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On the Pterosaur Remains from the Río Belgrano Formation (Barremian), Patagonian Andes of Argentina

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ABSTRACT
Pterosaur remains from the Río Belgrano Formation, Santa Cruz Province, Argentina, were found close to the Estancia Río Roble, along with several ammonoids that indicate a Barremian age for those strata. The specimens (MACN-SC 3617) consist of one ulna and one element tentatively identified as a portion of a wing metacarpal. The ulna shows morphological affinities with the Pteranodontoidea (sensu Kellner 1996), particularly with the members of the Anhangueridae by having a well developed ventral crest close to the proximal articulation, and is tentatively referred to this pterosaur clade. The oldest record of the Anhangueridae, previously limited to the Aptian/Albian, is therefore extended to the Barremian. The Argentinean material is preserved in three dimensions, an unusual condition for pterosaur fossils from that country, indicating that the site situated near the Estancia Río Roble has a great potential for new and well preserved specimens.

Key words: Pterosauria, Río Belgrano Formation, Lower Cretaceous, Argentina.

INTRODUCTION
The systematic geological survey of the southern Patagonian Andes done through the Servicio Geológico Nacional during the early eighties identified an important fossil locality of Cretaceous age in the region of the Belgrano Lake, approximately 48°S latitude. Although the fossil assemblage is dominated by ammonoids, some remains of pterosaurs were found in 1981 (Aguirre-Urreta and Ramos 1981). The material consists of two bones that were only briefly mentioned in the literature (Montanelli 1987, Bonaparte 1996).

The fossils were found along the Chorrillo Rivera, a small stream of the Roble river system, a few kilometers south of the Belgrano Lake in the province of Santa Cruz (Figure 1). The access to the area is done from the national road 40 to Estancia Río Roble, distant approximately 95 km. The nearest town is Gobernador Gregores situated about 140 km. The fossil locality is 5 km south of the Estancia Río Roble.

The purpose of this paper is to describe those pterosaur remains and document their precise geographic and stratigraphic location, and to constrain the age of the vertebrate horizon using the abundant micro and megafauna found at the site.
Fig. 1 – Location of the site with pterosaur remains in Santa Cruz Province, Argentina.
GEOLOGIC SETTING

The southern Patagonian Andes are characterized by a low-grade metamorphic core of Late Paleozoic age, emplaced by a series of arc related granitoids of Mesozoic and Cenozoic age. These metamorphic rocks were part of an accretionary prism developed during the Late Paleozoic along the western Pacific margin of Gondwana. Volcanic rocks of Jurassic age unconformably overly the previous rocks, deposited during the beginning of the Andean subduction along the western margin of Gondwana, coeval with the opening of the South Atlantic. At this stage a series of transgressive and regressive cycles from the Pacific sea characterizes a retroarc basin where important accumulations of continental and marine deposits are recorded during the Cretaceous. Final uplift during the Cenozoic produced the present Patagonian fold and thrust belt (Ramos 1989) where the fossiliferous rocks are found.

CRETACEOUS STRATIGRAPHY

A sequence of black shales of the Río Mayer Formation paraconformably overlies the Jurassic rocks (Figure 2). These rocks were deposited in a low energy marine platform environment, with restricted circulation, away from the littoral. About 50 m from the base of the sequence the first fossil level is found. Fossils in these rocks are preserved in ellipsoidal concretions and septarias, which indicate a reducing environment. The concretions vary from a few centimeters up to one meter in size.

Thin limestone beds of 5 to 7 cm in thickness are interfingered with the shales bearing small bivalves. Green sandstones are interfingered with the black shales, as small turbiditic layers with convolute sedimentation. Two other levels of fossiliferous concretions are at the top of this 175 m thick sequence of black shales (Figure 2).

The green sandstones of the Río Belgrano Formation are transitionally deposited over the black shales. The base of the unit is indicated by a 3 m thick bed of sandstone. The sandstones have parallel bedding, organized in coarsening-up sequences,
with green brownish shales at the base. Epidiagenetic red sandy concretions are common a few meters above the contact with the underlying Río Mayer Formation, and constitute the fourth fossiliferous level. Ammonoids, crustacean decapods and the pterosaur bones were found in this level. Bioturbation increases towards the top of the green sandstones, and laminar bedding gives place to cross laminated beds. Cut and fill structures become common and at the top, a coarse brown red sandstone marks the contact with the basal beds of the Kachaike Formation.

The green sandstones of the Río Belgrano Formation show the beginning of the marine regression in the area. Facies indicate the transition to a littoral near coast high energy environment, up to the continental fluvial deposits of the Kachaike Formation.

The pterosaur remains were found in a near-shore environment, which at the top shows an even higher energy facies that finally changes to fluvial continental facies. This occurrence corroborates with the hypothesis that pterosaur colonized marginal-marine deposits (Kellner 1994).

