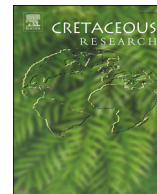


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## Discovery of the largest pterosaur from South America

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## ABSTRACT

A giant humerus (450 mm total length) belonging to one of the largest pterosaur recorded in South America is described. The specimen (UNCUYO-LD 350) was discovered in the Upper Cretaceous (upper Coniacian – lower Santonian) Plottier Formation of the Mendoza Province, northern Neuquén Basin, Argentina. It was found associated with a smaller pterosaur specimen represented by around thirty postcranial bones. The specimen is assigned to Tapejaroidea and show characters of both Tapejaridae and Azhdarchidae. Based on comparisons with other Azhdarchidae species, a wingspan of 9.1 m is estimated for UNCUYO-LD 350, showing that giant pterosaurs were present in South America during the Upper Cretaceous.

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## 1. Introduction

The pterosaur record is abundant in the Lower Cretaceous strata of South America. Most specimens have been discovered in Brazil, particularly in the Aptian-Albian deposits of the Araripe Basin (Wellnhofer, 1985; Kellner and Tomida, 2000; Unwin and Martill, 2007; Pêgas et al., 2016). In this basin different taxa such as *Tapejara wellnhoferi* Kellner 1989, *Tupuxuara longicristatus* Kellner and Campos 1988, and *Anhanguera blittersdorffi* Campos and Kellner 1985, were found. Moreover, pterosaurs have been recorded in the Lower Cretaceous of Chile. In this country, Casamiquela and Chong Diaz (1978) described the first remains of pterosaurs from Antofagasta, which were reinterpreted by Martill et al. (2000) as a Dsungaripteridae (*Domeykodactylus ceceliae*). Bell and Padian (1995) and Martill et al. (2006) described pterosaurs from Atacama, assigned them to the archaeoptero-dactyloid clade Ctenochasmidae. In Peru and Venezuela fragmentary and isolated bones were also reported (Bennett, 1989; Kellner and Moody, 2003)

that can be referred to the Pteranodontoidea sensu Kellner 2003. In Argentina, one of the most important sites of South American pterosaurs is located in the Lower Cretaceous strata of San Luis Province. The quarry has yielded hundreds of specimens of the archaeoptero-dactyloid *Pterodaustro guinazui* Bonaparte 1970; this monospecific association comes from the Lagarcito Formation (Albian) (Sánchez, 1973; Codorniú, 2005). Moreover, isolated bones have been recorded in Patagonia such as an incomplete right femur of a pterodactyloid from the La Amarga Formation, Neuquén Province (Montanelli, 1987), and an incomplete ulna and a metacarpal of a Pteranodontoidea from the Rio Belgrano strata (Barremian) of Santa Cruz Province (Kellner et al., 2003).

In contrast, South American record of the Upper Cretaceous pterosaurs is scarce and mostly of specimens are relatively fragmentary. One exception of this is *Caiuajara dobruskii* Manzig et al., 2014 from the southern of Brazil that yielded one of the few pterosaur bone beds known so far. Another Upper Cretaceous pterosaur from Brazil is only represented by an incomplete humerus of the pterodactyloid *Nyctosaurus lamegoi* Price 1953 (Kellner, 2006). In Argentina, Upper Cretaceous pterosaur fossils come from Patagonia. The only species described is *Aerotitan sudamericanus* Novas et al., 2012, an azhdarchid pterodactyloid discovered in the upper Campanian-lower Maastrichtian Allen Formation of the Neuquén

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Basin. Other Patagonian specimens are represented by fragmentary bones and described as Pterodactyloidea. In particular, in Neuquén Province fossils recovered in the upper Turonian – lower Coniacian Portezuelo Formation (Kellner et al., 2004, 2006) and in the Cenomanian Candeleros Formation (Haluzá and Canale, 2009) have been tentatively assigned to Azhdarchoidea. In Rio Negro Province (Cenomanian Candeleros Formation) fragmentary bones were assigned to Tapejaroidea (Haluzá et al., 2007).

