



PTEROSAUR BONES FROM THE PORTEZUELO FORMATION (CRETACEOUS), NEUQUÉN GROUP, PATAGONIA, ARGENTINA¹

(With 7 figures)

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ABSTRACT: The Futalognko quarry, located 90km northwest of Neuquén city, Argentina, has yielded several fossil vertebrates. All come from the upper part of the Portezuelo Formation (Turonian-Early Coniacian) and include some pterosaur remains, the first ones from the Cretaceous strata of the Neuquén Group. The material consists of a proximal end of a large ulna (MUCPv-358), the proximal part of a wing-phalanx (MUCPv-359), and another ulna associated with a radius (MUCPv-600). All specimens are referred to the Pterodactyloidea, and possibly represent members of the Azhdarchoidea. Histological sections of the large ulna (MUCPv-358) indicate that it belonged to an animal that was still growing at time of death. Comparisons with more complete specimens indicate that MUCPv-358 represents an animal with a wingspan of six meters, making it the largest pterosaur known from Argentina.

Key words: Pterosauria. Azhdarchoidea. Cretaceous. Patagonia. Argentina.

RESUMO: Ossos de pterossauro da Formação Portezuelo (Cretáceo), Grupo Neuquén, Patagônia, Argentina. O jazigo Futalognko está situado 90km a noroeste da cidade de Neuquén, Argentina, e forneceu uma grande quantidade de vertebrados fósseis, todos da parte superior da Formação Portezuelo (Turoniano-Eoconiaciano). Dentre os exemplares recuperados encontram-se alguns exemplares de pterossauros indicando a primeira ocorrência deste grupo para as rochas cretácicas do Grupo Neuquén. O material está representado pela parte proximal de uma ulna de grandes proporções (MUCPv-358), a parte proximal de uma primeira falange alar (MUCPv-359), e uma segunda ulna associada com o rádio (MUCPv-600). Todos estes exemplares são referidos a Pterodactyloidea e possivelmente representam formas de Azhdarchoidea. Seções histológicas da ulna maior (MUCPv-358) indicam que ela representa um animal jovem que estava em fase de crescimento quando morreu. Comparações com outros exemplares mais completos sugerem que MUCPv-358 tenha pertencido a um pterossauro com uma abertura alar em torno de seis metros, fazendo dele o maior réptil voador coletado até o presente momento na Argentina.

Palavras-chave: Pterosauria. Azhdarchoidea. Cretáceo. Patagônia. Argentina.

INTRODUCTION

The Futalognko quarry, discovered in 2000, is located about 90km northwest of the Neuquén city, at the margins of the Lago Barreales, Argentina (CALVO *et al.*, 2002) and has turned out to be one of the most productive fossil vertebrate site in South America. The rocks in that locality belong to the upper part of the Portezuelo Formation (Turonian-

Early Coniacian) of the Neuquén Group (LEANZA & HUGO, 2001) and have furnished several important specimens, such as plants (PRÁMPARO *et al.*, 2003), osteichthyan fishes (GALLO *et al.*, 2003), turtles, crocodylomorphs (POBLETE & CALVO, 2005), titanosaur sauropods (CALVO *et al.*, 2001), theropods (CALVO *et al.*, 2004a; CALVO *et al.*, 2004b), theropod teeth (POBLETE & CALVO, 2003; VERALLI & CALVO, 2003), and ornithopods (PORFIRI & CALVO, 2002).

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In February of 2001 the technician Federico Poblete collected a pterosaur bone lying on the surface, some meters away from the main excavation, which was briefly reported by KELLNER *et al.* (2004). Since then three more were recovered, all deposited in the Museo de Geología y Paleontología de la Universidad Nacional del Comahue (MUCP). Here we describe those specimens, which consists the first pterosaur evidences from the Late Cretaceous of the Neuquén Group.

DESCRIPTIONS AND COMPARISONS

The pterosaur bones from the Portezuelo Formation consist of a proximal end of a large ulna (MUCPv-358), one wing-phalanx (MUCPv-359), and another ulna associated with a radius (MUCPv-600). The first two were preserved in a concretion composed of fine red sandstone and carbonates. The ulna and radius (MUCPv-600) were collected in a sandstone layer right above the main fossiliferous level of the Futalogno site and presumably belong to the same individual. Despite being incomplete, all specimens are preserved in three dimensions, a rare feature among pterosaurs (KELLNER, 1994).

