General Palaeontology, Systematics and Evolution (Vertebrate Palaeontology)

Long-necked chelid turtles from the Campanian of northwestern Patagonia with comments on K/P survivorship of the genus *Yaminuechelys*

Tortues chélidées à cou long dans le Campanien du Nord-Ouest de la Patagonie, avec de commentaires sur la survie du genre Yaminuechelys *à la limite K/P*

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A B S T R A C T

The long-necked chelid turtle *Yaminuechelys* aff. *maior* is described on the basis of post-cranial material of two specimens from the Lower–Middle Campanian Anacleto Formation, nortwestern Patagonia (Argentina). These post-cranial remains are described macroscopically (external morphology) and microscopically (histological sections of the shell). Although minor carapace and plastral differences are reported (e.g., extension of the axillary buttresses on visceral surfaces of the first costal bone, curled bridge peripheral bones, absence of a sub-rectangular fenestra retained in adults) the specimens exibit the shell morphology and surface ornamentation of specimens referred to *Y. maior* (Staesche, 1929) from Paleocene levels of the Salamanca Formation (Central Patagonia). This assignment is supported by a phylogenetic analysis, in which the new material is the most closely related to *Y. maior*. As *Yaminuechelys* is hypothesized to be the sister taxon of *Hydromedusa*, the capability of *Hydromedusa tectifera* to adapt to changing environments and the survivorship of *Yaminuechelys* genus in K/P boundary is discussed.

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R É S U M É

La nouvelle tortue chélidée á long cou *Yaminuechelys* aff. *maior* est décrite, sur la base du matériau post-crânien de deux spécimens au membre inférieur-moyen de la formation Anacleto, campanienne, du Nord-Ouest de la Patagonie (Argentine). Les restes post-crâniens sont décrits macroscopiquement (morphologie externe) et microscopiquement (histologie de la carapace). Malgré des différences dans la carapace dorsale et le plastron (par

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exemple, extension du contrefort axillaire de la première costale sur les surfaces viscérales, os périphériques en arcade, absence d'une fenestra subrectangulaire conservée chez les adultes), les spécimens décrits ressemblent, par la morphologie de la carapace et son ornementation de surface, à ceux rapportés à *Y. maior* (Staesche, 1929) dans les niveaux paléocènes de la formation Salamanca (Patagonie centrale) du Paléocène. L'attribution du taxon présenté ici est étayée par une analyse phylogénétique, dans laquelle ce taxon est le plus proche qui soit lié à *Y. maior*. Comme *Yaminuechelys* était supposé être le groupe-frère d'*Hydromedusa*, la capacité de *Hydromedusa tectifera* à s'adapter à des environnements changeants et la survie du genre *Yaminuechelys* à la limite K/P sont ici discutées.

1. Introduction

The greatest specific richness among elements of the continental chelonian fauna of South America are the oldest clades with extant species, Chelidae and Pelomedusoides (de la Fuente et al., 2013; Van Dijk et al., 2012). Notably, the Chelidae clade is represented by 36 species (22 extant plus 14 extinct) assigned to 14 genera (de la Fuente et al., 2013). This species richness, along with a long Cretaceous fossil record in Patagonia and Australia (de la Fuente et al., 2011; Lapparent de Broin and de la Fuente, 2001; Smith, 2009, 2010), the peculiar disjointed geographic range limited to Australasia and South America (Iverson, 1992), and other chelid peculiarities (Pritchard, 1984; Pritchard and Trebbau, 1984) has lead multiple authors (Broin, 1987, 1988; Broin and de la Fuente, 1993; de la Fuente, 2003, 2007, 2013; Romano and Azevedo, 2006) to suggest that chelid diversity was the result of an ancient biogeographic and phylogenetic history developed in southern Gondwana landmasses.

Two different chelid clusters (short-necked forms and long-necked forms) have been recognized among both extant and extinct species since the nineteenth century (Boulenger, 1889). This assessment is based on the length of the eight cervical vertebrae of the neck in comparison with the length of the ten dorsal vertebrae attached to the carapace. The oldest record of a South American short-necked chelid dates back to the Aptian?-Albian (de la Fuente et al., 2011; Lapparent de Broin and de la Fuente, 2001) and is represented by *Prochelidella cerrobarcinae* de la Fuente, Umazano, Sterli and Carballido, 2011, whereas the long-necked South American chelid record goes back to the Late Santonian or Early Campanian based on *Yaminuechelys* species (de la Fuente et al., 2010), a hypothesis that is supported here. These South American long-necked species lineages are represented in Paleogene, Neogene, and Recent times by *Hydromedusa* species (*H. casamayorensis*, *H. tectifera*, and *H. maximiliani*), being also represented by *Yaminuechelys* species (*Y. gasparinii* and *Y. maior*) in the Coloradoan (Santonian-Early Campanian) and Allenian (Late Campanian-Early Maastrichtian) tetrapod assemblages (Leanza et al., 2004), and also in the Danian.

Turtle post-cranial remains recovered in the Early Campanian of the Anacleto Formation at the Paso Córdova site were referred to *Yaminuechelys* cf. *gasparinii* (de la Fuente et al., 2010). In the present contribution, additional remains assigned to one potentially new species of *Yaminuechelys* closely related to *Y. maior* (i.e., a long-necked Danian species from central Patagonia, see Bona and de la Fuente, 2005), and the circumstances of the survivorship of *Yaminuechelys* lineage through the K/P extinction are discussed.

2. Materials and methods

All the materials described are housed on the Museo Argentino Urquiza in Rincon de los Sauces, Neuquén Province, Argentina.

For the use, interpretation, and syntax of Open Nomenclature, we follow recommendations proposed by Bengtson (1988).

The phylogenetic analysis is based on the data set from Bona and de la Fuente (2005) data set. Character 37 (Claws in forefoot) was removed from this data set, four additional ones were scored (new Characters 37 to 40) and one taxon (*Yaminuechelys* aff. *Y. maior*) was added and codified during the present analysis. The data set includes 14 taxa and 40 characters. Multistate characters were considered unordered and all characters were considered equally weighted. The phylogenetic analysis was performed using TNT (Goloboff et al., 2008a, 2008b). The most parsimonious trees were found using a heuristic search tree-bisection-reconnection (TBR) with ten replicates. Bremer support values were also calculated with the same replicates to establish branch support for each node.

Histological analysis of the new material was done using two fragmentary costal plates from the carapace: MAU-Pv-N-475 (first costal) and MAU-Pv-PR-455 (third or fifth costal). The section-planes were oriented antero-posteriorly (perpendicular to the progression of the ribs). Thin sections were made at the Museo Egidio Feruglio, Trelew, Argentina. The sampling followed standard petrographic thin-sectioning procedures (see Scheyer and Sánchez-Villagra, 2007). The bone microstructure of the thin sections was studied under light microscopy using normal and polarized light. The histological descriptions follow Francillon-Vieillot et al. (1990) and Scheyer and Sánchez-Villagra (2007).

2.1. Institutional Abbreviations

MAU-Pv-N; Museo Argentino Urquiza of Rincón de Los Sauces; vertebrate paleontology collection; Puesto Narambuena site; MAU-Pv-PR; Ibídem; Puesto La Rinconada site.
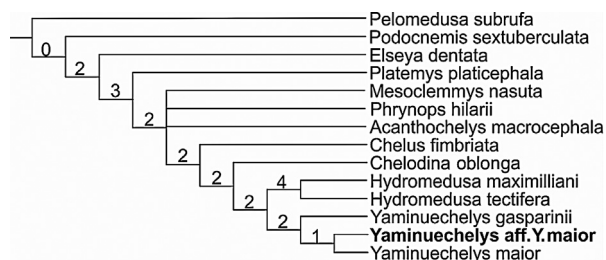
Fig. 1. Strict Consensus Tree showing the position of *Yaminuechelys* aff. *maior*. It forms a clade with the other named *Yaminuechelys* species. The numbers above the Branches are the Bremer Support.

Fig. 1. Arbre de consensus strict montrant la position de *Yaminuechelys* aff. *maior*, qui forme un clade avec les deux autres espèces *Yaminuechelys*. Les chiffres au-dessus des branches sont le support Bremer.