Here we describe a complete humerus of a new species which is so far, the largest pterosaur discovered in South America. This bone was found associated with a well preserved and smaller pterosaur specimen represented by around thirty postcranial bones which will be described elsewhere. The humerus described here was discovered in the upper levels of the Plottier Formation, Upper Cretaceous (upper Coniacian – lower Santonian) of El Padrillo site, Mendoza Province, northern area of the Neuquén Basin. The fossil is housed at the Laboratorio y Museo de Dinosaurios of the Universidad Nacional de Cuyo, Mendoza City, Argentina.

### 1.1. Stratigraphic context

In Mendoza, the most fossiliferous Cretaceous sedimentary sequences were deposited in the Neuquén Basin, which extends between the active magmatic arc along the Andes to the west, the Sierra Pintada System to the northeast, and the North Patagonian Massif to the southeast (Vergani et al., 1995). In this basin marine, littoral, and continental deposits are related to transgressive–regressive cycles of both the Pacific and the Atlantic oceans (Digregorio and Uliana, 1980; Legarreta and Uliana, 1991). The richest vertebrate record in South America comes from the Neuquén Basin, primarily from Upper Cretaceous strata of the Neuquén Group and the Allen Formation.

The Upper Cretaceous (Cenomanian – middle Campanian) Neuquén Group is the most important dinosaur-bearing unit in this basin. It comprises a thick succession of continental sandstones, conglomerates, and claystones that represent alluvial fan, fluvial, lacustrine, eolian and playa lake depositional environments. Recently, Garrido (2010) recognized two new geologic units, Los Bastos and Sierra Barrosa formations from deposits previously assigned to the upper section of Portezuelo Formation. The Portezuelo, Los Bastos, and Sierra Barrosa formations collectively range from late Turonian to late Coniacian in age.

In the south of Mendoza Province, four titanosaur sauropods were discovered: *Quetecsaurus rusconii* from the middle – upper Turonian Cerro Lisandro Formation exposed in the Cañada del Pichanal (González Riga and Ortiz David, 2014), *Malarguesaurus florenciae* comes from the lower – middle Coniacian Los Bastos Formation of the Paso de las Bardas (González Riga et al., 2009), *Mendozasaurus neguyelap* was discovered in Arroyo Seco site, in the South area of Cerro Guillermo, near the top of the middle – upper Coniacian Sierra Barrosa Formation (González Riga 2003, 2005) and *Notocolossus gonzalezparejasi*, one of the largest dinosaur ever discovered in the world, comes from the basal level of the upper Coniacian – lower Santonian Plottier Formation (González Riga et al., 2016). The pterosaur specimens were found in the upper levels of the Plottier Formation, around 8 km north of the *Notocolossus* quarry. In the same formation, but in different levels, we discovered different titanosaur specimens, some of them articulated and exceptionally preserved, including part of the skull, and most of the cervical, dorsal, sacral and caudal vertebrae. In this formation, remains and theropods, chelid turtles and fish are also recovered. The pterosaur humerus described herein was discovered in the same level and facies but 2 m of distance with respect a smaller pterosaur individual represented by disarticulated postcranial skeleton. In the sector of the quarry, the Plottier Formation

is characterized by a fluvial association of facies: red to purplish massive and mottled mudstones and siltstones (Fm after nomenclature of Miall, 1996) and, more rarely, laminated greenish grayish claystones (Fl) interbedded with thin-bedded tabular and lenticular sandstones (Sm, Sh, Sr). Fining-upward trends progressive and lateral accretion surfaces in channel (CH) sandstone bodies indicates lateral migration of high sinuosity rivers through low-gradient plains. Some key indicators of ephemeral flows are present toward the top of the formation: numerous internal scour surfaces, mud drapes and desiccation cracks. In particular, the bones are preserved in massive mudstone facies, interpreted as accumulations of bones in swamps of poorly drained floodplains. All bones are preserved in this same facies, most of them in contact each other. This evidences suggest that bones were deposited simultaneously under the same sedimentological regime.

## 2. Systematic paleontology

Pterosauria Kaup, 1834

Pterodactyloidea Plieninger, 1901

Tapejaroidea Kellner 2003

Azhdarchidae? Nessov, 1984

Genus and species indet.

