally broad, being more developed than in *Me. platyceps* and *Pr. quenstedti*. In its posterior part it bears the postzygapophysis, which articulates with the axis (Gaffney, 1990). The atlas neural arch also exhibits a small transverse process located in its posteroventral part. The ventral portion has well defined articular facets: anteriorly for the condylus occipitalis, mediolaterally for the atlas pleurocentrum, and ventrally for the atlas intercentrum.

The atlas intercentrum is a rectangular piece of bone, much wider than tall and than long as in *Me. platyceps* and in *Pr. quenstedti*, but contrary to most turtles (Gaffney, 1985, 1990). Dorsolaterally it contacts the atlas neural arch. Anteriorly there is an articular surface for the occipital condyle and posterodorsally there is another articular surface, smaller in size, for the atlas centrum. Posterolaterally the atlas intercentrum has a small process protruding laterally, process also seen in *Pr. quenstedti*.

The atlas centrum (atlas pleurocentrum + axis intercentrum) of *C. copelloi* is a robust, cube-shaped element. The ventral part (maybe the part corresponding with the axis intercentrum) is eroded and the dorsal part is not seen because it is still in the matrix. The anterior articular facet is convex and T-shaped. The posterior facet is concave and almost quadrangular. The presence of paired projections extending posteroventrally as seen in *Me. platyceps* (Gaffney, 1985) cannot be confirmed because the ventral surface is broken.

5.4.2. Thoracic vertebrae 1 to 3, 5, and 10 (Fig. 5, b)

Thoracic vertebrae 1 to 3 are preserved in the carapace fragment described by Gaffney et al. (2007); however no description of these vertebrae was published. Thoracic vertebra 1 is the shortest of the three first thoracic vertebrae. It is longer than wide and articulated with thoracic rib 1 anteriorly and thoracic rib 2 posteriorly. It seems thoracic rib 1 is long. The anterior articular surface is concave and facing anteriorly and slightly ventrally. Thoracic vertebrae 2 is much longer than wide and articulates with thoracic rib 2 anteriorly and probably with thoracic rib 3 posteriorly. Thoracic vertebra 3 is also much longer than wide. Its articulations with the thoracic ribs are not seen, but probably it contacted thoracic rib 3 anteriorly and 4 posteriorly. A similar morphology of these three thoracic vertebrae and the orientation of the central articulation of the first thoracic vertebra are seen in *O. cunicularius* (Gaffney et al., 1998: figs. 7–8). The posterior part of the thoracic vertebra here interpreted as a fifth thoracic, is preserved in the ventral part of the carapace. Due to the nature of the specimen, no more information of the thoracic vertebra 5 can be extracted.

Thoracic vertebra 10 is preserved in the ventral surface of a small fragment of carapace (left costal 8 and suprapygal). This vertebra has the anterior articular surface flat and the posterior slightly convex as in *Pa. gasparinae*. The thoracic rib is located in the anterior region of the centrum.

5.5. Pectoral girdle

5.5.1. Scapulae (Fig. 5, b; Fig. 6, a; Fig. 7)

Both scapulae were preserved in *C. copelloi*. Acromial and dorsal processes form an angle of 90° and a short web of bone unites them like in *K. bajazidi* and *Mo. efremovi*; however in those two taxa the web of bone is more developed. The dorsal process in *C. copelloi* is longer than the acromial process and the glenoid neck is present.

5.6. Humeri (Fig. 5, b; Fig. 6, a; Fig. 7, a)

The distal end of both humeri and only the head of left one are exposed in *C. copelloi* (MPEF-PV 1140). The humerus of *C. copelloi* is a long element, more than three times longer than wide. The distal end is expanded; however the expansion of the proximal end cannot be assessed with certitude. There is an enclosed ectepicondylar canal in the anterior view of the both humeri (as in *Pr. quenstedti*, *K. bajazidi*, *Me. platyceps*, among others), probably ending in an ectepicondylar foramen.

5.7. Pelvic girdle (Fig. 5, b)

The right ilium is complete, while only the iliac blade is preserved of the left ilium. The ilium is a robust element with an iliac blade developed towards posteriorly (as in *Mo. efremovi* and *K. bajazidi*). The right ilium is preserved in medial view, not allowing the description of the acetabulum. Other pelvic elements are preserved but their preservation precludes any description.