2.2. Antomical Abbreviations

Ab; abdominal scale; acet; acetabulum; An; anal scale; anc; anterior condyle; anct; anterior cotyle; ax but; axillar buttresses; co; costal bone; en; entoplastral bone; epi; epiplastral bone; hyo; hyoplastral bone; hypo; hypoplastral bone; Hu; humeral scale; il; ilium; ilsc; ilium scar; ing but; inguinal buttresses; is; ischium; ischsc; ischium scar; isf; interwoven structural fibre boundless; Fe; femoral scale; lb; lamellar bone; lppub; lateral process of pubis; M; marginal scale; meso; mesoplastral bone; nar; neural arch; ncr; neural crest; op; ornamentation pattern; pc; primary vascular channel; Pe; pectoral scale; per bone; peripheral bone; pfb; parallel-fibered bone; Pl; pleural scale; poc; posterior condyle; poct; posterior cotyle; prz; prezygapophyses; pu; pubis; pusc; pubis scar; py; pygal bone; pz; postzygapophysis; rl; resorbtion line; shf; sharpey's fibres; so; secondary osteon; spy; suprapygal bone; thyf; thyroid fenestra; tp; transverse process; tr; bone trabeculae; V; vertebral scale; vk; ventral keel; xi; xiphiplastral bone.

2.3. Results of the phylogenetic analysis

The phylogenetic analysis resulted in three trees of 83 steps (CI = 0.639, RI = 0.741), the strict consensus of which is provided in Fig. 1. *Yaminuechelys* aff. *maior* forms a monophyletic group with *Yaminuechelys maior*, which is supported by one synapomorphy (Character 37, Pygal bone trapezoidal). *Yaminuechelys gasparinii* is the sister taxon of this clade, and the relationship is supported by five synapomorphies (Character 6, Quadrate laterally expanded, forming part of temporal arch; Character 29, Presence of nuchal notch; Character 30, Nuchal bone width twice or more its length; Character 31, Peripheral bones anterior to bridge shorter than posterior ones; Character 35, Mesoplastral bones present). *Yaminuechelys maior*, *Y. aff. maior* and *Y. gasparinii* form the sister group of the *Hydromedusa* clade, and this relationship is supported by four synapomorphies present in all trees (Character 11, Large bony aperture narinum interna formed by reduction of palatines; Character 12, Large supraoccipital-squamosal contact; Character 22, Proportion of condyle of cervical vertebra 8 wider than high; Character 23, Outline of condyle of cervical vertebra 8 trapezoidal with shorter dorsal side).

2.4. Systematic Paleontology

TESTUDINES Batsch, 1788
PLEURODIRA Cope, 1865
CHELIDAE Lindholm, 1929
***Yaminuechelys* de la Fuente et al., 2001**
Type species. *Yaminuechelys gasparinii* de la Fuente et al., 2001

Yaminuechelys aff. *maior* (Staesche, 1929)
Figs. 2–7

Material. MAU-Pv-N-475 (Figs. 2–4): A partially preserved carapace (3–11 left peripherals, and 8–11 right peripherals, lateral-distal portion of the left costal bones 1, 4, 5 and 6, lateral fragments of 7 and 8 costal, lateral-distal portion of the right costals 5–8, a suprapygal and pygal), a left xiphiplastral fragment, one 7th cervical vertebra, one anterior caudal vertebra, and a right femur. MAU-Pv-PR-455 (Figs. 5–7): a partially preserved carapace (lacking the anterior margin, and most of the central and left part of the carapace), a complete plastron, remains of a sacral vertebra, eight articulated caudal vertebrae, and the pelvic girdle.

Localities. MAU-Pv-N-475: "Puesto Narambuena", about 20 km west from Rincón de los Sauces, Neuquén Province, Argentina. MAU-Pv-PR-455: "Puesto La Rinconada" northeastern flank of Auca Mauida ranges, about 10 km southwest from Rincón de Los Sauces, Neuquén Province, Argentina.

Horizon. Neuquén Group (Upper Cretaceous), Neuquén Subgroup, Anacleto Formation (Lower-Middle Campanian, according to paleomagnetic data by Dingus et al., 2000), referred to Coloradoan local tetrapod assemblage (Santonian-Lower Campanian) by Leanza et al. (2004). Additional information about the geological setting is provided by Filippi et al. (2011) for "Puesto Narambuena" and by Filippi and Garrido (2012) for "Puesto La Rinconada".

2.5. Comparative description

2.5.1. Cervical vertebra

A partially preserved seventh biconcave cervical vertebra is recognized as belonging to MAU-Pv-N-475 (Fig. 2). This is a long vertebra (maximum length = 78 mm) of a large, long-necked chelid turtle that preserves most of the vertebral centrum (Fig. 2A–E). The anterior condyle is sub-quadrangular in shape and slightly wider than high, while the posterior one is sub-circular in shape. The neural arch is not preserved, but the lateral process is situated in an anterior position. In ventral view the centrum is narrowed at mid-length and a ventral keel is preserved in poor condition.

2.5.2. Caudal vertebrae

An isolated caudal vertebra is preserved in MAU-Pv-N-475 (Fig. 3A–E) and an articulated caudal series formed by eight caudal vertebrae is seen in MAU-Pv-PR-455 (Fig. 3F–H). The isolated vertebra of the first specimen is preserved as a procoelus centrum with an oval condyle
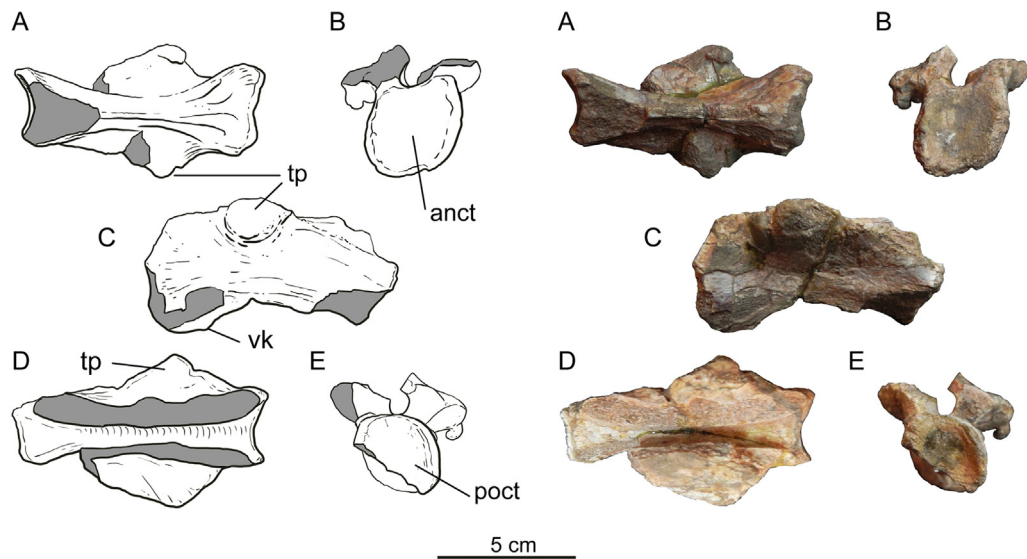
Fig. 2. (Color online.) *Yaminuechelys* aff. *maior* (Staesche, 1929), Upper Cretaceous, Puesto Narambuena, Neuquén Province, Argentina (MAU-Pv-N-475). Photographs and outline drawings of seventh cervical vertebra in: ventral (A), anterior (B), left lateral (C), dorsal (D), posterior views (E). Scale bar equals 5 cm.
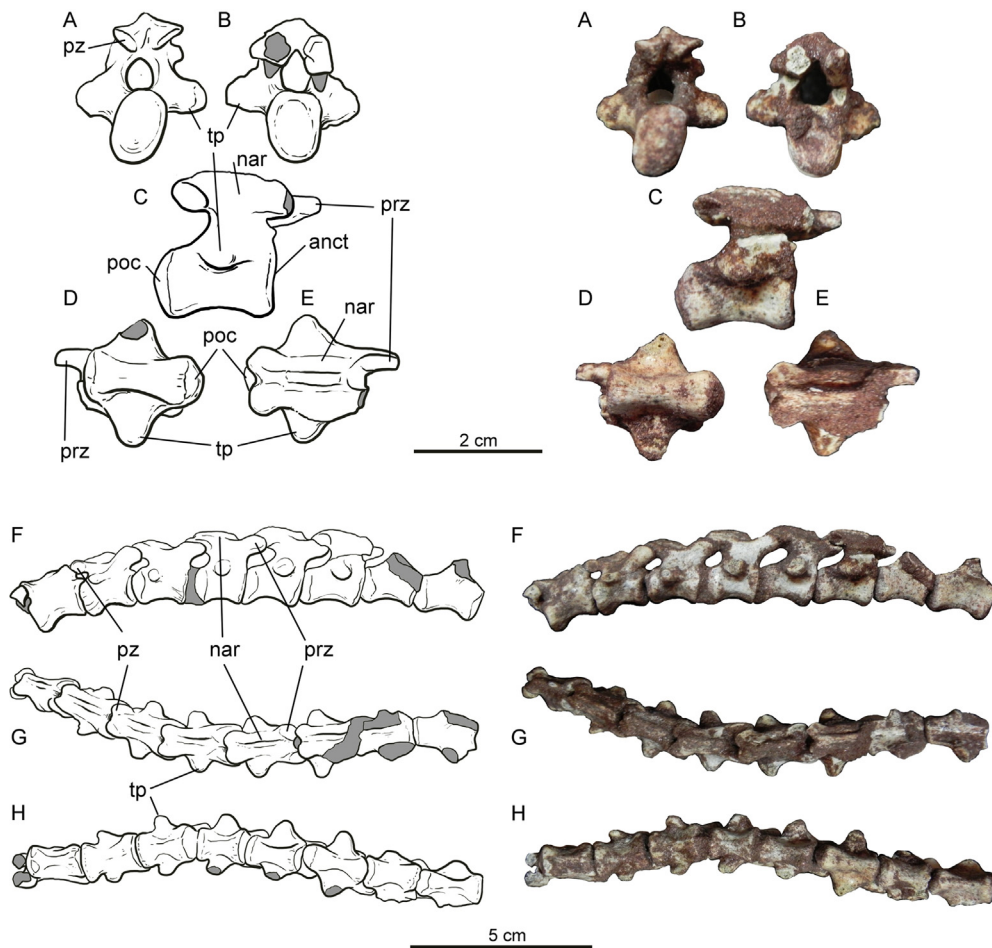
Fig. 2. (Couleur en ligne.) *Yaminuechelys* aff. *maior* (Staesche, 1929), Crétacé supérieur, Puesto Naranbuena, la vertèbre cervicale en vues : ventrale (A), antérieure (B), latérale gauche (C), dorsale (D), vues postérieures (E). Échelle : 5 cm.

