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Research Article

New Cretaceous lungfish material from southern South America, Argentina

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Abstract - Dipnoi is a large group of sarcopterygians which ranges from the Early Devonian to the present. Traditionally, it was considered that their taxonomic diversity decreased at the end of Paleozoic. Dipnoans are abundant in the fossil record and their preservation state varies. The material study herein was collected in La Invernada locality, at 50 km southwest from the Rincón de los Sauces city, Neuquén Province, Argentina. We present the first dipnoan skull record from the Mesozoic of South America and gives a preliminary description of the material. The new specimens have been identified as a Ceratodontidae indet.

Keywords: Dipnoi, Gondwana, Santonian, skull

1. Introduction

Dipnoi is a large group of sarcopterygians which ranges from the Early Devonian to the present. Traditionally, it was considered that their taxonomic diversity decreased at the end of Paleozoic (Schultze, 2004). However, a recent study, proposed that dipnoans presented two peaks of taxonomic diversification, one in the Middle Devonian, and the other in the Early Permian (Kemp *et al*., 2017). According to Nelson *et al*. (2016), Mesozoic and Cenozoic dipnoans are grouped together in Ceratodontiformes– an order that includes living lungfishes and their fossil relatives.

Dipnoans are abundant in the fossil record and their preservation state varies. In the Paleozoic they are represented by articulated specimens with heavily ossified skull (Miles, 1977; Campbell and Barwick, 1987; Schultze and Campbell, 1987). Taxonomy and systematics of most Mesozoic lungfishes are based on isolated tooth plates and jaw bones but little is known about their cranium and postcranium (e.g., Schultze, 1981; 2004; Martin, 1982; Kemp 1992; 1997a; 1998; Apesteguía *et al*., 2007; Cione and Gouiric-Cavalli, 2007; Soto and Perea, 2010). In the Triassic, most of the specimens show articulated skull bones (except those from North and South America), but no attached tooth plates (Kemp, 1994; 1998; Schultze, 2004). Jurassic and Cretaceous dipnoans consists mainly on isolated tooth plates (Kemp 1998; Schultze, 2004), exception are the Jurassic species *Potamoceratodus guentheri* (Pardo *et al*., 2010) and *Ferganoceratodus jurassicus* (Nessov and Kaznyshkin, 1985); *Ferganoceratodus martini* putatively Cretaceous in age (Cavin *et al*., 2007; Racey and Goodall, 2009) and the Cretaceous species, *Archaeoceratodus avus* (Kemp, 1997a). The variable degree of completeness could be explained by sampling bias (Pardo *et al*., 2010). However, a taphonomic bias may not be discarded especially if it is considered that skull bones tend to reduction and fusion through dipnoans evolution. Besides, these trends were accompanied by the reduction in ossification of the chondrocranium and the weakening of the articulation between skull bones (Kemp, 1992; 1998).

During the Cretaceous, dipnoans were widely distributed living on several Gondwana continents (e.g., Kemp, 1997a, b; Schultze, 2004; Cione and Gouiric-Cavalli, 2012). In South America, Cretaceous dipnoans tooth plates have an abundant record (Toledo and Bertini, 2005; Toledo *et al*., 2011; Alves *et al*., 2013; Madeiros *et al*., 2014; Pinheiro de Sousa *et al*., 2015). In Argentina, they are commonly found throughout Late Cretaceous sediments of Mendoza, Neuquén, Río Negro, Chubut, and Santa Cruz provinces (Ameghino, 1898; González Riga, 1999; Apesteguia *et al*., 2007; Cione *et al*., 2007; Salgado *et al*., 2009; Cione and Gouiric-Cavalli, 2012). To date, Argentinian dipnoans are extensively recorded in the Late Cretaceous, except in the Santonian.

The aim of this contribution is to present two nearly complete dipnoan skulls of the Late Cretaceous (Santonian) from Argentina. Also, the intention of this article is to discuss the importance of this finding in a global context including systematics and taphonomy.

