

## Oldest azhdarchid (Pterosauria) record from South America

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**Abstract:** Azhdarchid pterosaurs in South America were hitherto represented by two taxa coming from Coniacian-Santonian and Maastrichtian beds, of the Mendoza and Río Negro provinces, respectively, in Argentina. Here we report an incomplete pterosaur cervical vertebra from Cenomanian beds exposed at the east shore of Ezequiel Ramos Mexía Reservoir at the Río Negro Province (Patagonia, Argentina). The cervical vertebra is referred to Azhdarchidae by the presence of a notoriously slender centrum being sub-circular in cross-section at its mid-length, with well-developed postexpapophyses, and extremely reduced neural spine. The recovered specimen represents a pterosaur smaller in size than the previously found azhdarchids in Patagonia, and constitutes the oldest record for the clade in the South American continent. Thus, it constitutes an important addition to the knowledge of the diversity of the clade in Patagonia during the Cretaceous.

**Key words:** Pterosauria, Azhdarchidae, Patagonia, Cenomanian, Late Cretaceous.

**Resumen:** El registro más antiguo de Azhdarchidae (Pterosauria) en América del Sur. Los azdárquidos en América del Sur están representados por dos taxones provenientes de niveles del Coniaciano-Santoniano de Mendoza y Maastrichtiano de Río Negro, Argentina. Aquí presentamos una vértebra cervical incompleta de pterosaurio, proveniente de estratos cenomanianos de la provincia patagónica de Río Negro, Argentina. El espécimen es referido a Azhdarchidae por la presencia de una vértebra cervical notoriamente elongada con postexpapofisis bien desarrolladas, espina neural muy reducida y un centro vertebral que es subcircular en sección en la mitad de la longitud. La vértebra cervical recuperada representa un pterosaurio de menor tamaño que los azdárquidos previamente descubiertos en Patagonia, y constituye el registro más antiguo para el clado en el continente sudamericano. Por ende, el presente hallazgo constituye una importante adición al conocimiento de la diversidad del clado en Patagonia.

**Palabras clave:** Pterosauria, Azhdarchidae, Patagonia, Cenomaniano, Cretácico Tardío.

### INTRODUCTION

Azhdarchids represent a derived clade of long-necked pterodactyloid pterosaurs that were distributed in almost all continents, with exception of Antarctica (Averianov, 2014) and probably Australia (Andres, 2021). Most azhdarchids are known from Upper Cretaceous deposits (Andres *et al.*, 2014; Longrich *et al.*, 2018), with some possible records from Lower Cretaceous and Upper Jurassic deposits (Costa *et al.*, 2015; but see Andres, 2021). In spite of their wide geographi-

cal distribution, their record in South America is still very poor. Possible azhdarchid remains were reported from the Lower Cretaceous beds from the Crato Formation, Brazil (Martill & Frey, 1998), but its identification was heavily put into question by subsequent authors that regarded them as indeterminate tapejarids or pterodactyloids (Unwin & Martill, 2007).

More recently, Kellner & Calvo (2017) described the new genus and species of azhdarchoid *Argentinadraco barrealsensis* from the Portezuelo Formation (Late Turonian-Early Coniacian)

from Neuquén Province, Argentina, based on an incomplete lower jaw. Based on its general shape, Kellner & Calvo (2017) suggested that it may be allied to azhdarchids. However, this taxon has been recently found to be included in Thalassodrominae among Dsungaripteromorpha by Andres (2021).

The first undoubted record of azhdarchid in South America belongs to *Aerotitan sudamericanus*, a large-sized azhdarchid from Maastrichtian beds of northwestern Patagonia (Novas *et al.*, 2012). Because *Aerotitan* is known just by the tip of a beak, some authors doubted its affinities (Longrich *et al.*, 2018), but its unique morphology indicates that it belongs to a very large azhdarchid closely related to *Quetzalcoatlus* (Averianov, 2014; Vullo *et al.*, 2018; Pegas *et al.*, 2022). More recently, Ortiz-David *et al.* (2018, 2022) described the azhdarchid genus and species *Thanatosdrakon amaru*, based on postcranial remains from the Plottier Formation (Late Coniacian-Early Santonian, Neuquén Basin), Mendoza Province, Argentina.