and a sub-quadrangular cotyle. The procoelous condition and the anterior position of the transverse process in this vertebra suggest an anterior position in the caudal series (Fig. 3A–E). The central articulations of the caudal vertebrae MAU-PV PR-455 are procoelous (first to fifth), concavo-platycoelous (sixth), and amphicoelous (seventh and eight) (Fig. 3F–H). Procoely in *Yaminuechelys* aff. *maior* is not completely established but it is known in extant *Hydromedusa* species (*H. tectifera* and *H. maximiliani*). In MAU-Pv-PR-455 it is more developed than in *Y. gasparinii* which is characterized by a weakly procoelous (only first and second), amphicoelus (third), concavo-platycoelous (fifth, sixth), and amphicoelous (seventh) condition (see de la Fuente et al., 2001, and also de la Fuente et al., 2010). The central articulations are higher than wide in the five procoelous vertebrae, but wider than heigh in the remaining one. In MAU-Pv-PR-455 the transverse process is situated in an anterior position on the first four caudal centra, while in the remaining vertebral centra this process is more posteriorly located in the middle of the vertebral body (Fig. 3F–H). A relatively strong keel is developed on the preserved neural arches from the fifth to eight caudal vertebrae and it extends dorsally from the base of prezygapophyses to the base of the postzygapophyses. The preserved prezygapophyses (fourth to eight vertebrae) are oriented dorso-medially and they are in articulation with ventro-laterally oriented postzygapophyses of the previous caudal vertebra (Fig. 3F–H). In ventral view the vertebral bodies have no keels, and these centra are relatively narrow from first to third and continue to widen from fourth to eight (Fig. 3F–H).

2.5.3. Carapace

The carapace is flattened and oval in shape with convergent anterolateral margins (Figs. 4 and 5). The maximum length of the carapace is estimated to be 620 mm in MAU-Pv-N-475 (Fig. 4A and B) and 580 mm in MAU-Pv-PR-455 (Fig. 5A). The maximum width of the carapace at the seventh peripheral bone is estimated to be 430 mm in MAU-Pv-N-475. The dorsal surface of the carapace is sculptured by dichotomously branching sulci and a combination of the small and large polygons. In MAU-Pv-N-475 roughly equidimensional polygons are recognized on the peripheral bones, whereas more elongated ones are oriented along the width of the costal bones (Fig. 4A). The sculpture distribution of these polygons is slightly different in MAU-Pv-PR-455 with roughly equidimensional ones on dorsal surface of the carapace (Fig. 5A). Unfortunately the anterior margin of the carapace is not preserved in either specimen. However, a short third peripheral bone (Fig. 6A), suggests a non-expanded anterior margin in these specimens (with a correlated short and wide nuchal bone and cervical scale) as is characteristic in *Yaminuechelys* species (*Y. gasparinii* and *Y. maior*). This would be in contrast to the condition seen in *Hydromedusa* species (*H. casamayorensis* de la Fuente and Bona, 2002; *H. maximiliani* (Mikan, 1820), and *H. tectifera* Cope, 1870). Bridge peripheral bones 3–7 are not medio-laterally expanded, but they do have curled lateral margins that decrease from peripheral bones 3 to 7. The peripheral bones of the free posterior margin (8–11) are longer antero-posteriorly than transversely. Only two elements of the midline series are preserved in MAU-Pv-N-475 (suprapygal and pygal bones). The suprapygal is subpentagonal and the pygal is trapezoidal in shape. A similar pygal outline is recognized in the referred specimens of *Y. maior* (Bona and de la Fuente, 2005), whereas it is quadrangular in *Y. gasparinii* (de la Fuente et al., 2001, 2010). Although, neural bones, a suprapygal and pygal are present in MAU-Pv-PR-455, the sutures among these bones are not discernible in this specimen.

Fig. 3. (Color online.) *Yaminuechelys* aff. *maior* (Staesche, 1929), Upper Cretaceous, Puesto Narambuena, Neuquén Province, Argentina (MAU-Pv-N-475). Photographs and outline drawings of anterior caudal vertebra in: posterior (A), anterior (B), right lateral (C), ventral (D), dorsal views (E). *Yaminuechelys* aff. *maior* (Staesche, 1929), Upper Cretaceous, Puesto Rinconada, Neuquén Province, Argentina (MAU-Pv-PR-455). Articulated caudal vertebrae in: right lateral (F), dorsal (G), ventral views (H). Scale bars equals 2 cm for A–E; equals 5 cm for F–H.

Fig. 3. (Couleur en ligne.) *Yaminuechelys* aff. *maior* (Staesche, 1929), Crétacé supérieur, Puesto Naranbuena, province du Neuquén, Argentine (MAU-Pv-N-475). Photographies et dessins de vertèbre caudale antérieure en vues postérieure (A), antérieure (B), latérale droite (C), ventrale (D), dorsale (E). *Yaminuechelys* aff. *maior* (Staesche, 1929), Crétacé supérieur, Puesto Rinconada, province du Neuquén, Argentine (MAU-Pv-PR-455). Photographies et dessins de vertèbres caudales articulées en vues latérale droite (F), dorsale (G), ventrale (H). Échelle = 2 cm pour A–E ; échelle = 5 cm pour F–H.

In visceral view the axillary buttresses extend onto the third peripheral bone and the lateral extreme of the first costal in both specimens (Figs. 4B and 6B), whereas the inguinal buttress is attached to the seventh and eight peripheral and the lateral extreme of costal 5 and 6 in MAU-Pv-N-475, and on peripheral 7 and the lateral margin of the costal 5 in MAU-Pv-PR-455. The axillary and inguinal buttress attachment of the latter specimen fit with the attachment seen in referred specimens of *Y. maior* (Bona and de la Fuente, 2005). However, Pritchard and Trebbau (1984) pointed out variation of the extension of the plastral bridge as a case of sexual dimorphism in some extant chelid species (e.g. *Mesoclemmys zuliae*). The ilium scars are sub-triangular and located on the eighth costal bones and the anterolateral margin of the suprapygal bone (Fig. 4B).

Marginals 3 to 12 are seen on peripheral bones in both specimens; these scales are more complete on bones of the left side in MAU-Pv-N-475, but on the right one in MAU-Pv-PR-455 (Figs. 4A and 5A). In MAU-Pv-N-475, as in both *Yaminuechelys* species the marginal scales do not extend onto the suprapygal or costal bones. In both specimens the shape of marginal scales is similar: marginals 3–8 are sub-rectangular, 9–10 and 12 are sub-quadrangular, and 11 is pentagonal in outline. The third, fourth and fifth vertebral scales are recognized in MAU-Pv-PR-455 (Fig. 5A). The third and fourth vertebral scales are partially outlined in the incomplete carapace and likely hexagonal in shape, whereas the fifth is heptagonal. Unlike *Y. gasparinii*, in MAU-Pv-PR-455 the fourth vertebral scale is longer than the fifth. As typical in chelids, the fifth vertebral scale is wider than the third and fourth ones.