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2. Geological setting

The material study herein was collected in La Invernada locality, at 50 km southwest from the Rincón de los Sauces city, Neuquén Province, Argentina (Fig. 1 a - b). Specimens were recovered at the Bajo de La Carpa Formation, Río Colorado Subgroup of Neuquén Group in the Neuquén Basin (Fig. 1 c). According to Garrido (2010), the Bajo de La Carpa Formation is considered Santonian (85.8-83.5 My) in age. The depositional environment for this unit has been interpreted mainly as fluvial. Sediments of the Bajo de La Carpa Formation correspond to continental deposits of sandstone, mudstone, and laminated sandy siltstone, usually with thin evaporitic layers of gypsum. In addition, it has been inferred warm and semiarid climatic conditions for the Bajo de La Carpa Formation (Garrido, 2010).

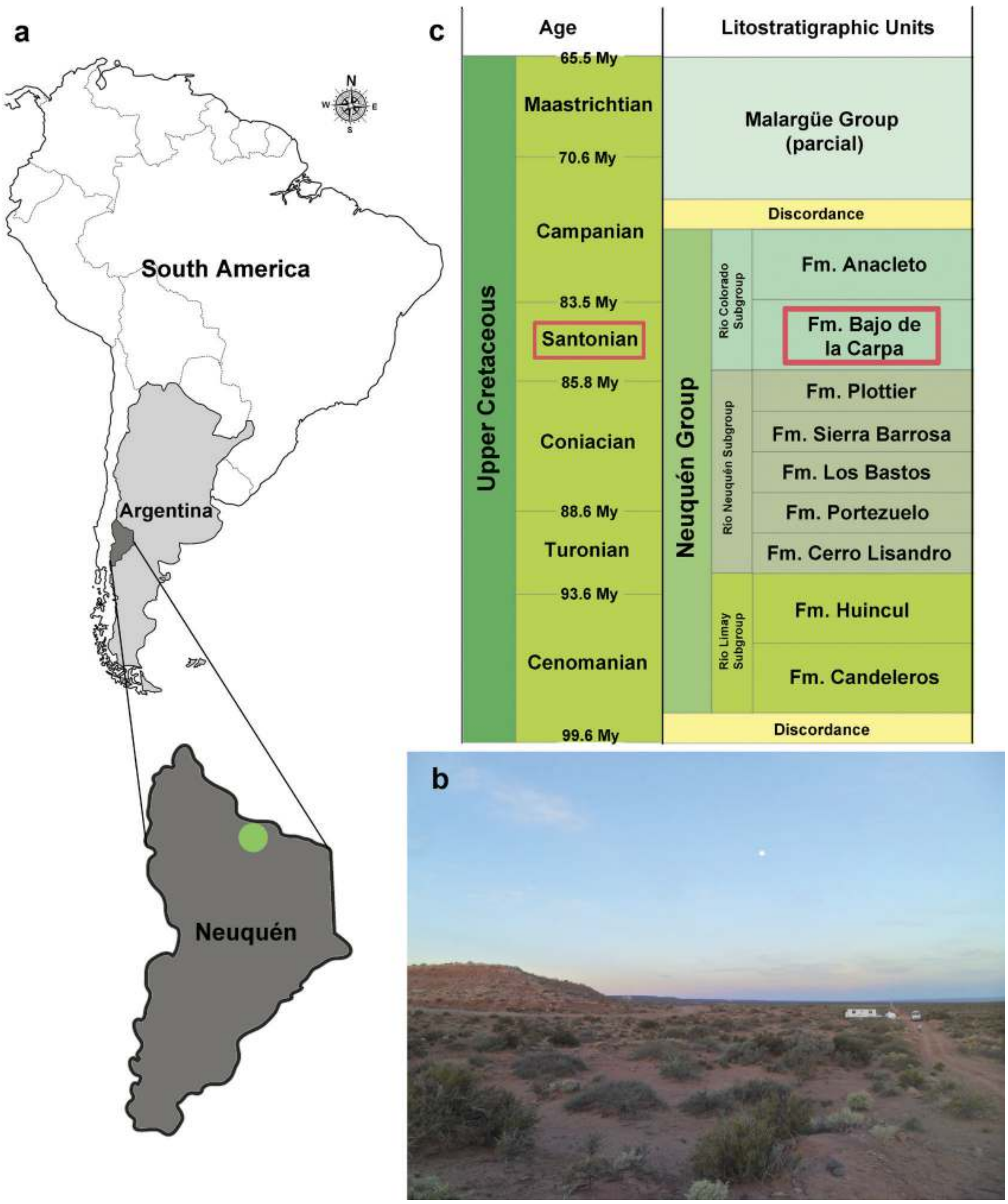

Figure 1. (a) Geographic location of La Invernada Locality, Neuquén, Argentina, South America. (b) Photograph of study area. (c) Stratigraphic location of Bajo de La Carpa Formation in Neuquén Group (Modified from Garrido, 2010).

3. Material and Methods

3.1Material

Specimens studied herein are held in the Museo Municipal "Argentino Urquiza", Rincón de los Sauces, Neuquén, Argentina (MAU). Material consists of two concretions with skulls three-dimensionally preserved. MAU-Pv-LI-612 (Fig. 2) is almost completely preserved having most of the skull roof bones, two pterygopalatine tooth plates attached to bone, and a fragmentary prearticular tooth plate. MAU-Pv-LI-613 has their skull roof bones badly preserved, two pterygopalatine tooth plates, the left one attached to pterygopalatine bone, the right one is not attached to the pterygopalatine bone, and has only one prearticular tooth plate.

3.2 Methods

The material were mechanically prepared at MAU. Both specimens were studied under binocular microscopy (Arcano ZTX 745L) and using digital photographs taken with a Canon EOS Rebel T2i with a compact macro lens Canon EF 50 mm f/2.5. Measures were taken using high resolution photographs with the free software, Fiji.

3.2.1 Anatomical terminology

Skull roof bones are described following topography criteria *sensu* Cavin *et al*. (2007). However, Kemp (1992; 1998) terminology is in brackets. Jaw bone terminology follow Kemp (1992).