**BIOSTRATIGRAPHIC CONTROLS**

The ammonoids recovered in the Río Mayer and Río Belgrano Formations at Chorrillo Rivera are mostly *Hatchericeras* Stanton, represented by several species. In the same level as the pterosaur remains, the ammonoids are dominated by *Hatcheri ceras patagonense* Stanton, associated with *Cryp tocrioceras yrigoyeni* (Leanza), and *Sanmartinoceras africanum insignicostatum* Riccardi, Aguirre-Urreta and Medina, and decapod crustaceans. In Patagonia, this association represents the *Hatcheri ceras patagonense* assemblage zone of the Lower Barremian (Riccardi 1984). The three species are known from Patagonia and Zululand only. In South Africa, *H. patagonense* and *C. yrigoyeni* are known from the Barremian I of Kennedy and Klinger (1975) equivalent to the Lower Barremian. *Sanmartinoceras africanum* has been reported from the Upper Barremian, associated with *Colchidites vulansis australis*. This latter species distinctively overlies the *Hatcheri ceras* fauna in Patagonia and characterizes the *C. vulansis assemblage* zone of the Upper Barremian (Riccardi 1984). Based on the evidence presented above, the *Hatcheri ceras patagonense* assemblage zone can be placed in the Lower-Middle Barremian.

**PTEROSAUR REMAINS**

The pterosaur material was found at a locality 5 km to the south of the Estancia Río Roble and consists of two long bones. Despite being incomplete, both are preserved in three dimensions, a rare condition among pterosaur fossils, and show no signs of distortion. Both are housed at the Museo Argentino de Ciencias Naturales “Bernardino Riva- davia” (MACN, Buenos Aires) and were cataloged under the number MACN-SC 3617. It should be noted that it is not sure whether both belong to the same individual.

The least complete (Fig. 3) is a long bone that lacks any articulation, making its identification difficult. The total preserved length is 197 mm, with the mid-section of the shaft compressed laterally (20 × 16 mm). The widest part has a length of 44 mm and is more expanded than the shaft, indicating that it was close to an articulation. Most of the external surface was broken away, but where observable, the bone walls are very thin with an average thickness of about 1 mm. In some parts, the internal trabecular structure can be observed, particularly close to the expanded area. This element was previously identified as a radius (Bonaparte 1996), but no feature is present that could confirm this. Furthermore, this bone seems rather robust for a radius. Due to its general shape and size, it can be rather identified as a first wing phalanx (F1D4) or the proximal portion of the fourth wing metacarpal (McIV); based on the expanded portion (less expanded than the proximal articulation of most known F1D4) the latter interpretation is favored here.

The second and most complete element is a left ulna, as identified by Bonaparte (1996). It is com-
posed of the distal articulation and most of the shaft, but lacks the proximal portion, with a total preserved length of 199 mm (Figs. 4 and 5). As common of pterosaur ulnae (particularly in pterodactyloids), this bone is compressed anteroposteriorly and has an elliptical circumference at the middle portion of the shaft (17.5 × 12 mm). It is a hollow structure with the bone wall very thin (average thickness around 1 mm). In some places the surface was broken off, revealing the presence of a well-developed internal trabecular structure. In lateromedial view, this bone shows a concave dorsal margin and a straighter ventral margin that becomes concave near the articulations.

The distal articulation is expanded (maximum width 49.2 mm), with the dorsal portion wider than the ventral part. Close to the articulation on the anterior side, part of the bone was broken off possibly prior to fossilization since it is filled with matrix. Whether this breakage was caused by scavenging or during the embedding process cannot be determined.

The articulation of the distal surface shows several pits and has a porous aspect, suggesting that the epiphyseal cartilage was not fully ossified in this specimen. Neither the tuberculum nor the fovea carpalis are very well developed. Those features suggest that this bone belonged to a young animal (perhaps a sub-adult).

Among the most interesting features of this el-
Complementation is the presence of a well developed ventral ridge. To date, only taxa of the Anhangueridae show such a feature, which is more developed in the Argentinean specimen (see discussion).

COMPARISONS

Despite the fact that the pterosaurian nature of the specimens found in the Río Belgrano Formation is indisputable (e.g., extremely thin-walled pneumatic bones), the classification of isolated postcranial elements can be quite challenging. The Belgrano specimens clearly belong to large animals. Up to date, the more primitive members of the Pterosauria (i.e., all non-pterodactyloids) are comparatively small, with wingspans less than 2 meters. The maximum estimation of the ulna of the largest reported specimen of *Rhamphorhynchus* (member of the Rhamphorhynchidae, the sister-taxon of the Pterodactyloidea) is about 115 mm (see Wellnhofer 1975). This size is less than half the size estimated for the ulna from the Río Belgrano Formation (estimated length: 282 mm), suggesting that the Argentinean material represents a member of the clade Pterodactyloidea.