2.5.4. Plastron

The plastron is represented by a left xiphiplastral tip in MAU-Pv-N-475 and a complete plastron in MAU-Pv-PR-455 (Fig. 5B and C). The following description is based on
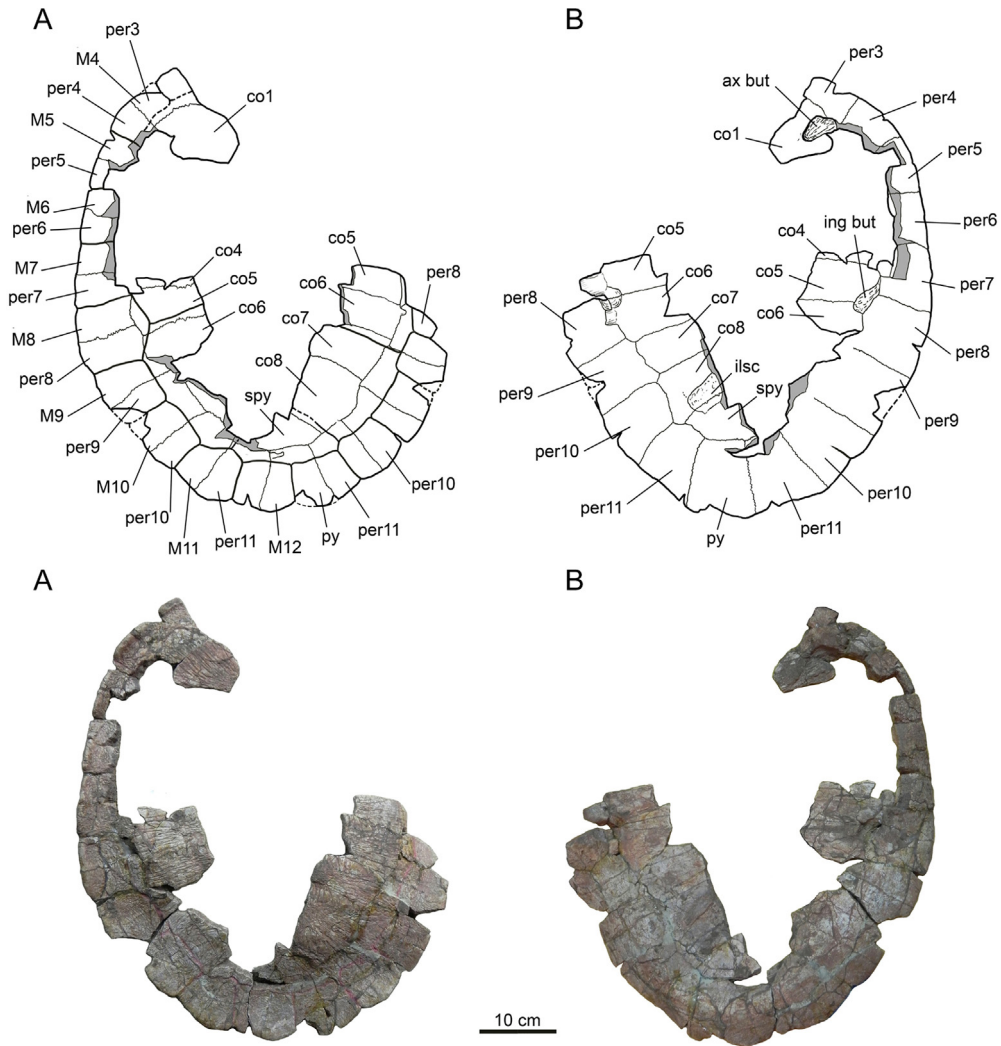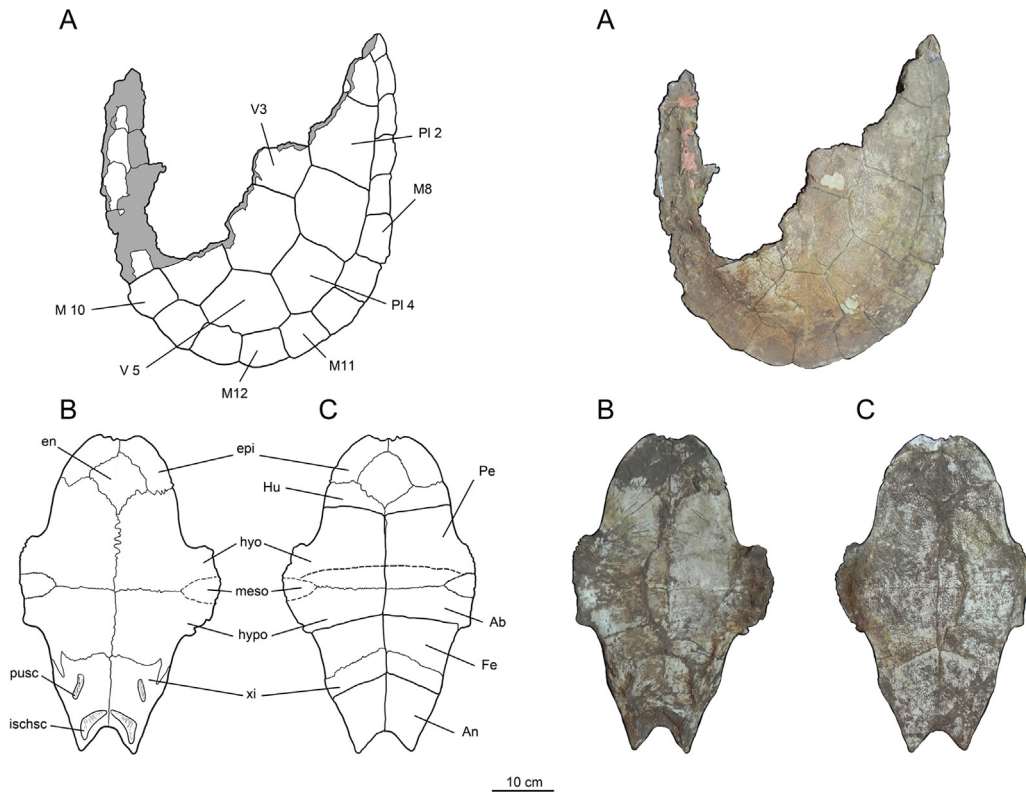
Fig. 4. (Color online.) *Yaminuechelys* aff. *maior* (Staesche, 1929), Upper Cretaceous, Puesto Narambuena, Neuquén Province, Argentina (MAU-Pv-N-475). Photographs and outline drawings of the carapace in: dorsal view (A), visceral view (B). Scale bar equals 10 cm.

Fig. 4. (Couleur en ligne.) *Yaminuechelys* aff. *maior* (Staesche, 1929), Crétacé supérieur, Puesto Narambuena, province du Neuquén, Argentine (MAU-Pv-N-475). Photographies et dessins de carapace en vues : dorsale (A), viscérale (B). Échelle = 10 cm.

the latter specimen. The plastron is relatively long: 472 mm midline length and 502 mm maximum length, but it is shorter than the carapace as is typical in turtles. The ventral surface of the plastron has strongly developed polygonal sculpturing made up of delicate sulci (Fig. 5C). A similar ornamentation is recognized in *Yaminuechelys*, *Chelodina* and *Hydromedusa* species.

The narrow anterior plastral lobe is roughly rounded in shape with lateral margin convergent proximally, in contrast to the enlarged anterior lobe in *Hydromedusa tectifera* and *H. maximiliani*. Although only slightly longer than the anterior lobe, the posterior lobe is the longest plastral element, while the bridge is shorter than either lobe (Fig. 5B and C). As in the specimens referred to *Y. maior* the margins of the posterior plastral lobe are strongly curved, contrary to the condition seen in the holotype of *Y. gasparinii*, in which the posterior plastral lobe margins are straight and convergent. The posterior tips of the xiphiplastra are