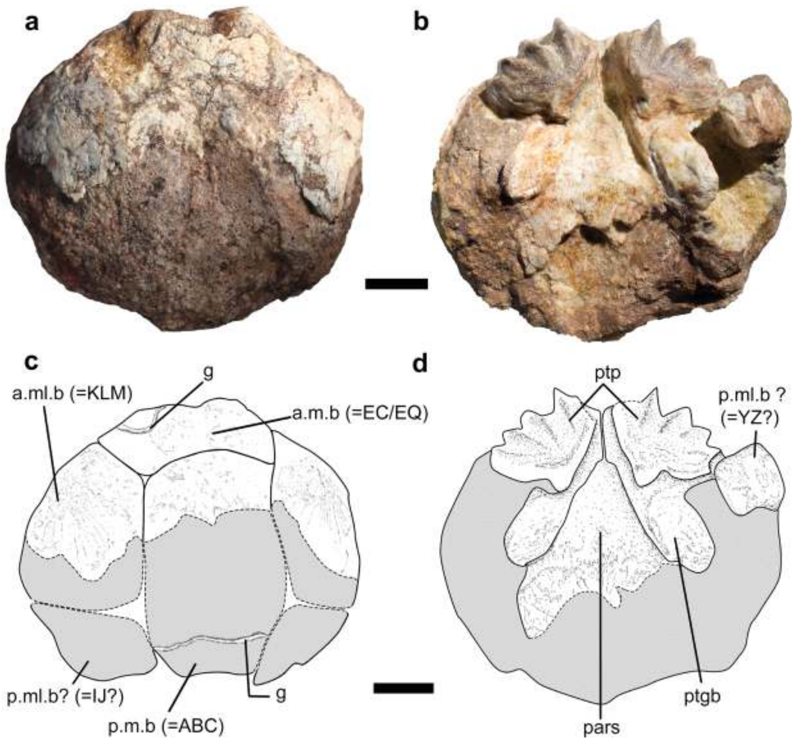

Figure 2. MAU-Pv-LI-612, Ceratodontidae indet. (a) Photograph on dorsal view. (b) Picture on ventral view. (c) Interpretative drawing on dorsal view. (d) Interpretative drawing on ventral view. Abbreviations: a.m.b (=EC/EQ), anterior median bone, a.ml.b (=KLM), anterior mediolateral bone, pars, parasphenoid, p.m.b (=ABC), posterior median bone, p.ml.b.? (=IJ?), posterior mediolateral bone, ptp, pterygopalatine tooth plate, ptgb, pterygoid bone, stc, supratemporal sensory canal. Scale bar= 10 mm.

4. Results

4.1Systematic paleontology

Dipnoi Müller, 1845

Family Ceratodontidae Gill, 1872

Ceratodontidae indet.

Figures 2

Description– The skulls are massive, robust, and heavily ossified. The general morphology of the skulls is more or less quadrangular to ovoid-shaped. They measure among 5–5. 5 cm antero-posteriorly, 4–5.5 cm wide, and 3 cm high (Figs. 2–3). The skull roof is composed of an unpaired anterior medianł bone (=EC/EQ bone of Kemp) and posterior median bones (=ABC bone of Kemp) plus paired anterior mediolateral bones (KLM bone of Kemp). Impressions at the posterior portion of the skull are interpreted here as posterior mediolateral bone? (=IJ? bone of Kemp and) bones (Fig. 2). Skull roof ornamentation consists of weak and straight lines and some punctuations present in the JLM bones. No tubercles or coarse ridges are present. The anterior median bone is short and quadrangular. The anterior mediolateral bones are more or less triangular. The supratemporal commissure is visible as a groove in the posterior margin of the posterior median bone. No cranial ribs are preserved. The palate is represented by the unpaired parasphenoid and paired pterygopalatine bones. The pterygopalatine supports the ankylosed tooth plates. Vomerine tooth plates are not preserved. The pterygopalatine bone is short. The upper tooth plates are short, thick, and have five ridges –first ridge of both upper tooth plates is broken–. The inner angle is not well developed and ridges seem to originate medially. Mesial angle is up to 90º. In occlusal view the mesial margin of upper tooth plates is slightly curved and has a well-developed posterior projection. Upper tooth plates are close to each other but not in contact. Punctuations are absent. Occlusal pits present over occlusal surface and between ridges. The ascending pterygopalatine process is not observed. Cleft between ridges are shallow and wide. Cusps are weakly developed in the labial profile of ridges extremities. The labial profile of the upper tooth plate ridges is steep and each tooth plate ends in a single last ridge. The enamel to bone junction rising up between ridges in buccal, lingual and medial surfaces. Wear facets are present on some ridges. The parasphenoid is partially preserved in both specimens lacking most of its posterior portion. It articulates antero-medially with the pterygopalatine bones. The lower jaw is represented by the paired prearticular bone which bears ankylosed tooth plates. The lower prearticular joint is long and straight. The prearticular bones form an angle with the horizontal of about 38º and has a short posterior process. The lower tooth plates are short, thick, and has five ridges that originate anteriorly. The inner angle is well developed and ridges originates anteriorly. Lower tooth plates are widely separated.