ULNA (MUCPv-358)

The specimen MUCPv-358 (cast at the Museu Nacional - MN7059-V) was the first pterosaur bone collected in the Portezuelo Formation (KELLNER *et al.*, 2004). It can be identified as the proximal end of a right ulna with a preserved length of 125mm (Figs. 1-5). The articulation is expanded dorsoventrally reaching 88mm. The external bone surface shows several pits and small grooves resembling those present in young pterosaur individuals from elsewhere (BENNETT, 1993; KELLNER & TOMIDA, 2000). The preserved distal part of the shaft has an oval transverse section that is more elongated dorsoventrally (46.2mm) than it is mediolaterally (36.4mm). The bone is hollow and the cortex extremely thin, varying from 1.7mm (dorsally, anteriorly, and posteriorly) to 1.2mm laterally, where it contacts the radius (not preserved in this specimen). The remains of a system of trabecular struts is observed (Fig.5), a common feature of derived pterosaurs (e.g., WELLNHOFER, 1991; KELLNER, 2006). The anterior surface of the shaft is almost straight, while the posterior one is convex. On the anterior surface, close to the proximal margin, there is a well-developed foramen (possibly pneumatic) piercing the shaft longitudinally (Fig.1). About 13mm from the

distal edge of this foramen there is a rugose surface that extends almost diagonally for about 18mm, possibly representing a muscle scar.

On the posterior surface the articulation is broken and part of the cortex has been lost. A small depression is observed close to the dorsal margin and is tentatively regarded as a puncture mark. Similar depressions (total of three) are observed on the dorsal surface near an area where the bone is broken and displaced toward the interior of the shaft (Fig.2). There are other small depressions scattered on the bone surface, but since they are not associated with any part where the cortical bone is broken and displaced from its natural position, it is not clear if they are puncture marks or the result of other processes (e.g., fossilization, collecting).

The articulation for the humerus is incomplete with the posterior part missing. There are two distinct articulation surfaces that are concave and subequal in size, with the ventral one more pointed and directed anteriorly while the dorsal one shows a more rounded margin (Fig.4).

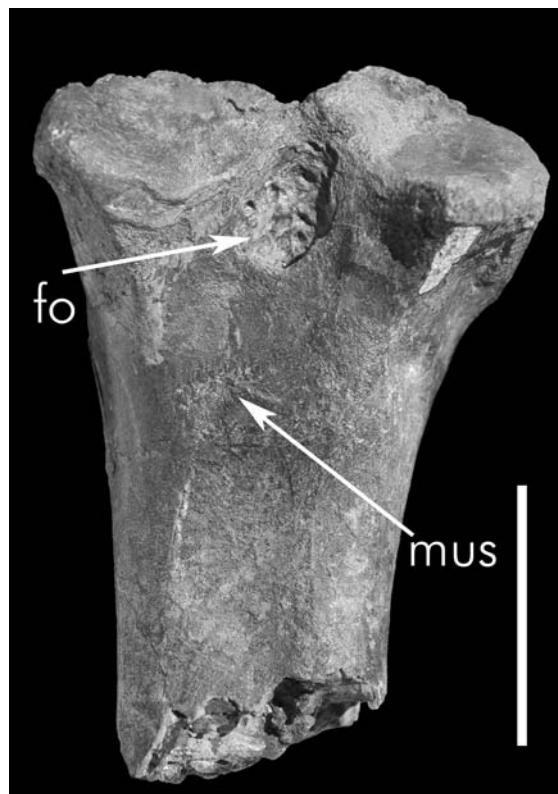


Fig.1- Proximal end of a right pterosaur ulna (MUCPv-358), in anterior view. Abbreviations: fo - foramen, mus - muscle scar. Scale bar: 50mm.