well developed, but the anal notch is not so deep and is opened open and U-shaped. The anterior lobe is composed of by a relative narrow epiplastron that embraces an entoplastron roughly rhomboidal in shape. The hypoplastra are the largest bone elements of the plastron. The hyo-hypoplastral suture is fused laterally on the right sided precluding the recognition of mesoplastron, whereas on the left sided a mesoplastral bone is recognized. Paired mesoplastra, cuneiform in shape, are recognized in a specimen referred to *Y. maior* from the Salamanca Formation (Bona and de la Fuente, 2005: Fig. 4D) and in the holotype of *Y. gasparinii* (de la Fuente et al., 2001, Fig. 2B–E; de la Fuente, 2007, Figs.3E and F and 5E and F). In visceral view the entoplastron is roughly arrow shaped with a relatively well-developed posterior process. The midline plastral suture is strongly interfingered in the midline hyoplastron contact, but becomes slightly sinuous posteriorly. On the xiphiplastra the scars produced by the narrow
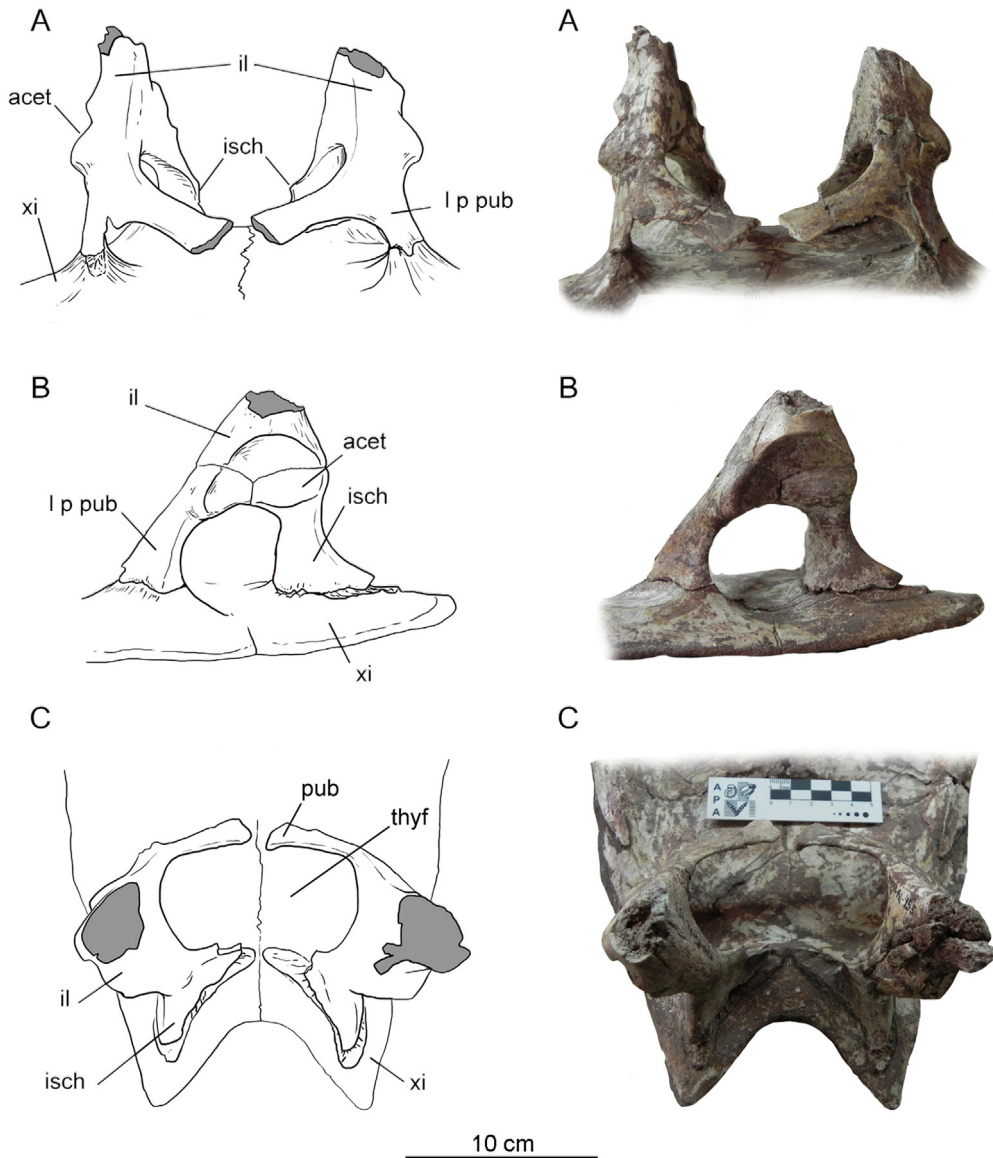
Fig. 5. (Color online.) *Yaminuechelys* aff. *maior* (Staesche, 1929), Upper Cretaceous, Puesto Rinconada, Neuquén Province, Argentina (MAU-Pv-PR-455). Photographs and outline drawings of the carapace in: dorsal view (A); and plastron in: visceral view (B), ventral view (C). Scale bar equals 10 cm.
Fig. 5. (Couleur en ligne.) *Yaminuechelys* aff. *maior* (Staesche, 1929), Crétacé supérieur, Puesto Rinconada, province du Neuquén, Argentine (MAU-Pv-PR-455). Photographies et dessins de la carapace en vue dorsale (A) et du plastron en vues viscérale (B) et ventrale (C). Échelle = 10 cm.
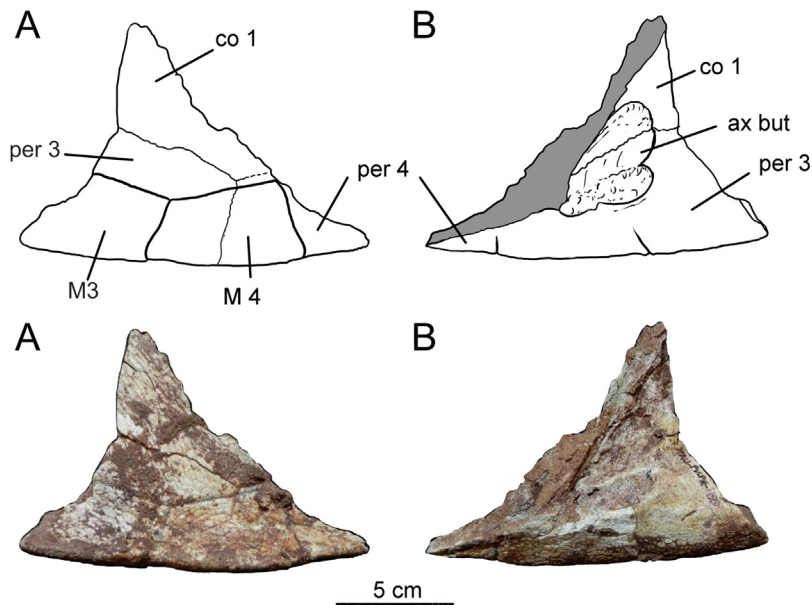
Fig. 6. (Color online.) *Yaminuechelys* aff. *maior* (Staesche, 1929) Upper Cretaceous, Puesto Rinconada, Neuquén Province, Argentina (MAU-Pv-PR-455) photographs and outline drawings of a left fragment of bridge (third, fourth peripheral bones) and lateral extreme of the first costal bone in: dorsal view (A), ventral view (B). Scale bar equals 5 cm.
Fig. 6. (Couleur en ligne.) *Yaminuechelys* aff. *maior* (Staesche, 1929) Crétacé supérieur, Puesto La Rinconada, province du Neuquén, Argentine (MAU-Pv-PR-455). Photographies et dessins d'une portion gauche de carapace de la région antérieure du pont (troisième et quatrième périphériques) et de l'extrémité latérale de la première costale en vues dorsale (A) et ventrale (B). Échelle = 5 cm.

Fig. 7. (Color online.) *Yaminuechelys* aff. *maior* (Staesche, 1929), Upper Cretaceous, Puesto La Rinconada, Neuquén Province, Argentina (MAU-Pv-PR-455). Photographs and outline drawings of the pelvic girdle sutured to xiphiplastron in: anterior view (A), left lateral view (B), dorsal view (C). Scale bar equals 10 cm.

Fig. 7. (Couleur en ligne.) *Yaminuechelys* aff. *maior* (Staesche, 1929), Crétacé supérieur, Puesto La Rinconada, province du Neuquén, Argentine (MAU-Pv-PR-455). Photographies et dessins de la ceinture pelvienne fixée par suture au xiphiplastron en vues antérieure (A), latérale gauche (B) et dorsale (C). Échelle = 10 cm.

sutural contact of the lateral pubis process and the ischium are recognized (Fig. 5B).

Although the gular-intergular scales are not discernible, the remaining scale patterns seen in MAU-Pv-PR-455 are recognized in chelid turtles (ie., humeropectoral sulcus well posterior to a large entoplastron) which fits well with the plastral scale formula suggested in the plastral reconstruction of *Y. maior* (Bona and de la Fuente, 2005: Fig. 9C) Fe > = An > Ab > Pe > Hu (Fig. 5C).

