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A new large panchelid turtle (Pleurodira) from the Loncoche Formation (upper Campanian-lower Maastrichtian) of the Mendoza Province (Argentina): Morphological, osteohistological studies, and a preliminary phylogenetic analysis

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ABSTRACT

A new genus and species of panchelid turtle (*Mendozachelys wichmanni* gen. et sp. nov.) from the upper Campanian–lower Maastrichtian Loncoche Formation (southern Mendoza Province, Argentina) is described here. This species is represented by only one complete and articulated large specimen (carapace length estimated in 950 mm) that was recovered from tidal flat deposits. A detailed morphological and osteohistological description is made, recognizing autapomorphic characters that allow differentiating this taxon from the rest of extant and extinct panchelids. Osteohistological characters suggest an aquatic to semi-aquatic life style for *Mendozachelys wichmanni* gen. et sp. nov. Phylogenetic analysis based on morphological data suggested that this new taxon is nested within crown Chelidae. Both phylogenetic signals (morphological and molecular) about the assessment of long-necked chelids monophyly or polyphyly are discussed.

1. Introduction

The large turtle described herein (carapace length estimated in 950 mm) was found in upper Campanian–lower Maastrichtian strata of the Loncoche Formation that crops out at the locality of Ranquil-Có (Southern Mendoza Province) Argentina. It was collected in 1990 by José Bonaparte and his crew. Posteriorly, some authors of this paper (BGR and MdlF) explored the area between 1995 and 2004 and found several fossil remains increasing the knowledge of the vertebrate fauna from this Formation (González Riga, 1999; González Riga et al., 2004).

The goal of this contribution is to describe the morphology and osteohistology of the new genus and species to enhance the knowledge of extinct panchelids and to explore the new taxon phylogenetic position within pleurodiran turtles in a cladistic framework. The specimen is articulated and is one of the most complete specimens of panchelid turtles of the Upper Cretaceous of South America. It is represented by skull remains, lower jaw, cervical and caudal vertebrae, carapace, plastron and appendicular skeleton. This specimen was preserved under particular taphonomic conditions associated with tidal flat deposits (see Geological Settings). This relatively complete specimen increases the diversity of panchelid turtles from the cuspidal part of the Upper Cretaceous of southern Gondwana. A preliminary approach to the anatomy and phylogenetic position of this species was given by de la Fuente et al. (2015a); here, the detailed study is provided. Pan-Chelidae is used to refer the total group that includes the crown chelids and its stem

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(Joyce et al., 2004). Pan-Chelidae is the sister group of Pan-Pelomedusoides within Pleurodira but has an opposing geographic distribution and evolutionary history (Broin, 1988; Broin and de la Fuente, 1993; de la Fuente, 2003; Romano and Azevedo, 2006; de la Fuente et al., 2014). Members of Pleurodira (pan-chelids plus pan-pelomedusoids) could be recognized by the presence of a processus trochlearis pterygoidei, by the sutural articulation of the pelvis with the shell, presence of a well-developed anal notch, a pair of mesoplastra lacking a medial contact, single gular scute, central articulation in the cervical column and absence of inframarginals and supramarginals. Pan-chelids are differentiated from pan-pelomedusoids by the cervical formula of 1((2((3((4((5))6))7((8) and by the symplesiomorphic presence of a cervical scute (Maniel and de la Fuente, 2016), characters recognized in the new genus and species presented herein. The pan-chelid phylogeny is still controversial. The morphological approach, based on cranial and post-cranial characters, suggest that the long-necked chelids, *Chelodina* (Australia), *Hydromedusa* (South America), and *Chelus* (South America) form a monophyletic group spanning in both continents (Gaffney, 1977; Bona and de la Fuente, 2005). On the other hand, the molecular and serological analyses (Burbidge et al., 1974; Seddon et al., 1997; Georges et al., 1998; Guillon et al., 2012) conclude that the Australian short-necked and long-necked species are more closely related to each other than to the South American species. The molecular analyses suggest an independent radiation of the chelids following the separation of the Australian and South American continents, and contradicts the monophyly of long-necked chelids proposed by Gaffney (1977) and Bona and de la Fuente (2005).

1.1. Institutional abbreviations

MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina.

UNCUYO-LD, Laboratorio de Dinosaurios of the Universidad Nacional de Cuyo, Mendoza, Argentina.

MZUSP, Museo de Zoologia Universidade de São Paulo, São Paulo, Brazil.

SMF, Senckenberg Museum Frankfurt, Germany.