6. Cladistic analysis

Two hundred and seventy MPTs of 900 steps with a CI of 0.336 and RI of 0.764 have been found. A strict consensus was calculated (Appendix D). The general topology of the strict consensus is similar to that calculated for Sterli and de la Fuente's (in press) paper, except for a basal polytomy (Appendix D). As *C. copelloi* and other taxa were involved in a polytomy we run the script of Pol and Escapa (2009). This script showed *P. gasparinae* from the Late Cretaceous of Patagonia as the most unstable taxon. *Patagoniaemys gasparinae* acquires different phylogenetic positions (Fig. 9; Appendices E and F) in all the MPTs collapsing several nodes in the strict consensus, causing the polytomy (Appendix C). A simplified reduced consensus is presented in Fig. 9 showing the alternative positions of *P. gasparinae*. Although *P. gasparinae* takes

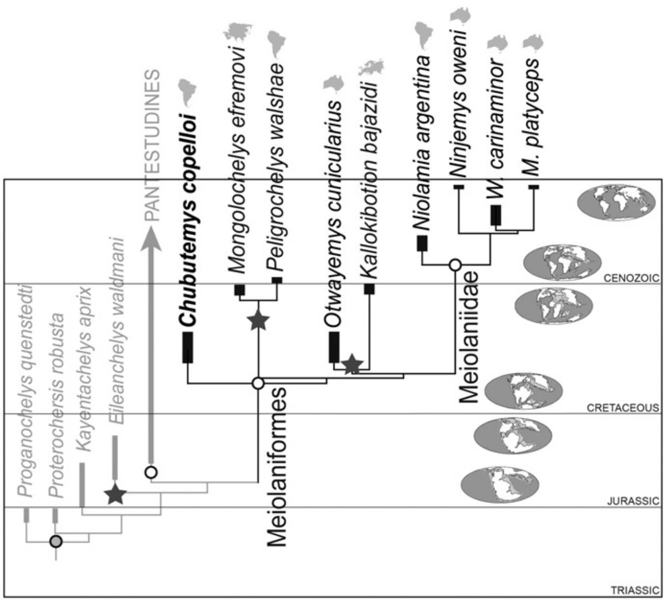

Fig. 9. Simplified reduced consensus tree showing the inferred phylogenetic position of *Chubutemys copelloi*. Stars show the alternative position for *Patagoniaemys gasparinae*. Grey circle: synapomorphy based definition. White circle: stem-based definition.

different phylogenetic positions, the exclusion of this taxon in the strict consensus (not in the matrix) produces the same topology as in Sterli and de la Fuente's (in press) analysis. In this regard, *C. copelloi* is recovered, as the most basal taxon of Meiolaniformes and Meiolaniformes is located outside crown Testudines. The clade Meiolaniformes has a Bremer support of 1 and is characterized by 5 characters present in all trees and 2 characters present in some trees (see Appendix G). Those 5 characters are (numbers as given by TNT): prefrontal exposure large [character 6 (0)], no contribution of frontal to the orbit [character 9 (0)], presence of a ventral crest on the vomer [character 45 (1)], processus pterygoideus externus as in *Pr. quenstedti* [character 69 (0)], and crista supraoccipitalis protruding significantly beyond the occipital condyle [character 71 (1)]. The two characters not present in all MPTs are: absence of a vertical flange on the lateral process of the pterygoid [character 66 (0)] and presence of formed cervical vertebrae [character 186 (1)]. *Chubutemys copelloi* is the sister group of all remaining Meiolaniformes because the squamosal and the supraoccipital are not in contact [character 25 (0)]. Meiolaniformes are located outside crown Testudines because they have vertebral scales broader than pleurals [character 140 (0)], long to intermediate first thoracic rib [character 199 (0, 1)], among others (see Appendix F).