2.5.5. Pelvic girdle

The pelvic girdle (MAU-Pv-PR-455) is represented by right and left halves (Fig. 7A–C). Each one is tri-radiated in lateral view. As typical in pleurodires the pubis and ischium of each half is attached by two sutures to the xiphiplastron. Although, the iliac blade is not preserved, the ilium likely expanded dorsally to be attached by suture with the eight costal and the anterolateral margin of the suprapygal, as suggested by the iliac scar seen in the visceral surface of the carapace (see carapace description above and Fig. 4B). The pubis is sutured by only the lateral process, whereas the ischium is attached by suture over a broad surface extending from its symphysis to a lateral process. As typical in pleurodires the paired pubes and ischia are separated by a large and confluent thyroid fenestra. According to Walker (1973) in pleurodires this enlarged

fenestra is largely filled by the puboischiofemoralis externus, muscle which arises from the reduced pubis and ischium, the membrane in the fenestra, and the adjacent plastron.

2.5.6. Femur

An almost complete left femur is preserved in MAU-Pv-N-475. In this specimen the femoral head is roughly oval in end view. In lateral view, the head of the femur forms an angle of 130 degrees with the shaft of the bone. The proximal end includes partially preserved minor and major trochanters and the intertrocanteric fossa. The expanded distal end of the femur bears subequal fibular and tibial condyles. The morphology and size of this femur is similar to the left femur (MPEF-599) described in the material referred to *Y. maior* by Bona and de la Fuente (2005) from Danian levels of the Salamanca Formation and to the right femur (MEF 954) referred as Chelidae gen. et sp. indet. 1 by Gasparini and de la Fuente (2000) from the Maastrichtian La Colonia Formation.

2.6. Microanatomy and histology

2.6.1. Histological description

The two thin-sectioned carapacial elements show similar microstructures, and are described together. Individual variation between the two specimens will be mentioned where applicable. The external cortex consists of an inner region of interwoven structural fibers (ISF sensu Scheyer and Sánchez-Villagra, 2007) and an outer region mainly composed of highly remodellated parallel-fibered bone tissue. The ISF mostly extends sub-parallel to the bone surface, although perpendicular and diagonal arrangements are also present (Fig. 8A and B). The outer zone of the external cortex, which corresponds to the plate ornamentation, consists of parallel-fibered and lamellar bone tissue formed during successive stages of osseous resorption and deposition (Fig. 8C–E). Bone cell lacunae within the parallel-fiber bundles are mostly elongated and their orientation typically parallels the spatial arrangement of fibers. Branching canaliculi are often observed. Resorption lines are clearly visible in the inner zone and also within the outer zone. The cortical tissue is well vascularized by a mixture of simple vascular canals, scattered primary osteons, and few secondary osteons. Primary canals commonly exhibit anastomosis. In MAU-Pv-N-475 short Sharpey's fibers are scattered in the compact tissue.

The cancellous bone is rather poorly developed and consists of primary trabecular bone with little secondary reconstruction (Fig. 8). The transition between both external and visceral cortices and the cancellous bone is rather gradual. Cancellous bone is formed by short and thick bone trabeculae which bound inter-trabecular spaces. These spaces are small to medium sized in the periphery of the cancellous bone, becoming larger toward the inner core. The Inter-trabeculae spaces of the cancellous bone are rounded to irregular in shape and they commonly coalesce to form larger cavities. The walls of the trabeculae are coated by lamellar bone. The bone cell lacunae are flattened and exhibit thin canaliculi. The primary bone tissue

is totally formed by ISF. The cell lacunae are more circular and arranged in clusters.

The visceral cortex is composed of parallel-fibered bone, which can locally turn into lamellar bone. The arrangement of the fibers is roughly sub-parallel to the internal bone surface. Cortical bone is mainly avascular (Fig. 8G), with only occasionally scattered radial primary vascular. Sharpey's fibers are only found directly adjacent to the rib of the costal plate in MAU-PV-N-475. Growth marks in the form of lines of arrested growth (LAGs) are observed in the compacta. Bone cell lacunae are slightly flattened and elongated with long canaliculi.

The sutures are only preserved in MAU-Pv-N-475 (Fig. 8H). These are moderately developed with short to medium sized interfingered bone (pegs and sockets). The sutural area of the element is composed of interwoven structural fibers. Sharpey's fibers extend perpendicular to the bone margins.

3. Discussion

3.1. Taxonomic and phylogenetic comments

The long-necked chelid *Yaminuechelys* was named by de la Fuente et al. (2001) on the basis of an almost complete specimen from the Allen Formation (Upper Campanian-Lower Maastrichtian) of northern Patagonia. The type species of this genus *Yaminuechelys gasparinii* preserves several cranial and post-cranial characters that are recognized in the specimen described as neotype and the additional referred specimens of *Y. maior* by Bona and de la Fuente (2005). This Danian species has a long and confused taxonomic history summarized by Bona and de la Fuente (2005). According to these authors Staesche (1929) referred the largest specimens from the Punta Peligro (Chubut Province, Argentina) chelonian fauna to two taxa that he described from Paleocene levels of the Salamanca Formation (as Upper Cretaceous in Staesche's paper) as: "?*Najadochelys maior* n. sp. (Bothremydidae) and *Osteopygis sculptus* n. sp. (Cryptodira: Thalassemydidae)". Both species were described on the basis of fragmentary shell bones. In accordance with Broin (1987) and Broin and de la Fuente (1993), Bona and de la Fuente (2005) assigned *N. maior* to the family Chelidae, but these authors (on the basis of new and more complete cranial and post-cranial material recovered during a field trip in the austral summer of 1998) pointed out that *Osteopygis sculptus* is a junior synonymous of *N. maior* and transferred this species to the genus *Yaminuechelys* as a new combination: *Y. maior* (Staesche, 1929). The phylogenetic analyses preformed by Bona and de la Fuente (2005) suggest that *Yaminuechelys* (*Y. gasparinii* and *Y. maior*) is the sister group of *Hydromedusa* species (*H. maximiliani* and *H. tectifera*), and that together they form a monophyletic clade which is supported by two synapomrphies (large apertura narium interna formed by osseous reduction of palatines, and a wide contact between supraoccipital and squamosal) and one homoplasy (condyle of the 8th cervical vertebra wider than high).

In the present study we analyze the affinities of the specimens here described within the Chelidae. This analysis suggests that the two new specimens referred
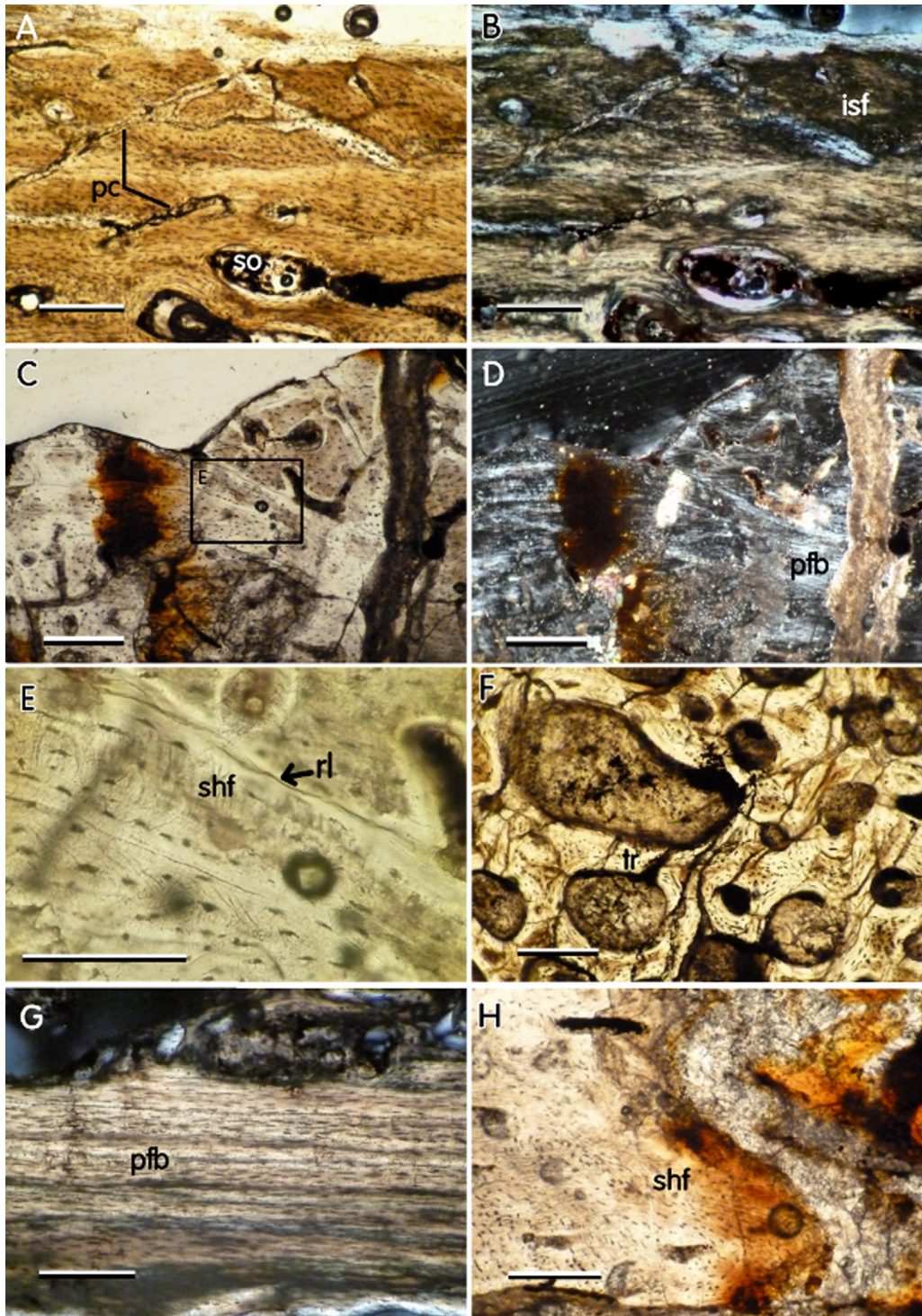
Fig. 8. (Color online.) *Yaminuechelys* aff. *maior.* Histological sections of carapace bones (A and B. MAU-Pv-PR-455. C–F. MAU-Pv-N-475); A and B. Interwoven structural fibres in the inner portion of the external cortex showed under normal (A) and polarized (B) light. C–D. Outer portion of the external cortex composed of parallel fibred bone viewed under normal (C) and polarized (D) light. E. Detail of the parallel fibred bone tissue (box inset in C) (normal light). F. Enlarged view of the cancellous bone tissue (normal light). G. Internal cortex composed of avascular parallel fibred bone (polarized light). H; detailed view of the suture margins of two adjacent plates (normal light). Scale bar equals 0.03 mm (A–D, F–H) and 0.1 mm (E).