The aim of the present contribution is to describe a single, partial cervical vertebra assignable to Azhdarchidae from Cenomanian beds of the Candeleros Formation (early Late Cretaceous) from northern Patagonia (Fig. 1). This represents the oldest record for this clade in South America.

## MATERIAL AND METHODS

### Locality and horizon

The specimen here reported was found close to the bonebed that yielded the skeletal remains of the coelurosaur theropod *Bicentenaria argentina* (Novas *et al.*, 2012). The specimen was found during a field trip performed under the project of relocation and georeferencing of fossil sites in the Río Negro province, carried out by the former Dirección de Patrimonio y Museos from the Río Negro government and supported by some professionals of the Universidad Nacional de Río Negro (UNRN) in June, 2019. The fossiliferous locality is placed on the east shore of Ezequiel Ramos Mexía Reservoir, in the northwestern part of the Río Negro Province, Northern Patagonia, Argentina. GPS coordinates of the fossil site are 39° 28' 9.82" S, 68° 54' 25.01" W (Novas *et al.*, 2012) (Fig. 1). The specimen here described was found together with some turtle plates belonging to a small Chelidae.

These fossils come from the upper levels of the Candeleros Formation (Early Cenomanian, early

Late Cretaceous; Leanza *et al.*, 2004), Río Limay Subgroup, Neuquén Group. The rocks that yielded the remains of *Bicentenaria* and the pterosaur here described are composed of red medium-sized sandstones and mudstones, with abundant dark brownish paleosoils (Leanza *et al.*, 2004; Garrido, 2010, 2011). These beds represent a fluvial environment under braided and meandering regimes, as well as aeolian conditions (Garrido, 2010).

### Institutional abbreviations

MPCA-PV, Vertebrate Paleontology Collection, Museo Provincial "Carlos Ameghino", Río Negro province, Argentina; TMM, Texas (Texas Vertebrate Paleontology Collections, Austin, Texas, USA.

## SYSTEMATIC PALEONTOLOGY

Pterosauria Kaup, 1834

Pterodactyloidea Plieninger, 1901

Azhdarchoidea Unwin, 1995 (sensu Kellner, 2003)

Azhdarchidae Nessov, 1984

Indeterminate genus and species

**Referred material.** MPCA-PV 2003, posterior half of a middle cervical vertebra (Fig. 2A-D).

**Description.** The specimen MPCA-PV 2003 consists of the posterior half of a cervical vertebra having the surface of the centrum and the left postzygapophysis slightly eroded, and lacking the right postzygapophysis. The strongly convex condyle suggests that this element was procoelous. The notably elongated and compressed centrum, which is tubular in cross section at its mid-length and with a reduced neural spine are features present in cervical vertebrae IV to VI of azhdarchids (see Averianov, 2010), and consequently, MPCA-PV 2003 is tentatively identified as a middle cervical element.

The neural arch is dorsoventrally low (Fig. 2D'). The neural spine is a very low and narrow ridge, and is confluent with the centrum at mid-length of the vertebra (Fig. 2A, C'). The neural canal is relatively small and subcircular in cross-section. Lateral to the neural canal there is a subcircular, much smaller, pneumatic foramen (Fig. 2D'). The postzygapophysis is relatively robust and ovoidal in cross-section, being separated from the neural spine by a concave dorsal surface. In posterior view, the preserved postzygapophysis has a deep ventral groove near its