7. Discussion

7.1. Remarks on the phylogenetic relationships of Meiolaniform species and related taxa

Recent studies (e.g., Gaffney et al., 2007; Sterli et al. 2013b; Sterli and de la Fuente, in press) have suggested Meiolaniidae and related taxa originated at least in the Early Cretaceous. Although several taxa have been reported as related to the exclusively Gondwanan clade Meiolaniidae (sensu Gaffney, 1996), only two species have been properly described (e.g., *O. cunicularius* and *C. copelloi*). Moreover, only one of these two species is relatively complete (*C. copelloi*). The poor record of Early Cretaceous continental turtles makes the origin of several clades, including meiolaniforms, difficult to evaluate. In the following paragraphs we summarize the Early Cretaceous turtles that have been considered related to Meiolaniidae and the plausible shared characters supporting these relationships. Although several of these clades have been related to Meiolaniidae, some of them have not yet been described in detail (e.g., Sinochelyidae, *Naomichelys speciosa* Hay, 1908) precluding any revaluation of their phylogenetic relationships. After this description, *C. copelloi* turns to be the most complete described species from the Lower Cretaceous related to the clade Meiolaniidae. Future work on the taxa mentioned below will shed light on the origin and early steps of meiolaniforms, a peculiar clade of turtles.

7.1.1. Chubutemys copelloi Gaffney, Rich, Vickers-Rich, Constantine, Vacca and Kool 2007

Since the original description of *C. copelloi* by Gaffney et al. (2007), this taxon has been considered to be related to Meiolaniidae (Sterli and de la Fuente, in press, this study). Gaffney et al. (2007) mentioned the only unambiguous character uniting *C. copelloi* and meiolaniids is the presence of a contact between the prefrontal and postorbital preventing the frontal being part of the orbit. Another putative character shared by *C. copelloi* and meiolaniids suggested by Gaffney et al. (2007) is the large parietal lacking temporal emargination. The authors also pointed out that the carotid circulation in *C. copelloi* could be the plesiomorphic condition for meiolaniids, but they did not discard that condition as plesiomorphic for crown-cryptodirans. In later analyses (e.g., Sterli and de la Fuente, in press; this study) *C. copelloi* has been also recovered at the stem of Meiolaniidae. The characters involved in this close relationship are described above (see Cladistic analysis). Although Gaffney et al.'s (2007) phylogenetic hypothesis differs in several points (e.g., position of *Ka. aprix*, general position of meiolaniids and related taxa relative to crown cryptodirans) from the hypothesis presented here, *C. copelloi* is recovered in both analyses as a stem Meiolaniidae and in a basal position.

7.1.2. Otwayemys cunicularius Gaffney, Kool, Brinkman, Rich, and Vickers-Rich 1998

Otwayemys cunicularius (Lower Cretaceous, Australia) has been recovered in several phylogenetic analyses as a close relative to Meiolaniidae (Hirayama et al., 2000; Gaffney et al., 2007; Anquetin, 2011; Sterli and de la Fuente, 2011a). Characters uniting *O. cunicularius* and Meiolaniidae in Hirayama et al. (2000) and Anquetin (2011) are described below under Sinochelyidae. *Otwayemys cunicularius* and Meiolaniidae are united in Gaffney et al.'s (2007) cladistic analysis by the presence of transverse processes in cervical vertebrae in the middle of the centra. In Sterli and de la Fuente (2011a) analysis, the clade *O. cunicularius* +*P. gasparinae* + *Mo. efremovi* + Meiolaniidae is supported by the ambiguous synapomorphy presence of the contact between supraoccipital and squamosal bones. Unfortunately, published material of *O. cunicularius* is fragmentary. Hopefully, new specimens will help to elucidate the phylogenetic relationships of this taxon with remaining turtles.

7.1.3. Sinochelyidae Chkhivadze, 1970 (=Peishanemydidae Nessov, 1981 sensu Hirayama et al., 2000)

Sinochelyidae is a poorly known group of turtles from the Lower Cretaceous of Asia. Following Sukhanov (2000) Sinochelyidae has two genera with three species (*Sinochelys applanata* Wiman, 1930, *Peishanemys latipons* Bohlin, 1953, and *Peishanemys testudiformis* Nessov 1981). In a summary of the Chinese fossil reptiles, Brinkman et al. (2008) suggest *S. applanata* is synonymous of *Scutemys tecta* Wiman, 1930, *Pe. latipons*, and *Heishanemys imperfectus* Bohlin, 1953. According to Hirayama et al. (2000), the clade Sinochelyidae + *O. cunicularius* + *Mo. efremovi* + Meiolaniidae is supported by the following synapomorphies: formed cervical vertebrae, anterior and posterior caudal vertebrae opisthocoelous, ventral knob or keel in cervical 8 absent, and plastral fontanella present. Sinochelyidae has also been related to Testudinidae because they share the general shape of the shell, the presence of shortened plastron, relatively short humerus and femur, among others (Nessov and Verzilin, 1981). They have also been related to Platysternidae by the extensive development of the skull roof, the strengthened mandibular symphysis, and the nuchal emargination in the carapace (Sukhanov, 2000). The deficient knowledge on the detailed anatomy and phylogenetic relationships of Sinochelyidae precludes the evaluation of this group as a plausible taxon related to Meiolaniformes. New studies on Sinochelyidae will bring more information about this enigmatic group of Lower Cretaceous Asian turtles.

