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A Late Jurassic-?earliest Cretaceous ctenochasmatid (Pterosauria, Pterodactyloidea): The first report of pterosaurs from Uruguay

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ABSTRACT

The Tacuarembó Formation contains a faunal assemblage with some taxa clearly indicative of a Late Jurassic-Early Cretaceous age. In this context, the first remains of Uruguayan pterosaurs are described. These correspond to a dorsoventrally compressed and narrow fragment of a rostrum widening anteriorly, with alveoli and a very fragmentary dentition including a tooth base. The orientation of the alveoli and preserved tooth base allows the assumption that the teeth were projected laterally and forward from the dental borders. The deep interdental concavities make up a wavy contour of the lateral margins of the rostrum. Both morphology and size correspond to that observed in the ctenochasmatid gnathosaurines. The Uruguayan pterosaur remains represent the oldest ctenochasmatid found in South America and suggest an age of the fossiliferous horizon no older than Late Jurassic, which was already established on the basis of other fossils, such as *Priohybodus arambourgui* d'Erasmo, 1960.

1. Introduction

During the last two decades the knowledge of the vertebrate assemblage of the Tacuarembó Formation has significantly increased (Perea et al., 2001, 2003; 2009, 2014; Soto and Perea, 2008, 2010; Soto et al., 2012a; b; Mesa and Perea, 2015). Here we describe and analyze the first remains of pterosaurs ever found in Uruguay. The studied material, the fragment of anterior part of a rostrum, was originally classified erroneously as a probable sawfish (Perea et al., 2016). However, more detailed studies by high resolution computed tomography, refuted that hypothesis.

Pterosaurs were the first vertebrate group that conquered the skies. In South America, pterosaurs are known from spectacular findings, such as those from the Early Cretaceous Santana Group (Neumann and Cabrera, 1999), where a variety of exceptionally preserved crested forms, belonging to different taxa, were found (Maisey, 1991; Kellner and Tomida, 2000). However, Jurassic pterosaurs from this continent are poorly known. They include forms from the lacustrine Cañadón Asfalto Formation (Middle Jurassic of Patagonia, Codorniú et al., 2016) and the marine Vaca Muerta Formation (Late Jurassic of Patagonia, Casamiquela, 1975, Codorniú and Gasparini, 2013). Herein we report a valuable addition to the Jurassic record of South American pterosaurs.

2. Material and methods

Regular and frequent fieldwork was undertaken at the diverse outcrops of the Tacuarembó Formation in northern Uruguay in order to collect fossil material and observe the stratigraphic distribution of the fauna of this unit.

A new locality, situated about 2 km northwest of Batoví Hill (close to Batoví Quarry and the homonimous locality mentioned by Soto et al., 2012b), is reported here for the first time. This locality has yielded the rostrum fragment described below.

In order to collect the here described rostrum fragment it was necessary to use electro pneumatic hammer, because of the hardness of the sandstone. In the laboratory, mechanical preparation techniques were used under binocular magnifying glasses. To reinforce the specimen, cyanoacrylate consolidating agents were used.

The detailed anatomical study of the material had to be complemented necessarily with conventional and high resolution computerized tomography (micro-CT).

A preliminar CT scan of the studied rostrum fragment was performed in a Siemens Somaton Sensation 64 CT scanner device, at Unidad de Radiología - Hospital de Clínicas, Universidad de la República (Uruguay). The specimen was scanned in the coronal plane with a voltage of 100 KV and a current of 155 mA, with a resolution of

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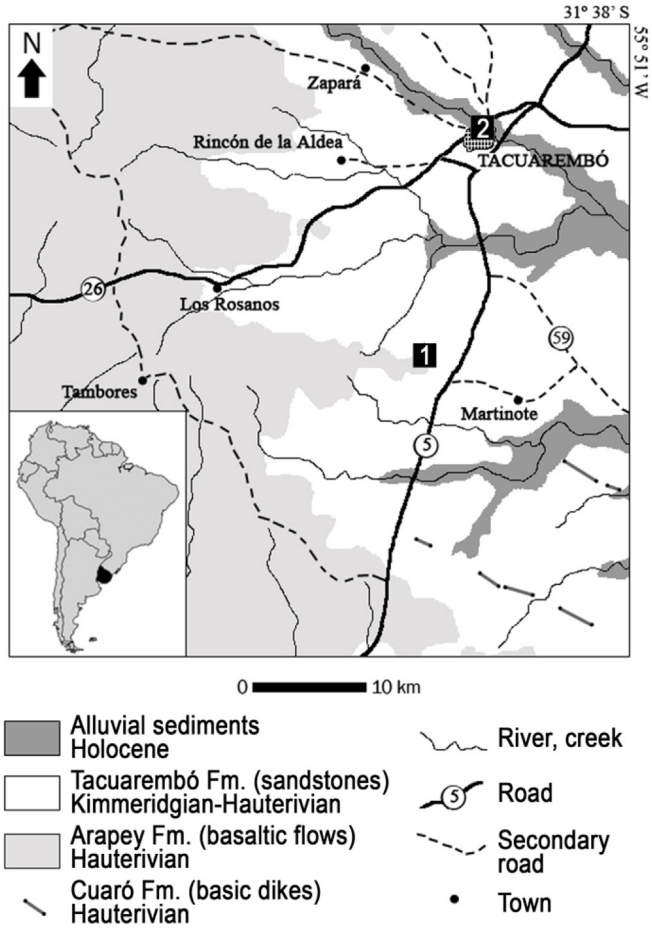

Fig. 1. Map showing pterosaurian fossil localities (black squares) for the Tacuarembó Formation discussed in the text. 1, FC-DPV-2869, rostral fragment. 2, FC-DPV-3090, isolated teeth.