**Material.** UNCUYO-LD 350 is a complete left humerus discovered very close to an associated but disarticulated smaller specimen (UNCUYO-LD 307) represented by around thirty postcranial bones. **Locality and Horizon.** Agua del Padrillo, south of Malargüe Department, Mendoza Province, Argentina; upper-most levels of the Upper Cretaceous (upper Coniacian – lower Santonian) Plottier Formation of Neuquén Basin. (Fig. 1).

## 3. Description

The specimen UNCUYO-LD 350 (“Padrillo pterosaur”) is represented by an almost complete left humerus lacking a small portion of the distal border of the ulnar crest (Fig. 2). It has a strongly dorso-ventral taphonomic compression, showing several longitudinal fractures. The saddle-shaped of the proximal articular head, common in pterosaur humeri (e.g., Wellnhofer, 1978), is particularly elongated antero-posteriorly. The bone exhibits one oval pneumatic foramina on the ventral surface, close to the deltopectoral crest, near the humerus head.

The deltopectoral crest is fractured and has the main axis oriented parallel to the ventral surface. It is relatively long and well developed, placed proximally, and curves ventrally, similar to the general shape of azhdarchids and tapejarids (Averianov 2010; Kellner, 2013). The base of the crest is very robust and short, extending along approximately 25% of the shaft.

The ulnar crest is separated from the proximal articulation by a marked ventro-dorsal constriction. In ventral view the separation is not very visible. The ulnar crest is massive, with developed proximal ridge, medially expanded and directed posteriorly.

Although the bone has a dorso-ventral taphonomic compression, the surface of the distal end, is well preserved. The humerus presents expanded distal and bearing condyles for articulation with the radius and ulna. The capitulum is oval and prolonged towards the medial part. It is separated from the trochlea by a conspicuous intertrochlear sulcus. The capitulum is larger than the trochlea. On the capitulum extends the fovea supratrochlearis ventralis, which forms a depression that extends to the lateral border. The ectepicondyle is large, has a size similar to that of the capitulum, a condition not observed in another pterosaur. The entepicondyle is elongated toward the medial border and is larger than the trochlea.

This character is uncommon, because in most known pterosaurs the entepicondyle is reduced (Fig. 3).

Broken areas of the bone show that the outer bony walls were extremely thin, varying between 1.2 mm and 1.5 mm on the ventral surface of the diaphysis. In the region of the deltopectoral crest and ulnar crest, the interior of the bone have a highly cancellous tissue consisting of paper-thin bony trabeculae enclosing large alveoli. A similar condition has been described in the deltopectoral crest of the giant azhdarchid *Hatzegopteryx thambema* Buffetaut, Grigorescu and Csiki 2002, from the Maastrichtian of Romania. The proximal and distal diaphysis (proximal articular head and distal articular condyles) present a compact tissue.

3.1. Measurements

Total length as preserved: 450 mm  
 Minimum diameter of shaft: 97 mm  
 Proximal width: 171 mm  
 Distal width: 186 mm

4. Discussion

4.1. Comparisons

The humerus UNCUYO-LD 350 possesses a well-developed deltopectoral crest and proximal saddle-shaped articulation, which support the allocation to Pterosauria. This specimen is referred to the Pterodactyloidea based on the presence of long deltopectoral crest that is proximally placed and curves ventrally (synapomorphic character of this clade after Kellner, 2003). The bone lacks the warped and the hatched-shaped deltopectoral crest of Pteranodontoidea and Nyctosauridae (Bennett, 2001a; Wang et al., 2005), indicating that it does not represent a member of those clades. One of the most peculiar feature of this bone is the strong development of the ulnar crest, which is a sinapomorphic character of Tapejaroidea (Dsungaripteridae + Azhdarchidae + Tapejaridae) (Kellner, 2003), and is easily observed in the genus *Caupedactylus*, *Montanazdarcho* and *Quetzalcoatlus*.