7.1.4. Naomichelys speciosa Hay, 1908

Solemydidae is a poorly known group of turtles from the Cretaceous of Europe and North America and all the species have a unique shell ornamentation formed by tubercules (vermiculated texture). In a recent revision made by Joyce et al. (2011) identified *Helochelydra nopcsai* Lapparent de Broin and Murelaga, 1999, *Plastremys lata* Owen in Parkinson, 1881, *Na. speciosa* (=*Tretosternon* sensu Hirayama et al., 2000), *Solemys gaudryi* (Matheron, 1869) and *Solemys vermiculata* Lapparent de Broin and Murelaga, 1996, plus two undeterminate solemydids as members of Solemydidae. Also recently, Anquetin (2011) has proposed *Na. speciosa* (Aptian–Campanian North America) together with *O. cunicularius* as the sister taxa of *Mo. efremovi* plus Meiolaniidae (Clade G of Anquetin, 2011). This clade is supported by the following unambiguous synapomorphies: vertebral scale 5 does not overlap onto peripherals and pygal, the central plastral fontanelle is retained in adults, and the central cervical articulations are formed (cervical vertebrae procoelous or opisthocoelous).

Hirayama et al. (2000) were the first to include *Na. speciosa* in a cladistic analysis. Contrary to Anquetin (2011), Hirayama et al. (2000)

recovered *Na. speciosa* forming a clade together with *K. bajazidi* (Upper Cretaceous, Europe), clade which is the sister group of Paracryptodira +Eucryptodira. Following Hirayama et al. (2000) *Na. speciosa* and *K. bajazidi* would share the presence of the second pygal much smaller than the first. The clade Meiolaniidae + *Mongolochelys* +Sinochelyidae + *Otwayemys* is located more basal than *Na. speciosa* +*K. bajazidi* in Hirayama et al.'s (2000) phylogeny.

7.1.5. *Spoochelys ormondea* Smith and Kear 2013

Spoochelys ormondea is a recently named and described turtle from the Lower Cretaceous of Australia (Smith and Kear, 2013). These authors have modified Gaffney's et al. (2007) and Sterli and de la Fuente's (2011a) matrices to test the phylogenetic relationships of *S. ormondea*. Although Smith and Kear (2013) have claimed that *S. ormondea* is a meiolaniid-like form, the inclusion of this taxon in the two competing hypotheses about turtle evolution did not recovered such affiliation. In all phylogenetic analyses *S. ormondea* has been recovered as a stem-Testudine. Following Smith and Kear (2013), *S. ormondea* would share with meiolaniids the cranial scale pattern and the incisura columella auris confluent with the Eustachian tube. However, as Sterli and de la Fuente (in press) have shown, the presence of scales in the skull is plesiomorphic for turtles. It seems that there are more characters supporting the basal position of *S. ormondea* among turtles than those shared with meiolaniids. As it was pointed out by Smith and Kear (2013), new findings of this taxon will help to clarify its phylogenetic relationships.

Several species of Meiolaniforms from the Lower and Upper Cretaceous are under study nowadays (e.g., Joyce et al., in prep.; Sterli and de la Fuente, in prep.). The detailed description of *C. copelloi* and the taxa under study (e.g., *Na. speciosa*, *P. gasparinae*) will bring more information on the general anatomy, evolution, and phylogenetic relationships of Meiolaniformes. In different cladistic analyses (e.g., Gaffney et al., 2007; Sterli and de la Fuente, in press) *C. copelloi* was recovered as the most basal taxon of Meiolaniformes. Consequently, the detailed description presented here together with new information gathered from other species under study will help to understand the origin and diversification of this peculiar clade of turtles. Furthermore, the discovery and description of more specimens from the Lower Cretaceous and related to Meiolaniidae will shed new light on this clade as well.