Fig. 8. (Couleur en ligne.) *Yaminuechelys* aff. *maior.* Section histologique d'os costal de la carapace (A and B. MAU-Pv-PR-455. C–F. MAU-Pv-N-475). Fibres structurelles enchevêtrées dans la portion intérieure du cortex externe en lumière naturelle (A) et polarisée (B). C–D. Cortex externe composé d'os pseudolamellaire en lumière naturelle (A) et polarisée (B). E. Vue détaillée d'os pseudolamellaire (encart en C). F. Vue agrandie d'os spongieux en lumière naturelle. G. Cortex interne composé d'os pseudolamellaire avascularisé (lumière polarisée). H. Vue détaillée de la suture de deux plaques adjacentes (lumière naturelle). Échelle = 0,03 mm (A–D, F–H) et 0,1 mm (E).

to *Yaminuechelys* aff. *maior* nest within *Yaminuechelys*. This arrangement is supported by three synapomorphies (Characters 6, state 1: Quadrate laterally expanded, forming part of temporal arch; Character 30, state 1: Nuchal bone width twice or more its length; Character 31, state 0: peripheral bones anterior to bridge shorter than posterior ones) and two homoplasies (Characters 29, state 1: presence of nuchal notch; Character 35, state 1: mesoplastral present). Although the presence of a nuchal notch or mesoplastral bones are shared with the outgroup (*Podocnemis sextuberculata*), this could be also recognized in extinct species of different chelid lineages (e.g. *Bonapartemys bajobarrealis, Lomalatochelys neuquina, Prochelidella portezuelae*). The nuchal bone width twice or more its length and the size of the anterior peripheral bones shorter than the posteriors could be recognized in Cretaceous species that have been suggested related to other lineages of chelids (de la Fuente, 2007; Lapparent de Broin and de la Fuente, 2001).

The post-cranial morphology of MAU-Pv-PR-455 and MAU-PV-N-475 matches with that of chelid pleurodiran turtles. The attachment by suture between the pelvic girdle and the visceral surface of the shell is a synapomorphy of Pleurodira (Broin, 1977; Gaffney and Meylan, 1988). This derived character and the presence of an elongated seventh biconcave cervical vertebra associated with one of the specimens suggest the assignment of these specimens to a long-necked chelid species. Likewise, the relatively shortened anterior peripheral bones in comparison with the posterior ones (Character 31 of Bona and de la Fuente, 2005; this paper) in association with a strong decoration allow us to refer both specimens to the genus *Yaminuechelys*. Although the post-cranial material is insufficient for formal assignment, both specimens appear to be most closely related to *Y. maior* because of the large size and general carapace and plastral morphology (e.g. pygal shape, posterior plastral outline). Nevertheless, minor differences in carapace and plastral morphology (a curled peripheral bridge margin, lesser extension of the axillary buttresses on the visceral lateral surface of first costal, absence of a sub-rectangular plastral fenestra) suggest the use of open nomenclature to express the specific uncertainty in the identification of these specimens. Bengtson (1988) recommend the utilization of the term *affinis (aff.)* to point out affinity of a new undescribed species to a named taxon. Hence, the specimens are assigned to *Yaminuechelys* aff. *maior*, because the intraspecific variation of this species is unknown. The materials here referred to *Yaminuechelys* aff. *maior* are insufficient to formally name a new species, but it can be a potential different species most closely related to *Yaminuechelys maior*.

Even though there is general agreement concerning the monophyly of the Chelidae (Gaffney, 1977; Gaffney and Meylan, 1988; Georges et al., 1998; Seddon et al., 1997; Shaffer et al., 1997), resolution of the phylogenetic relationships within this pleurodiran clade is still under discussion. Phylogenies based on morphological data support the monophyly of the long-necked chelid turtles of Australasia and South America (Bona and de la Fuente, 2005; Gaffney, 1977, 1979; Gaffney and Meylan, 1988; Scheyer, 2009; Shaffer et al., 1997), whereas the

phylogenetic analyses based on molecular and serological data suggest that long-necked chelid group represents a polyphyletic assemblage (Fujita et al., 2004; Georges et al., 1998; Guillon et al., 2012; Krenz et al., 2005; Near et al., 2005; Seddon et al., 1997; Shaffer et al., 1997). Likewise, among these studies some analyses (i.e., Seddon et al., 1997) weakly support the hypothesis that the Australian long-necked chelids are more closely related to short-necked ones than to South American long-necked. The most parsimonious tree obtained by Seddon et al. (1997) could be expressed in parenthetic notation as: ((*Hydromedusa* ((*Batrachemys, Mesoclemmys*) ((*Acanthochelys, Platemys*) (*Chelus, Phrynops*)))) ((*Chelodina rugosa* (*Chelodina oblonga, Chelodina longicollis*)) (*Pseudemydura*(*Elusor* (*Elseya latisternum* (*Emydura* (*Elseya dentata, Rheodytes*))))))). The results of the Seddon et al. (1997) suggest that the differentiation of two chelid lineages (Australasian and South American) occurred after the separation of Australia from the remaining South Gondwanan landmasses. Other results obtained by Seddon et al. (1997) (Fig. 4) with Neighbour Joining algorithm suggest that the South American genus *Hydromedusa* is closely related to the monophyletic clade of Australasian chelids which expressed in parenthetic notation is: (*Hydromedusa* ((*Chelodina rugosa* (*Chelodina oblonga, Chelodina longicollis*)) (*Pseudemydura* (*Elusor* (*Elseya dentata* (*Rheodytes* (*Elseya latisternum, Emydura*))))))).

Even though Pritchard (1984a, 1984b) pointed out that the elongated neck seems to be correlated with an anterior expanded shell in chelids, Bona and de la Fuente (2005) stated that species of the extinct long-necked clade *Yaminuechelys* show non-expanded anterior carapace and plastron marking that this condition does not necessarily imply a different ecological status. Maniel and Stefanini (2014) in a preliminary morphometric study on extant chelids found that the short-necked *Mesoclemmys nasuta, Mesoclemys tuberculata* and *Platemys platycephala* show expanded anterior margin and were more closely related in the morphospace with *Chelodina + Hydromedusa* group than with the short-necked group.

Pritchard (1984a, 1984b) mentioned that *Hydromedusa* is more closely related to *Chelus* than to *Chelodina*, and proposed an adaptive condition to relate *Hydromedusa* with *Chelodina*. In our cladistic analysis we retained an alternative hypothesis in which *Chelodina* is the taxon most closely related to *Hydromedusa + Yaminuechelys*, which is supported by a series of morphological characters. We tested the Pritchard hypothesis by forcing the monophyly of *Chelus* with *Hydromedusa + Yaminuechelys*. We obtained as the best score 93 steps (10 more than the most parsimonious trees), so in a morphological context *Chelus* presents some states of characters that differ from the rest of long-necked chelids. As mentioned by Bona and de la Fuente (2005) three of the synapomorphies recovered from the consensus tree are autopomorphies of the clade *Chelodina + Hydromedua + Yaminuehelys* (Characters 17, 18 and 20). All of these characters are related to cervical vertebrae. In this phylogenetic context functional correlation among characters is difficult to demonstrate.