1.2. Anatomical abbreviations

Morphological abbreviations (see figures in the text and the figures included in Online Supplementary Material Appendix 3)

acst, aditus canalis stapedio temporalis; AN, anal; ang, angular; art, articular; ax but, axillar buttress; bo, basioccipital; bs, basisphenoid; co, costal; C, cervical; con, condyle; conm, condylus mandibularis; cor, coracoid; coro, coronoid; cot, cotyle; csa, canalis semicircularis anterior; csh, canalis semicircularis horizontalis; ct, cavum tympani; cv, caudal vertebra; de, dentary; dip, diapophysis; EG, extragular; en, entoplastron; ep, epiplastron; ex, exoccipital; fe, femur; FEM, femoral; fi, fibula; for ner trig, foramen nervi trigemini; fr, frontal; fs meck, fossa meckelii; gln fs, glenoid fossa; GU, gular; hu, humerus; HUM, humeral; hy, hyoplastron; hyp, hypoplastron; il sc, iliac scar; isch sc, ischial scar; ju, jugal; lab r, labial ridge; lin r, lingual ridge; M, marginal; mar inc col au, margin incisura columellae auris; meso, mesoplastron; mh, mandibular hook; mt, metatarsals; mtc, metacarpals; mx, maxilla; n, neurals; nc, neural channel; ncr, neural crest; nu, nuchal; op, opisthotic; Pl, pleural; pa, parietal; pe, peripheral; PEC, pectoral; ph, phalanges; po, postorbital; pr, prootic; pra, prearticular; proc troch pt, processus trochlearis pterygoidei; prz, prezygapophysis; pt, pterygoid; pz, postzygapophysis; qu, quadrate; rd, radius; rlp, recessus labyrinticum prooticus; scp, scapula; sh pl, shell plates; sp, splenial; sup, suprapygal; sur, surangular; sym r, symphisial ridge; ti, tibia; un ph, ungual phalanges; V, vertebral; vc, ventral crest; xi, xiphiplastron.

Osteohistological abbreviations

CB, cancellous bone; ECO, external cortex; ICO, internal cortex; ISF, interwoven structural collagenous fiber bundles; lsFB, longitudinal fiber bundles; PO, primary osteon; ShF, Sharpey's fibers; SO, secondary osteon; SVC, simple vascular canal; TR, bone trabeculae; trFB, transverse fiber bundles.

2. Materials and methods

2.1. Materials

The turtle here described is represented by one articulated specimen recovered in the lower member of the Loncoche Formation. This specimen was found in articulation, and cranial and postcranial remains were separated during the technical preparation of the material. The skeleton of this specimen is one of the most complete panchelids from South America, composed of skull, lower jaw, carapace, plastron, cervical and caudal vertebrae, shoulder girdle, and elements of the appendicular skeleton.

2.2. Methods

Phylogenetic relationships of the new species of turtle presented here in particular, and those of the panchelid turtles in general, were evaluated through the cladistic method. A dataset of 18 taxa and 61 morphological characters (see Appendix 1) based on those proposed by several authors (Gaffney, 1977; de la Fuente, 2003; Bona and de la Fuente, 2005; Cadena Rueda and Gaffney, 2005; Joyce, 2007; Cadena et al., 2008; Thomson and Georges, 2009) was assembled for the present analysis. Only taxa with cranial and postcranial remains were included in this analysis. Three taxa (*Notoemys laticentralis*, *Araripemys barretoi*, and *Podocnemis sextuberculata*) were considered as the outgroup, while 15 taxa of extinct and extant turtles were considered as the ingroup (see Appendix 1). *Notoemys laticentralis* was the taxon selected to root the analysis. All characters were weighted equally and twelve characters were considered ordered (see Appendix 1). In order to evaluate the phylogenetic relationships of these turtles, an implicit enumeration algorithm search was performed in the phylogenetic program TNT (Goloboff et al., 2008a, 2008b). If more than one MPT was found, a strict consensus tree was calculated. Clade support was calculated using Bremer, Bootstrap and Jacknife supports. Two analyses were performed, unconstrained and constrained using molecular scaffolds for extant taxa. The extant taxa were constrained considering the topology of Guillon et al. (2012) (see Appendix 2). In the last case the extinct taxa where treated as floaters.

For the osteohistological analysis five fragmentary shell bones from the same specimen where used, three costal and two peripheral plates. Thirteen thin sections where prepared based on the methodology outlined in Chimsamy and Raath (1992). Planes of sectioning varied among the different shell bones: costals were cut parallel to the anteroposterior axis (perpendicular to the incorporated ribs), while peripherals were cut perpendicular and parallel to the anteroposterior axis of the turtle shell. Thin sections were described using petrographic polarizing microscopes (Nikon ECLIPSE E200). Nomenclature and definitions of structures follow Francillon-Vieillot et al. (1990). The terms "external" and "internal" are used throughout the text instead of "dorsal" and "ventral" to prevent confusion between dorsal carapacial and ventral plastral bones of the turtle shell (*e.g* the "dorsal" surface of a neural plate corresponds to the external surface of the bone, whereas the