7.2. Paleobiogeography

The continental Cretaceous turtle fauna from Gondwana has been dominated by two clades, Meiolaniformes and Pleurodira (e.g., Gaffney, 1981; Lapparent de Broin, 2000a,b; de la Fuente et al., 2013; Sterli and de la Fuente, in press). In Africa the record of continental turtle fauna from the Cretaceous is scarce and it was represented exclusively by one of the extant pleurodiran clades, Pelomedusoides (e.g., Lapparent de Broin, 2000a; Gaffney et al., 2006, 2011). On the other hand, the paleobiogeographical history of turtles from other Gondwanan continents such as Australia and South America is more complex. The continental Cretaceous turtles from Australia and Southern South America are integrated exclusively by two clades, Meiolaniformes and Pleurodira, while the paleobiogeographical history of the Northern part of South America is more similar to Africa than to Southern South America and Australia. Romano and Azevedo (2006) recognized the differentiation of pleurodires into two clades (Chelidae and Pelomedusoides) as the first vicariant event, which resulted in the isolation of the pelomedusoids in northern Gondwana (northwestern South America–northeastern Africa) and chelids in Patagonia and Australasia (Broin, 1987, 1988; Broin and de la Fuente, 1993; Lapparent de Broin, 2000a, b; de la Fuente, 2003) in the Early Cretaceous. This vicariant event could be related with the basaltic volcanic activity recorded in the Serra Geral Formation (Renne et al., 1992) occurred during the Early Cretaceous (Romano and Azevedo, 2006).

Contrary to pelomedusoids, the biogeographic history of chelids and meiolaniforms seems to be very similar to each other because they have been found associated in the fossil record since the Lower Cretaceous until the Holocene both in Southern South America and Australasia (Sterli and de la Fuente, in press). Southern South America was connected to Australasia via Antarctica at least until the Eocene (Grunow, 1992; Lawver et al., 1992). The paleobiogeography of turtles is consistent with the occurrence of other amniotes like monotremes in the early Paleocene of Patagonia (Pascual et al., 1992) and ratites in the Eocene of Seymour Island (Antarctic Peninsula) (Tambussi et al., 1994). The occurrence of these amniotes in Patagonia, Antarctic Peninsula, and Australia would be suggestive of a much older and widespread distribution of these taxa in Southern Gondwana prior to its final breakage (de la Fuente et al., 2013). Although in this contribution we are focused on the clade Meiolaniformes, the integration of the paleobiogeographical patterns of Chelidae and Pelomedusoides in future works will help to understand the evolution of Gondwanan's turtles.

In particular Meiolaniforms is a clade built up mainly by Gondwanan taxa. Its fossil record spans from the Early Cretaceous (*C. copelloi* and *O. cunicularius*) to the Holocene (?*Meiolania damelipi* White et al., 2010). During the Cretaceous, members of this clade have been recorded in Australia (*O. cunicularius*), South America (*C. copelloi*; *P. gasparinae*; *Trapalcochelys sulcata* Sterli, de la Fuente and Cerda, 2013b), Asia (*Mo. efremovi*), and Eastern Europe (*K. bajazidi*). According to the historical biogeographic analysis performed by Sterli and de la Fuente (in press) meiolaniforms originated at least during the Early Cretaceous in present day South America (mainly in Southern South America) (Fig. 9). These authors have recognized a long ghost lineage leading to meiolaniforms extending from the Early Jurassic to the Early Cretaceous (circa 60 Ma). During that time span, the location and relationships of the continents changed radically from only one big landmass, called Pangaea, into two large landmasses, Gondwana and Laurasia (Fig. 9). Whether Meiolaniformes originated in the Early Jurassic or in the Early Cretaceous is key to determine if this clade originated in Pangaea (Early Jurassic) or in Gondwana (Middle Jurassic to Early Cretaceous). The phylogenetic hypotheses proposed by Hirayama et al. (2000), Sterli and de la Fuente (2011a), and this work (Fig. 9) agree with the idea that meiolaniforms originated and diversified in the Early to Middle Jurassic before the breakup of Pangaea.

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