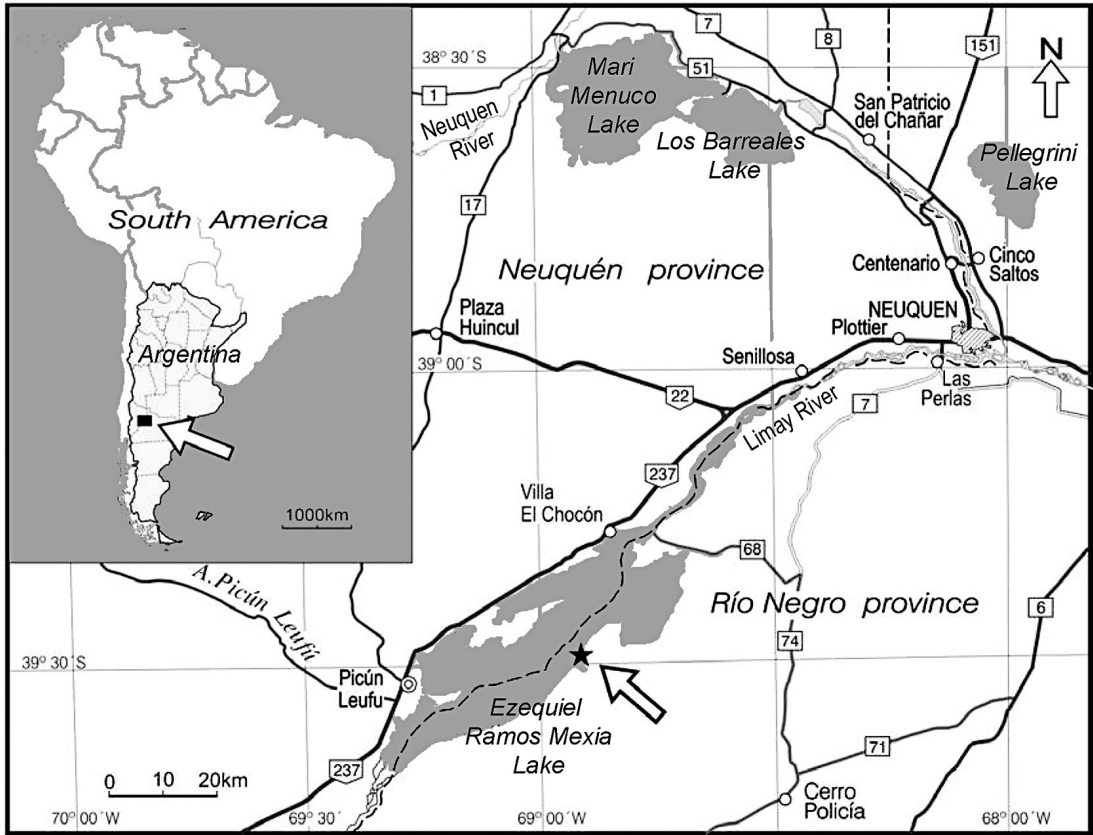


Fig. 1. Map showing the fossiliferous locality (star) where MPCA-Pv2003 was found (modified from Novas *et al.*, 2012).

base, resulting in a ventrally pendant lateral end (Fig. 2D'). In lateral view, the postzygapophysis is located at the posterior end of a lateral ridge that gets dorsoventrally thicker posteriorly.

The condyle projects posterior to the neural arch and postzygapophyses (Fig. 2A'). In posterior view, this articular surface is transversely broad and notably dorsoventrally flattened. It is higher than the neural canal and has convex dorsal and ventral margins (Fig. 2D'). In dorsal view, the posterior condyle has a convex articular surface, extending onto the lateral surfaces of the centrum on either side (Fig. 2A'). In posterior view the condyle has an even, convex profile, which slopes ventrally towards the postexapophyses (Fig. 2D'). The postexapophyses are tongue-shaped and posterolaterally directed (Fig. 2A', B'). These are located at the posteroventral corner of the vertebra and are posteriorly separated from the articular condyle by a shallow groove. The ventral surface of the postexapophyses is flat, while the dorsal one is smoothly convex (Fig. 2D'). The lateral surface of the centrum is

shallowly concave (Fig. 2C'), as also the ventral surface between the postexapophyses (Fig. 2B'). Anteriorly, the ventral surface of the centrum becomes straight close to the mid-length of the element. This results in a tubular-shaped centrum at the mid-length of the element. The centrum lacks any foramen on its lateral surface (Fig. 2C').