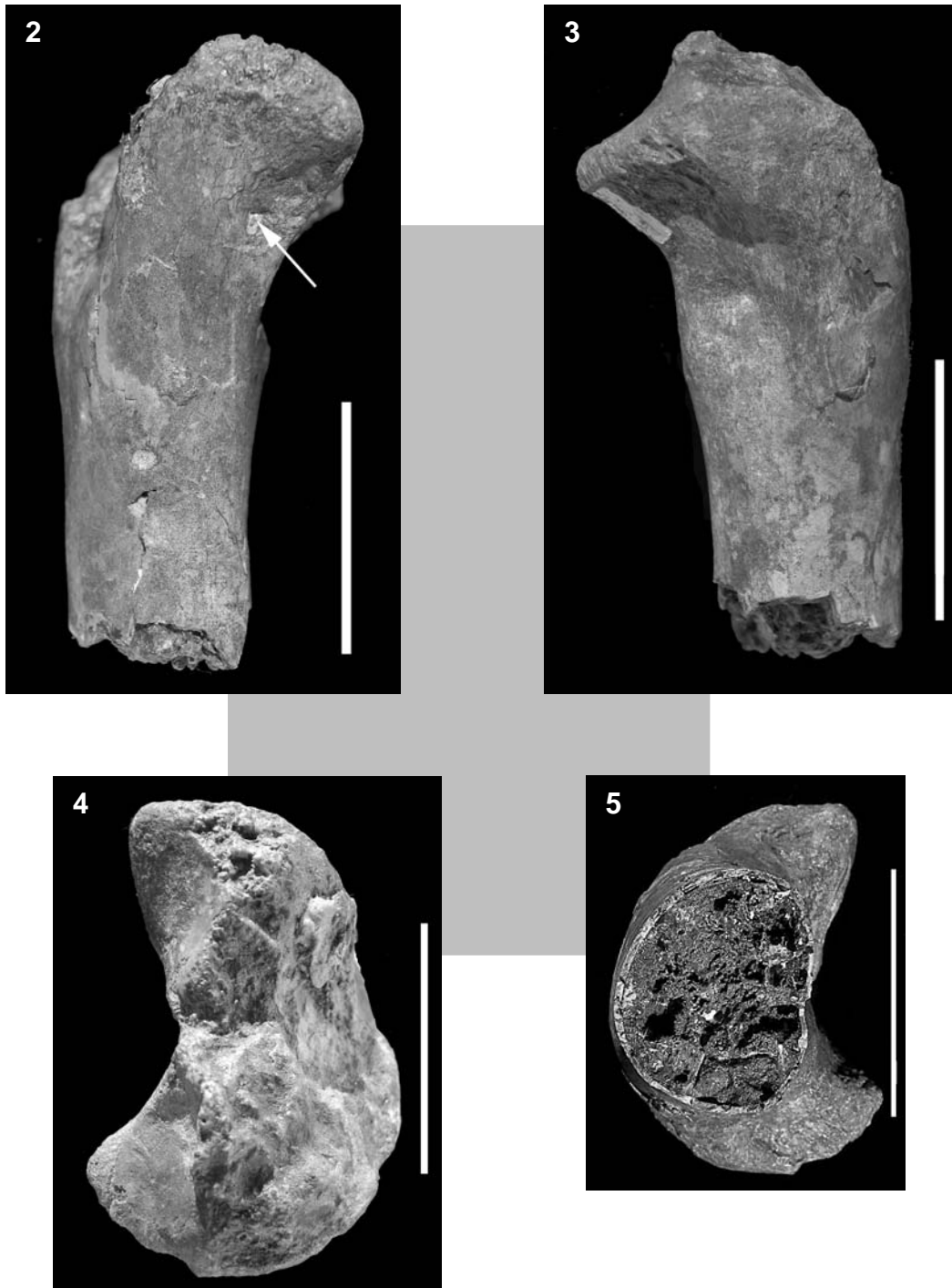


Fig.2- Proximal end of a right pterosaur ulna (MUCPv-358), in dorsal view. Arrow indicates puncture mark; fig.3- proximal end of a right pterosaur ulna (MUCPv-358), in ventral view; fig.4- proximal end of a right pterosaur ulna (MUCPv-358), in proximal view; fig.5- proximal end of a right pterosaur ulna (MUCPv-358), in distal view. Note the trabeculae inside the bone. Scale bars: 50mm.

RADIUS AND ULNA (MUCPv-600)

The radius and ulna (MUCPv-600) were found associated and are incomplete (Fig.6). They belong to the right side and compared to MUCPv-358, are massively constructed. This suggests that they belonged to an comparatively older animal. The radius is the best preserved element showing the proximal articulation (preserved length: 102.3mm). The proximal articulation is expanded dorsoventrally and compressed anteroposteriorly (70.4mm x 36.0mm). It shows a dorsoventrally elongated depression on the articulation surface with the humerus. The bone thickness is generally around 1.3mm. In several parts the bone surface is crushed and no trabeculae are observed.