5. Discussion

To date almost all valid Mesozoic dipnoan taxa are based on tooth plates (e.g., Kemp, 1993, 1997, Cione *et al*., 2007, Cione and Gouiric-Cavalli, 2012). Thereby, the pterygopalatine tooth plates of the specimens herein presented were compared with other Mesozoic dipnoans, especially with those of Cretaceous. The new Argentinian specimen are assigned to Ceratodontidae because show several characters shared among members of this family i.e., five ridges on pterygopalatine tooth plates and wide and shallow clefts between ridges like in *Ceratodus, Atlantoceratodus, Ferganaceratodus,* and some *Metaceratodus* specimens; ridges of medial origin as in *Ceratodus* and *Metaceratodus*. Like *Metaceratodus*, the Argentinian material have a similar occlusal profile. A medio lingual angle up of 90º is shared with *Atlantoceratodus*, *Metaceratodus*, and *Lupaceratodus*. Occlusal pits widely distributed and covering all the occlusal surface are present in the Argentinian material as well as in *Ferganaceratodus*, *Metaceratodus,* and *Lupaceratodus*. Subtriangular tooth plates are present also in *Metaceratodus*. The last two characters are also present in members of Ptychoceratodontidae (i.e., *Ptychoceratodus cuyanus, P. serratus*). The new Argentinian material differs from *Lupaceratodus* in the lower number of ridges, in having a different occlusal profile, a larger first crest, and straight and radiating ridges (see Gottfried *et al*., 2009 for comparison). The new Argentinian material agrees with *Atlantoceratodus* in the number of ridges, but differs from it in having a larger pterygopalatine posterior process. Also, the new Argentinian material differs from *Metaceratodus* in having the enamel to bone junction rising up between each ridge labially, upper tooth plates not in contact, a shorter and wider pterygopalatine posterior process, and in the absence of punctuations. The new Argentinian material differs from all the genera previously mentioned by having a marked process in the lingual margin of the tooth plates.

Also, the combination of the above mentioned characters with a the general morphology of upper and lower tooth plate (i.e., robust, thick, and with five ridges), allowed us the allocation of the studied specimens to Ceratodontidae Characters related to skull especially those regarding number and relative position of skull roof bones, show some similarities with *Ceratodus* as well as with other Ceratodontiformes, such as *Arganodus*, *Ferganoceratodus* and *Mioceratodus* (Kemp 1997a, b; 1998; Cavin *et al*. 2007). All these dipnoan genera share a general skull morphology, (i.e., short and wide) and also a similar or the same skull roof bones disposition (i.e., presence of a median anterior and posterior bones and a pair of anterior and posterior mediolateral bones).

Information relative to dipnoan skulls is useful to improve the understanding of their morphological diversity. Also, it allows test those nominal species based only on tooth plates (see Schultze, 2004 for a discussion). In this context, the new Argentinian finding seems to be quite remarkable and may provide useful information relative to skull structures and their association with tooth plates. This gives a more complete outline to make a more accurate taxonomic approach.

During the Mesozoic –particularly during the Cretaceous– dipnoans shows a wide distribution in many Gondwana continents being recorded by tooth plates (Kemp 1997a, b; Schultze, 2004; Cione and Gouiric-Cavalli, 2012). The new Argentinian finding is a very significant contribution because it represents the first dipnoan skull material collected in the Mesozoic of South America. In addition, there are records of dipnoan tooth plates almost over all the Late Cretaceous of Argentina (Apesteguia *et al*., 2007) yet, this is the first Santonian report and fill the Argentinian record of dipnoans for the Upper Cretaceous.

A detailed study of this new dipnoans skull in association with tooth plates, will provide new morphological information to discuss the pattern and characters of post-Paleozoic dipnoans skull, especially from the Cretaceous of Gondwana. Knowledge concerning skull of Cretaceous dipnoans is scarce compared with Paleozoic or Triassic information. The new data might contribute to a better understanding regarding the evolution and paleobiogeographic implications of dipnoans groups.

6. Conclusions

We present the first dipnoan skull record from the Mesozoic of South America and gives a preliminary description of the material. The new specimens have been identified as a Ceratodontidae indet. However, it is imperative to deep in comparisons to clarify the taxonomic position as well as the systematic affinities of this new Argentinian material.

The further and detailed study of the specimens will bring new information about the Cretaceous dipnoans skull anatomy. Also, it will contribute to the knowledge about taxonomic diversity of dipnoans from Argentina and Gondwana.

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