The preserved width of MPCA-PV 2003, measured across the postexapophyses, is 16.9 mm. In *Quetzalcoatlus* (specimen TMM 42889-1) the comparable measurement reaches a maximum of approximately 70 mm, whereas in *Arambourgiania* it reaches 90 mm (Frey & Martill, 1996). This indicates that the specimen here described belonged to a relatively small azhdarchid.

## DISCUSSION

In spite of its incomplete nature, MPCA-PV 2003, may be nested among azhdarchid pterosaurs. Azhdarchids exhibit notably modified cervical vertebrae that show a unique combination of characters absent in other flying rep-

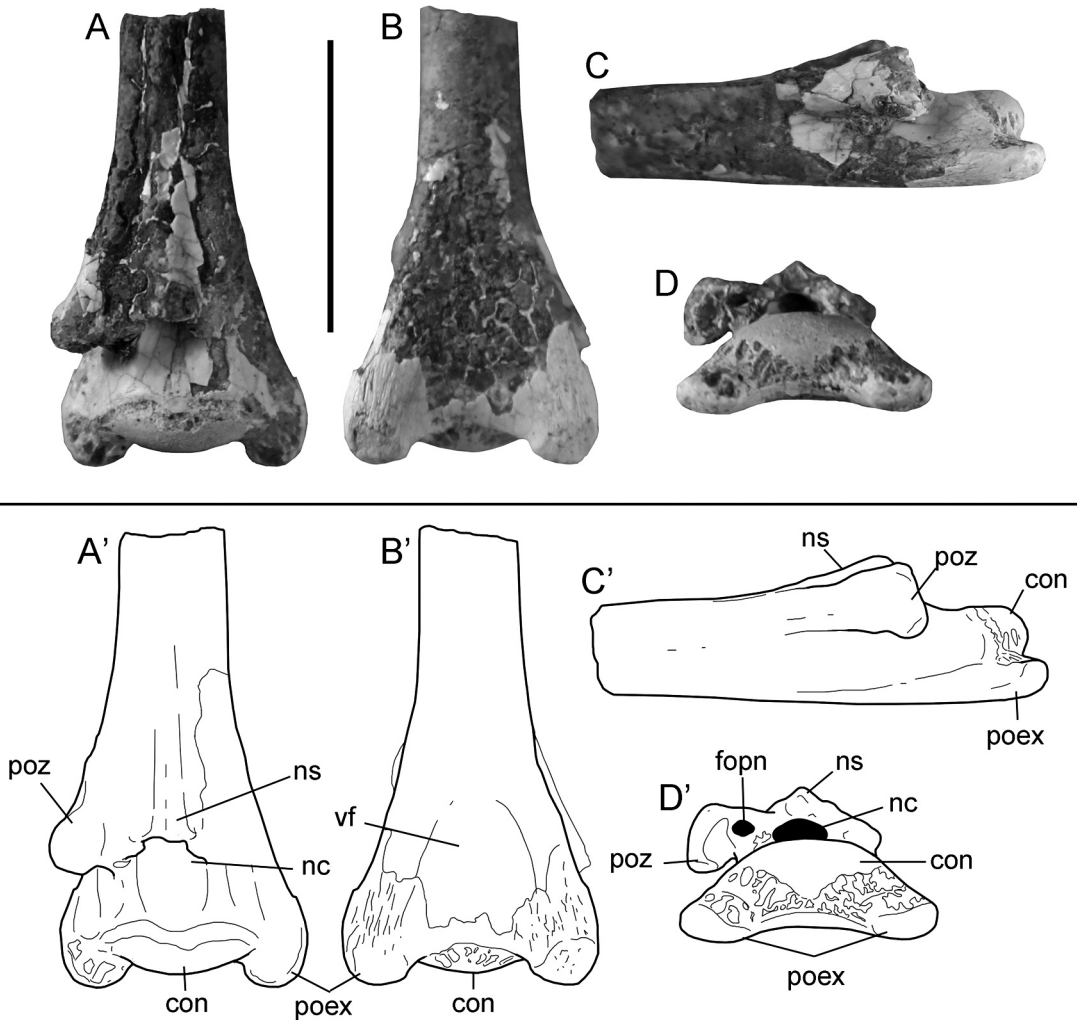


Fig. 2. Azhdarchid cervical vertebra (MPCA-PV 2003) in (A, A') dorsal, (B, B') ventral, (C, C') lateral and (D, D') posterior views. Abbreviations: con, posterior condyle; fopn, pneumatic foramen; nc, neural canal; ns, neural spine; poex, postexapophyses; poz, postzygapophysis; vf, ventral fossa. Scale bar: 3 cm.

tiles, which were recognized as unique since the recognition of the clade in 1984 by Lev Nesson. MPCA-PV 2003 is referred to Azhdarchidae because of the occurrence of very elongate and transversely narrow vertebrae with well-developed postexapophyses, notoriously reduced neural spine which disappear at mid-length of the centrum, and centrum that is tubular in cross-section at mid-length (Nesson, 1984, 1991; Company *et al.*, 1999; Pereda-Suberbiola *et al.*, 2003; Osi & Weishampel, 2005; Averianov, 2014; Andres & Langston, 2021; Longrich *et al.*, 2018) (Fig. 2). The lack of well-developed neural spine in MPCA-PV 2003 is a feature shared with azhdarchids, such as *Azhdarcho*, *Arambourgiania*

and *Quetzalcoatlus*. This differs from basal azhdarchoids that retained well-developed neural spines as is the case of the African Cenomanian taxon *Alanqa* (Rodrigues *et al.*, 2011). MPCA-PV 2003 lacks the deep ventral fossa and compressed posterior half of vertebral centrum present in *Quetzalcoatlus* (Andres & Langston, 2021; Longrich *et al.*, 2018).