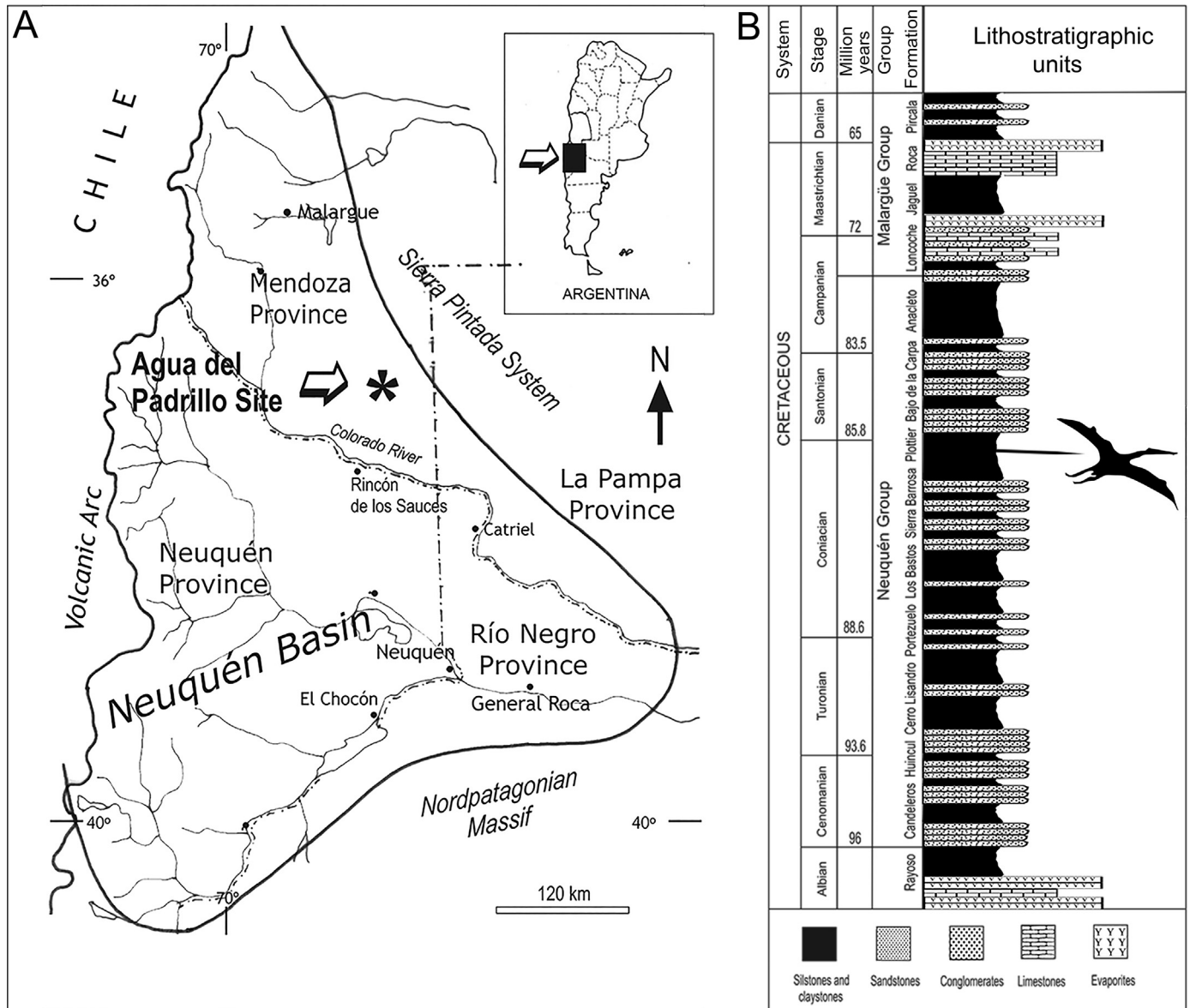