According to Kellner (1996, 1997), the Pterodactyloidea can be divided into two groups: the Archaeopterodactyloidea and the Dsungaripteroidea. Again, based on the size and the general morphology of the ulna (i.e., greater expansion of the distal end), the pterosaur material from the Río Belgrano Formation can be excluded from the Archaeopterodactyloidea, which includes taxa such as *Pterodactylus*, *Germanodactylus*, and *Galloactylus* (see Kellner 1996, 1997). The same differences apply to the Argentinean genus *Pterodaustro*, from the Lower Cre-
taceous strata of the Sierra de las Quijadas of San Luis (Bonaparte 1996, Chiappe et al. 2000), whose ulna is less than half the size of the Belgrano specimen.

The Dsungaripteroidea includes the following clades: Nyctosauridae, Pteranodontoidea, and Tapejaroidea. Among those, the ulna of the Río Belgrano Formation shows more affinities with the pteranodontid clade Anhangueridae, that (where known) shows a well developed ventral ridge on the distal end of the ulna (more developed in the Argentinean specimen). Such a feature is absent in tapejaroids like *Tupuxuara* and *Quetzalcoatlus* (Kellner pers. observ.) and in the pteranodontoids *Pteranodon* (Bennett 2001) and *Istiodactylus* (Hooley 1913; recently renamed by Howse et al. 2001). The Argentinean ulna also lacks any evidence of a pneumatic foramen on the posterior side, which is present in *Pteranodon* (Bennett 2001). Furthermore, the ulna from the Río Belgrano Formation has the dorsal edge of the distal articulation well developed and dorsally expanded, which is also found in anhanguerids. In the Argentinean material, however, this dorsal edge is less developed than in *Anhanguera araripensis* (see Wellnhofer 1985: p. 122) and *Anhanguera piscator*.

A gross estimate of the wingspan of the pterosaur from the Río Belgrano Formation can be obtained by the comparison of the ulna with the one known from *Anhanguera piscator*, the most complete anhanguerid known (Kellner and Tomida 2000). Based on direct comparisons, the complete ulna of the Argentinean form was around 282 mm, which would correspond to an anhanguerid with a wingspan of approximately 3.6 meters. This corresponds to a large but not gigantic member of this pterosaur clade.

**CONCLUSIONS**

The pterosaur record in South America is meager (Kellner 2001) and therefore any new occurrence is of interest and should be documented. The ulna found in the Río Belgrano Formation shows some affinities with the Anhangueridae, sharing with the member of this clade a well developed ventral ridge, that is absent in other pterodactyloids. Based on this feature the Belgrano specimen is here regarded as representing either a member of this clade or at least a closely related taxon.

To date, anhanguerids have been found in the following deposits: Aptian/Albian Khuren-Dikh, Central Mongolia (Bakhurina and Unwin 1995, Kellner and Tomida 2000); Albian strata of the Romualdo Member (Santana Formation), Araripe Basin (e.g., Campos and Kellner 1985, Wellnhofer 1991); late Albian strata of the Paw Paw Formation, Texas (Lee 1994, Kellner and Tomida 2000); Cenomanian strata of Ksar es Souk, Morocco (Mader and Kellner 1999), and Cenomanian Cambridge Greensand Formation, United Kingdom (Kellner 1990). Therefore the Argentinean material further extends the anhanguerid record to the Barremian.

Despite being incomplete, both pterosaur bones show no signs of compaction and are preserved in three dimensions, contrasting with most pterosaur material found in Argentina (Chiappe et al. 2000) and in most deposits (Kellner 1994). So far, such well preserved pterosaur specimens have been reported in abundance only in a few deposits like the Early Cretaceous Strata of the Dsungari Basin in China (e.g., Young 1973) and the Early Cretaceous Romualdo Member (Santana Formation) of the Araripe Basin (e.g., Price 1971, Wellnhofer 1985, Campos and Kellner 1985). The material described here indicates that the site close to the Estancia Río Roble has a great potential for new and well preserved finds of those volant archosaurs.

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RESUMO

Restos de pterossauros da Formação Río Belgrano, Santa Cruz, Argentina são descritos. O material foi encontrado nas proximidades da Estancia Río Roble, associado com diversos ammonóides que sugerem uma idade Barremiana para estas camadas. O material consiste de dois ossos longos (MACN-SC 3617), formados por uma ulna e o outro tentativamente identificado como parte de uma metacarpo alar. A ulna apresenta semelhanças morfológicas com os Pteranodonidae (*sensu* Kellner 1996), sobretudo com membros de Anhangueridae devido a presença de uma crista ventral próxima à articulação proximal, sendo referida à este clado. O registro mais antigo de Anhangueridae, previamente limitado para o Aptiano/Albian, é extendido ao Barremiano. O material argentino está preservado em três dimensões sem maiores distorções, que é raro nos registros de pterossauros daquele país, indicando que a localidade situada perto da Estancia Río Roble tem grande potencial para o encontro de restos destes animais voadores bem preservados.

Palavras-chave: Pterosauria, Formação Río Belgrano, Cretáceo Inferior, Argentina.

REFERENCES