0,6 mm.

With the aim to obtain higher resolution images, a second scan was performed in a General Electric Phoenix x-ray micro CT scanner device, at Laboratório Multiusuário de Processamento de Imagens de Microtomografia Computadorizada de Alta Resolução - Museu de Zoologia da Universidade de São Paulo (Brazil). In this last case the specimen was scanned with a tube voltage of 90 KV and a tube current of 265 μA, with a resolution of 0,02 mm in the three axes.

Taxonomy follows Witton (2013) and Andres et al. (2014). Stratigraphic nomenclature follows Perea et al. (2009).

Institutional abbreviations: FC-DPV, Vertebrate Fossil Collection, Facultad de Ciencias, UdelaR, Montevideo, Uruguay.

3. Geological setting, age, and taphonomy

The sandstones that form the Tacuarembó Formation (Bossi, 1966), which crops out in the northern region of Uruguay (Fig. 1), are divided into two members (Bossi et al., 1975), later named Batoví (lower) and Rivera (upper) members, respectively (Perea et al., 2009). Most of the thickness of the unit is formed by the Batoví Member, which is so far the only fossiliferous one.

Intensive field work carried out in this member yielded abundant fossils of bivalves, gastropods, conchostracans, hybodontid sharks, ginglymodians, actinistians, dipnoans, crocodyliforms, and theropod dinosaurs (see Perea et al., 2009). Moreover, ichnofossils attributed to sauropod, theropod and ornithopod dinosaurs have been recently described (Mesa and Perea, 2015).

The Tacuarembó Formation has a peculiar fossil assemblage, some members of which are unique to this unit, including the bivalve *Tacuaremboia caorsi* Martínez et al., 1993, the crocodyliform *Meridiosaurus vallisparadisi* Mones, 1980, and the turtle *Tacuarembemys kusterae* Perea et al., 2014. Other taxa are more widespread, with occurences in other units of Western Gondwana, such as the shark *Priohybodus arambourgi* d'Erasmo, 1960, the lungfish *Arganodus tiguidiensis* (Martin, 1982), and the coelacanth *Mawsonia* Woodward in Mawson and Woodward (1907) (see Perea et al., 2001; Soto and Perea, 2010; Soto et al., 2012a; b). Most of the taxa with a wider geographic distribution indicate a chronological interval spanning the Late Jurassic-Early Cretaceous (e.g. Perea et al., 2009; see below). This is corroborated by radiometric dates from overlying basalts, indicating that the Tacuarembó Formation cannot be younger than the Hauterivian (Perea et al., 2001, 2009, and references therein).

Dinosaurs are the only strictly terrestrial members of this faunal assemblage. They are represented by shed theropod teeth (Perea et al., 2003, 2009; Soto and Perea, 2008), and ichnites of sauropods, theropods and ornithopods (Mesa and Perea, 2015). The vertebrate assemblage of the Tacuarembó Formation mostly consists of aquatic or amphibian animals, which clearly depended on the ephemeral and perennial fluvial systems in which the fossiliferous sediments of this unit, were deposited. In the semi-arid conditions, under which the Batoví Member Formation supposedly formed (Perea et al., 2009), the dinosaurs would have also depended substantially on these water bodies.

The rostral fragment described herein was found in a 2.5-m thick yellowish, fine grained sandstone (Fig. 2). The sandstone starts with a basal horizon of pelitic intraclasts, and is massive, showing low-angle cross-bedding towards the top. Overall, this sedimentary log (Fig. 2A) is indicative of an ephemeral river, characterized by episodes of higher and lower discharge. The pterosaur rostrum fragment was found spatially associated with etched ganoid scales and unidentified bone fragments in a patchy bonebed (Fig. 2C). Fossil preservation is poor compared to other Tacuarembó Formation bonebed material, such as those from the localities of Martinote, Los Rosanos and Bidegain Quarry from where the isolated teeth here described came (e.g. Perea et al., 2001, 2003; 2009; Soto et al., 2012b).

The taphonomy of the remains described here indicates a probable transport away from the original habitat of the living organisms, in particular the rostral fragment showing a high degree of wear, which is herein interpreted as a parautochthonous component of the assemblage.

4. Systematic Paleontology

PTEROSAURIA Kaup, 1834.
PTERODACTYLOIDEA Plieninger, 1901.
CTENOCHASMATIDAE Nopsca, 1928.
GNATHOSAURINAE Unwin, 1992.
GNATHOSAURINAE gen. et sp. indet.
Figs. 3, 4, 5.

4.1. Material

FC-DPV-2869, fragment from the anterior part of a maxillopremaxillary rostrum with 18 alveoli (Fig. 3), including the root of one tooth (Fig. 4).

4.2. Locality and horizon

The specimen comes from near the Batoví Quarry, Tacuarembó province, northern Uruguay (Figs. 1 and 2; see Geological Setting above), Batoví Member, Late Jurassic-?earliest Cretaceous of the Tacuarembó Formation.