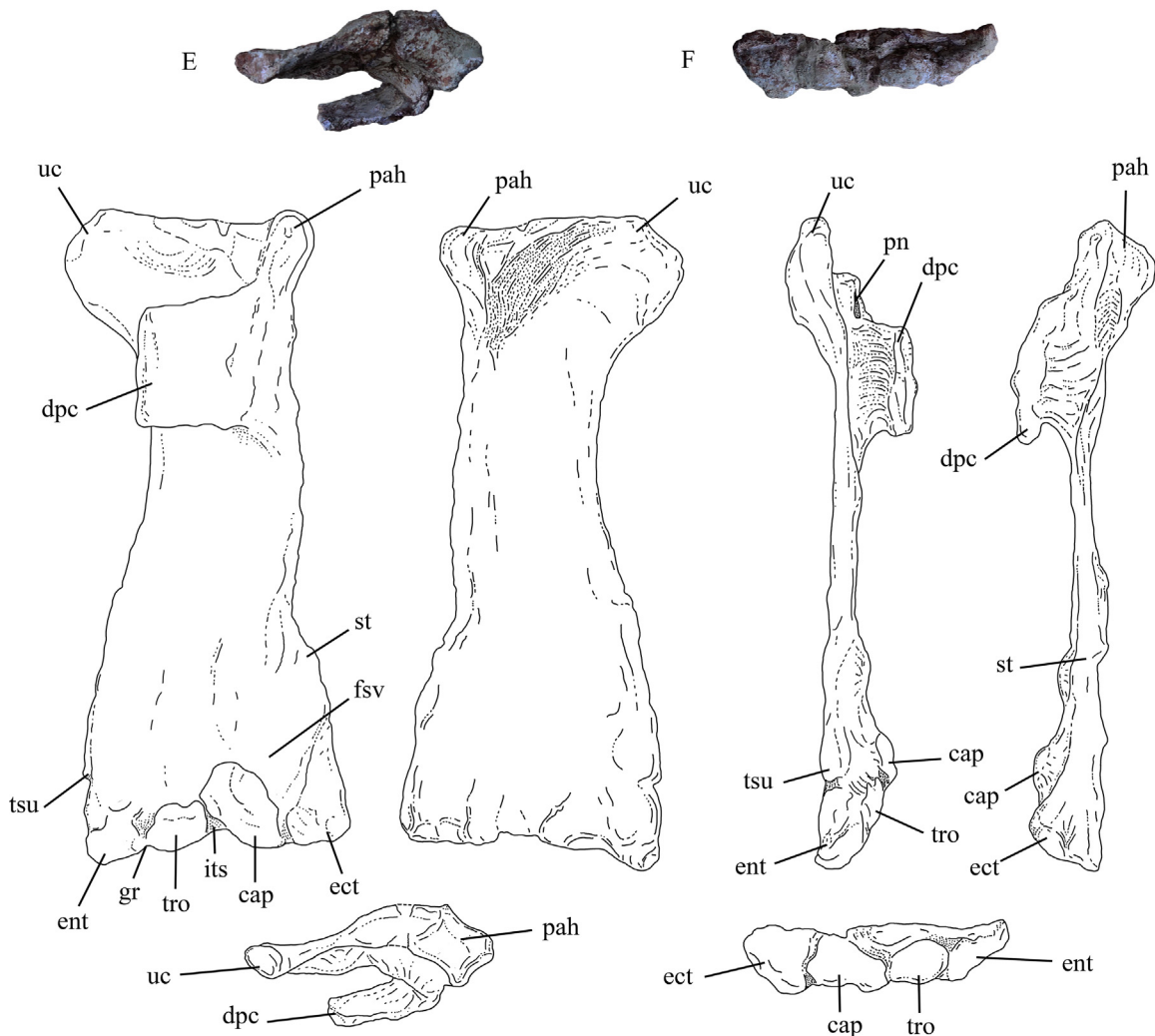
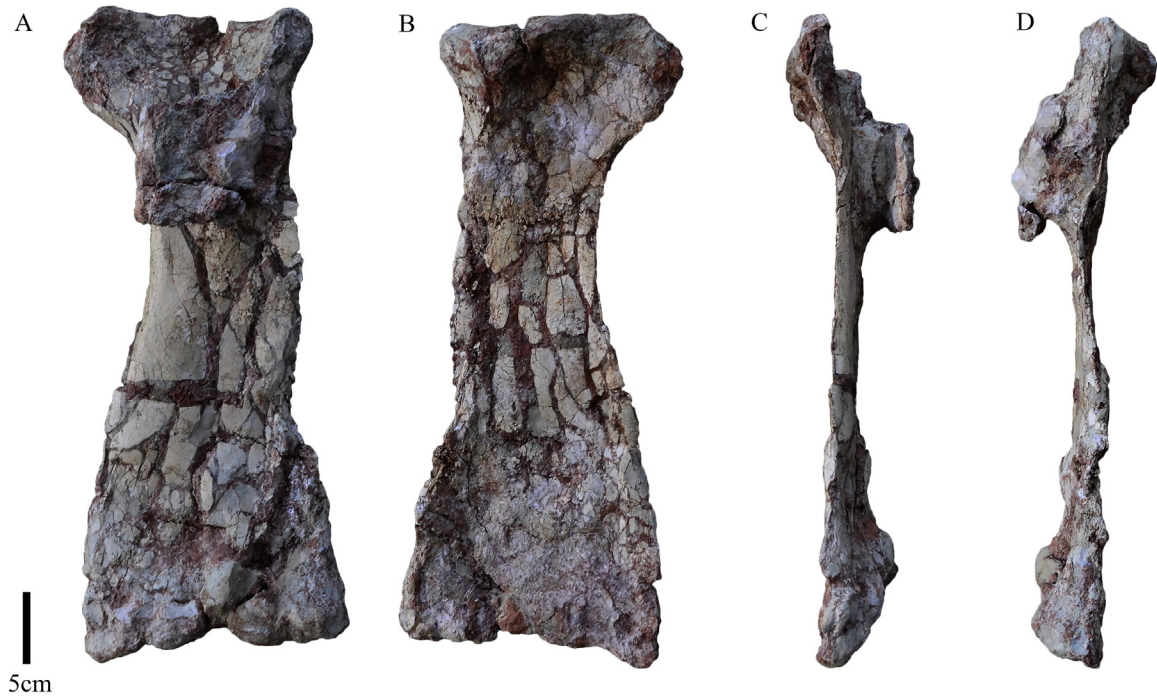