MPCA-PV 2003 is very fragmentary, and thus, a referral to a genus or species is not warranted. Furthermore, direct comparisons with other South American azhdarchids (i.e., *Aerotitan*, *Thanatosdrakon*) are not possible because of the lack of overlapping material. *Thanatosdrakon* preserves the posterior end of a posterior cervical

vertebra, which has a higher and more complex neural arch, with dorsoventrally higher neural spine and a very large pneumatic foramina lateral to the neural canal, unlike the specimen here studied (Ortiz-David et al., 2022). It should be pointed out that MPCA-PV 2003 belongs to a species much smaller than *Aerotitan* and *Thanatosdrakon*, as inferred by its vertebral width.

The record of pterosaurs in the Cretaceous of Patagonia is very patchy and incomplete (Bonaparte, 1996; Kellner et al., 2003, 2006; Codorníu & Gasparini, 2007; Martinelli et al., 2007; Ibiricu et al., 2012; Novas et al., 2012; Kellner & Calvo, 2017; Bellardini & Codorníu, 2019; Díaz-Martínez et al., 2022). For the Cenomanian age (the earliest age of the Upper Cretaceous), pterosaurs are represented by still unpublished remains from the “La Buitrera” locality in Río Negro province (Haluza et al., 2007). Here we expand this patchy record with the first description of a pterosaur coming from Cenomanian beds of Patagonia. Furthermore, it constitutes the oldest record for azhdarchids in the South American continent, which were so far represented by the Coniacian-Santonian *Thanatosdrakon amaru* (Ortiz-David et al., 2022) and the Maastrichtian *Aerotitan sudamericanus* (Novas et al., 2012).

In sum, this finding constitutes an important addition to the knowledge of the poorly known pterosaur faunas from completely continental assemblages of the Upper Cretaceous of South America, and also indicates that the diversification and evolution of the clade in South America is still poorly known.

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