The record of *Yaminuechelys* cf. *gasparinii* and *Y.* aff. *maior* in the Anacleto Formation (de la Fuente et al., 2010;
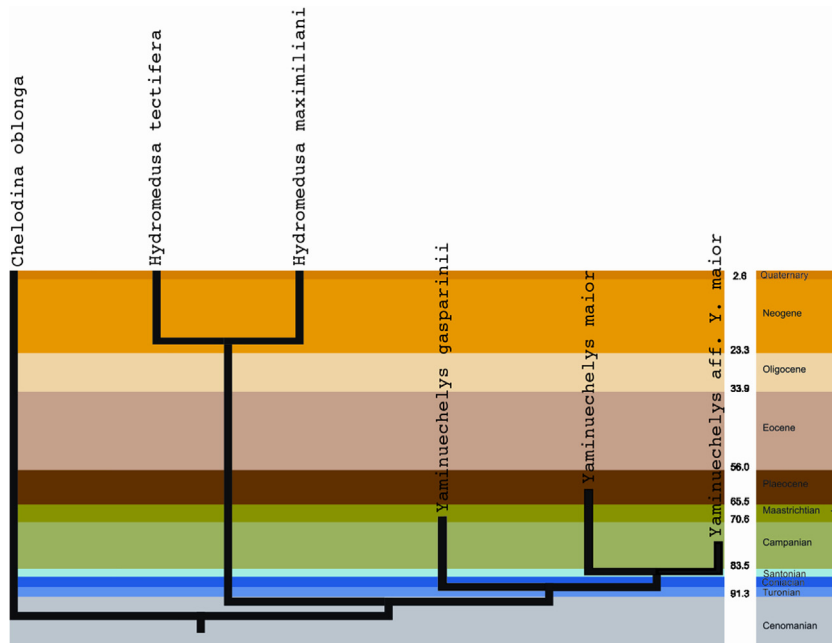
Fig. 9. (Color online.) A pruned tree showing the stratigraphic adjust between *Yaminuechelys* species and the other long-necked chelids. The divergence points between Australasian and South American forms had to be in the limit between the Lower Cretaceous and the Upper Cretaceous. The *Yaminuechelys* clade would have diverged at least in the Turonian age.

Fig. 9. (Couleur en ligne.) Arbre élagué montrant l'ajustement stratigraphique entre les espèces de *Yaminuechelys* et les autres chélidés à long cou. Les points de divergence entre les formes d'Australasie et d'Amérique du Sud ont dû se trouver à la limite entre le Crétacé inférieur et le Crétacé supérieur. Le clade *Yaminuechelys* aurait divergé au moins au Turonien.

this paper) extends the record of long-necked chelid at least to the Early Campanian (Dingus et al., 2000) or the Late Santonian (Leanza et al., 2004).

These old records are significant when the chelid diversification is assessed in a morphological phylogenetic framework (e.g., Bona and de la Fuente, 2005). As the basis of the Campanian is dated in 83.4 Ma (Gradstein et al., 2012) the common ancestor of *Hydromedusa* and *Yaminuechelys* would have inhabited southern South America in an age that predates this geological time (Fig. 9) Taking into account that the phylogenies based on morphological data suggest that the Australasian long-necked *Chelodina* is the sister taxon of *Hydromedusa* (i.e., Gaffney, 1977) or the *Hydromedusa + Yaminuechelys* (Bona and de la Fuente, 2005; this paper) these results suggest a chelid differentiation before the breakup of southern Gondwana.

3.2. Bone histological comments

Several microstructural features observed in MAU-PV-N-475 (e.g. diploe structure, external cortex formed by ISF, remodelled cancellous bone trabeculae, visceral cortex formed by parallel fibred bone) have been considered plesiomorphic for Testudines (Scheyer, 2007; Scheyer and Sánchez-Villagra, 2007). On the other hand, the presence of parallel-fibered and lamellar bone secondarily formed in the outer portion of the external cortex appears to be a derived character. This feature is associated with the typical ornamentation pattern of the external surface of the plates. The same histological pattern has been recently described for *Y. maior* (Jannello et al., 2014), which contributes to the

morphological systematic hypothesis enunciated in this paper.

The carapace microstructure has been used as a valuable tool in palaeoecological studies (Scheyer, 2007; Scheyer and Sander, 2007; Scheyer et al., 2014). These studies are based on the degree of development of compact and cancellous bone and the degree of cortical vascularization. Scheyer (2007) proposed four categories according to their degree of aquatic adaptation (I: terrestrial; II: semi-aquatic to mainly aquatic; III: fully aquatic; and IV: extreme aquatic/marine adaptation). The microstructure of the shell bone of MAU-PV-N-475 and MAU-PV-PR-455 fits with the fully aquatic condition (i.e. reduction of compact bone layers, especially the internal cortex, high degree of vascularisation in the cortical bone). Our findings are congruent with previous palaeoecological hypotheses (e.g., Bona and de la Fuente, 2005; de la Fuente et al., 2001).

3.3. Survivorship of Yaminuechelys genus to K/P boundary

The survivorship of turtle species through the K/P boundary was assessed taking into account mainly the turtle fauna from the Northern Hemisphere. One of the main studied cases is the chelonian fauna from the northern Great Plains in North America (i.e., Archibald, 1996; Archibald and Bryant, 1990; Holroyd and Hutchison, 2002; Hutchison and Archibald, 1986). Preliminary evaluation of the K/P survivorship of chelonians in the Southern Hemisphere was recently attempted by Sterli and de la Fuente (2013). According to these authors two lineages of

meiolaniforms survived the K/P boundary: *Peligrochelys walshae*, a member of a lineage with close related taxa in Laurasia, and Meiolaniidae, a lineage with only Gondwanan species. Sterli and de la Fuente (2013) pointed out the high frequency association of two different clades in the Southern Hemisphere, meiolaniforms and chelids. This association is found in horizons from the Early Cretaceous to Eocene in Patagonia and from the Early Cretaceous, and Miocene to Pleistocene in Australia. Besides this typical association of these turtle lineages (meiolaniforms and chelids) among the chelids, the South American longnecked lineage has shown examples of survivorship to the K/P boundary. The record of the long-necked chelids as *Yaminuechelys* aff. *Y. maior* (this paper) or *Yaminuechelys* cf. *Y. gasparini* (de la Fuente et al., 2010) in Coloradan assemblage sensu Leanza et al. (2004) (Lower and Middle Campanian), *Y. gasparinii* and *Yaminuechelys* cf. *maior* in Allenian assemblage (Campanian- Maastrichtian), or *Y. maior* in Danian levels of the Salamanca Formation (Bona and de la Fuente, 2005) in Patagonia provide empirical data of the survivorship of the *Yaminiechelys* genus through the K/P boundary in Patagonia. As mentioned above, a sister group relationship is suggested between species of *Yaminuechelys* and *Hydomedusa* (Bona and de la Fuente, 2005). In accordance with this phylogenetic hypothesis a close relative of the extinct *Yaminuechelys* species is the extant *Hydromedusa tectifera*. This long-necked chelid species is adapted to survive in extreme conditions, showing a peculiar capacity to hibernate underwater in a small creek of Buenos Aires Province by means of slowing down its metabolism (de la Fuente, personal observation). *H. tectifera* is also a typical freshwater inhabitant, whose range extends southward up to Samborombón Bay (Buenos Aires Province, Argentina) (Cabrera, 1998; de la Fuente et al., 2013; Iverson, 1992), that has been occasionally captured in brackish waters of the Río de la Plata with barnacles on the carapace (de la Fuente, 1999; Frazer, 1986). A similar estuarine estuarial paleoenvironment has been suggested for the Danian levels of the Salamanca Formation, where the remains of *Yaminuechelys maior* were found (Bona et al., 1998, and references therein). In contrast, fluvial environments have been inferred for the sediments of different outcrops of the Anacleto Formation that yielded *Yaminuechelys* aff. *maior* (Filippi et al., 2011; Filippi and Garrido, 2012) and *Y.* cf. *gasparinii* (de la Fuente et al., 2010, and references therein). The ecological plasticity and the peculiar behaviour of the extant species *H. tectifera* and the different paleoenvironments inhabited by the species of the extinct *Yaminuechelys* may help to explain how these aquatic species could have survived the K/P boundary.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.crpv.2015.04.008.

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