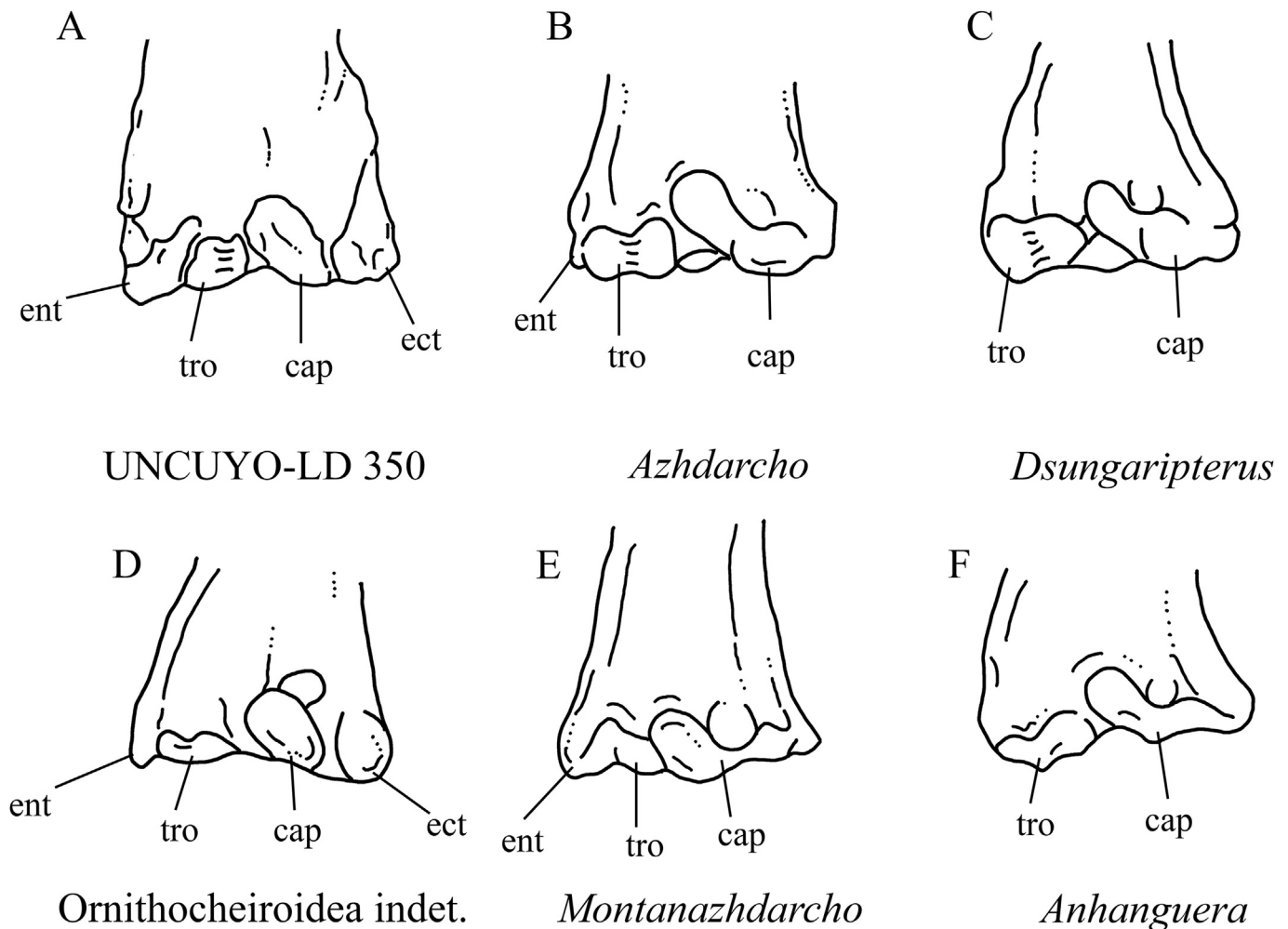


Fig. 1. A.- Neuquén Basin showing the Agua del Padrillo site where the specimen was found. B.- Stratigraphic column of the Upper Cretaceous strata of Neuquén Group with indication of the fossiliferous level of the Plottier Formation.





**Fig. 3.** Distal humerus of pterosaurs. A. “Padrillo pterosaur”; B. *Azhdarcho lancicollis* Nessov 1984 (Averianov 2010) (reversed); C. *Dsungaripterus weii* Young 1964 (reversed); D. *Ornithocheiroidea* indet. (Averianov et al., 2005); E. *Montanazhdarcho minor* Padian, De Ricqlès and Horner 1995 (McGowan et al., 2002) (reversed); F. *Anhanguera piscator* Kellner and Tomida 2000. Not to scale. Modified from Agnolin and Varricchio (2012).

The shapes of the trochlea and capitulum are similar to those of *Azhdarcho lancicollis* Nessov 1984 (Averianov 2010) and *Montanazhdarcho minor* Padian, De Ricqlès and Horner 1995 (McGowan et al., 2002). The pneumatic foramen located in the ventral face of the proximal end is characteristic of *Dsungaripteroidea*, although the present or absence of this feature is unknown outside this clade (Kellner, 2004). The oval foramen is similar to that of *Pteranodon* (Bennett, 2001a) and *Caupedactylus ybaka* Kellner 2013. In the dorsal side, the humerus does not possess any pneumatic foramina, contrary to the condition observed in tapejarine tapejarids (e.g., Kellner and Campos, 2007). Also unlike other pterosaurs, such as *Pteranodon*, *Santanadactylus* (De Buissonjé, 1980; Wellnhofer, 1985), *Anhanguera*, and pteranodontid indet. from Perú (Bennett, 1989), the humerus described herein does possess any pneumatic foramina at the dorso-posterior border.

#### 4.2. Wingspan estimate

The fossil remains of giant pterosaurs are scarce and only restricted to the Cretaceous: *Arambourgiana philadelphiae* in

Jordan (Arambourg, 1959; Frey and Martill, 1996); *Pteranodon sternbergi* in Kansas – United States of America (Miller, 1972; Bennett, 2001a), *Tropeognathus* cf. *T. mesembrinus* in Brazil (Kellner et al., 2013), *Quetzalcoatlus northropi* in Texas – United States of America (Lawson, 1975; Langston, 1981; Kellner and Langston, 1996), and *Hatzegopteryx thambema* in Romania (Buffetaut et al., 2002).

The largest known specimen of *Pteranodon* (FMNH-PR 464) comprises a radius and ulna from the Pierre Shale Formation and has an estimated wingspan of 7.25 m (Bennett, 2001b). Other pterosaurs are larger. For instance, *Tropeognathus* cf. *T. mesembrinus* (Kellner et al., 2013) has a wingspan of 8–9 m. Martill et al. (1998) tentatively estimated the wingspan of *Arambourgiana* as 12 m, but Pereda-Superbiola et al. (2003) suggested 7 m and other authors suggest 10 m (Frey and Martill, 1996; Martill et al., 1998). An estimate of the wingspan of *Hatzegopteryx thambema* would be about 10 m–12 m (Buffetaut et al., 2002; Witton and Habib, 2010; Naish and Witton, 2017). *Quetzalcoatlus northropi* is considered the largest pterosaur with a wingspan of 11–12 m (Langston, 1981; Witton and Habib, 2010).

**Fig. 2.** Left humerus UNCUYO-LD 350 in: A. ventral view, B. dorsal view, C. posterior view, D. anterior view, E. proximal view, F. distal view. Abbreviations: uc: ulnar crest, pah: proximal articular head, dcp: deltopectoral crest, tro: trochlea, cap: capitulum, its: intertrochlear sulcus, ent: entepicondyle, ect: ectepicondyle, tsu: tuberculum supracondyloideum ventralis, gr: Groove, st: supracondylar tubercle, fsv: fovea supratrochlaris ventralis. Scale bar 50 mm.

Estimates of wingspan in incomplete specimens have many limitations. The remains can be compared with complete specimens and appendicular bones to calculate the wingspan. Taking the data of [Witton and Habib \(2010\)](#) corresponding to the maximum size of *Quetzalcoatlus* (wingspan of 11 m, humerus of 544 mm in length), we can estimate a wingspan of ~9.1 m for the “Padrillo pterosaur” based on the humerus of 450 mm in length. This estimation allows to include the ‘Padrillo Pterosaur’ in the group of truly giant pterosaurs *sensu* [Kellner et al. \(2013\)](#).

In South America there are other two large pterosaurs: the pteranodontoid MN 6594-V (cf. *Tropeognathus mesembrinus* from the Lower Cretaceous of Brazil; [Kellner et al., 2013](#)) and the azhdarchid *Aerotitan sudamericanus* from Upper Cretaceous of Argentina ([Novas et al., 2012](#)). It is important to mention that the specimen MN 6594-V presents a wingspan of 8.26 m–8.70 m, a bit smaller than those of the “Padrillo pterosaur”. However is important to keep in mind that Pteranodontoidea have relatively large wings in relation with other members of Tapejaroidea (particularly Azhdarchidae and Tapejaridae) In this context we have different wingspan for the same size of humerus length, depending if they belong to the clade Pteranodontoidea or Tapejaridae (particularly Azhdarchidae and Tapejaridae) (e.g., [Kellner, 2003](#)).

In sum, although there is a notable difference of size between of humerus of the “Padrillo pterosaur” and MN 6594-V, the wingspan of both taxa are almost similar.

## 5. Conclusions

The “Padrillo pterosaur” comes from the northeast sector of the Neuquén Basin and is the first pterosaur record for the Mendoza Province, Argentina. The specimen described herein, a giant humerus, can be assign to the clade Tapejaroidea ([Kellner, 2003](#)), which includes Dsungaripteridae, Tapejaridae, and Azhdarchidae (and also Chaoyangopteridae, [Pinheiro et al., 2011](#)). Due to the specimen is only represented by a humerus, it is not possible to make more detailed taxonomic determinations. However, the bone presents characters related to Azhdarchidae (e.g. morphology of the distal portion of the humerus, similar to *Azhdarcho* and *Montanazhdarcho*) and to Tapejaridae (e.g. morphology of the proximal part of humerus and deltopectoral crest, similar to *Caupedactylus* and *Caiuajara*). The bone size and its characters allow it refer the specimen tentatively to Azhdarchidae. The ‘Padrillo pterosaur’ belongs to a group of giant pterosaurs with a wingspan approximately of 9.1 m. In this way, it represents the largest pterosaur registered in South America and one of the largest flight animal that lived in the world.

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