A long bone associated with the radius with no articulation is here interpreted as the ulna. The preserved length is 207mm. The part close to the proximal articulation of radius has an oval section (28.2mm x 20.9mm) while the preserved distal end is comparatively stouter (40.0mm x 45.0mm). Overall, the ulna has a thicker shaft than the radius, but it is not twice as thick (or more), a condition observed in *Istiodactylus latidens* (Seeley, 1901), *Nurhachius ignaciobrito* Wang, Kellner, Zhou & Campos, 2005, *Pteranodon longiceps* Marsh, 1876 and anhanguerids (KELLNER, 2003; WANG *et al.*, 2005).

WING PHALANX (MUCRv-359)

A fragmentary bone (Fig.7) is here interpreted as the incomplete proximal articulation of a right wing

phalanx (length: 67.4mm). Most of the bone surface is broken and not preserved, indicating that this specimen was eroding at the surface for some time before being collected. The cross section of the preserved distal end of the shaft is slightly triangular, with the longest axis directed anteroposteriorly (37.4mm) and the deepest part closer to the anterior edge (20.0mm). A depression is observed on the ventral part, which is typical of a pneumatic foramen present in more derived pterosaurs (Dsungaripteroidea *sensu* KELLNER, 2003). No extensor tendon process is preserved, suggesting that it was not fused to the main part of the wing phalanx, a common feature to young pterosaurs (BENNETT, 1993; KELLNER & TOMIDA, 2000).

DISCUSSION AND CONCLUSION

The fossil record of pterosaurs in Argentina is restricted to five localities (KELLNER, 2001). The most important one is the Lagarcito Formation, where hundreds of bones of the archaeoptero-dactyloid *Pterodaustro guinazui* Bonaparte, 1970 were found (BONAPARTE, 1971; CHIAPPE *et al.*, 2000). In Neuquén, evidence for pterosaurs is restricted to an isolated bone from the Upper Jurassic (GASPARINI *et al.*, 1987) and tracks (CALVO & MORATALLA, 1998).

As far as comparisons are possible all specimens collected in the Portezuelo Formation so far appear to belong to the Pterodactyloidea, more specifically to the Dsungaripteroidea (e.g., presence of pneumatic foramina, size). The large ulna (MUCPv-358) and the radius (MUCPv-600) have an overall

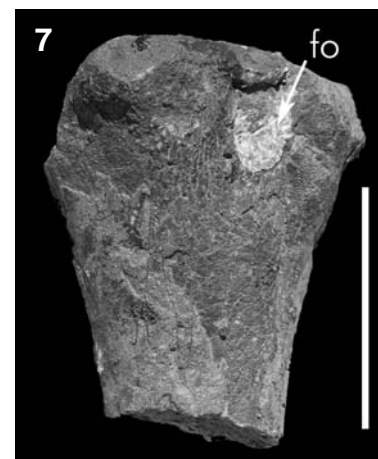
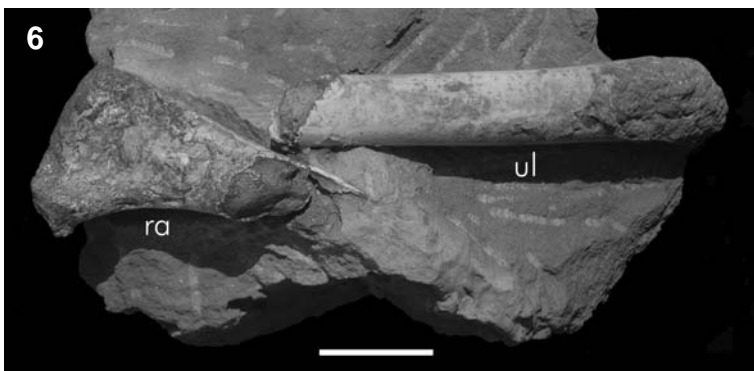


Fig.6- Pterosaur radius and ulna (MUCPv-600): (ra)- radius, (ul) ulna. Scale bar: 50mm; fig.7- proximal end of first wing phalanx of a pterosaur (MUCPv-359), in ventral view: (fo) foramen. Scale bar: 40mm.

shape similar to the members of the Azhdarchoidea that is formed by the Azhdarchidae and the Tapejaridae, both toothless pterosaur clades (KELLNER, 2003). The Azhdarchidae are characterized by features in the cervical vertebrae (e.g., HOWSE, 1986) while the Tapejaridae show several unique features in the skull and coracoid (KELLNER & CAMPOS, 2002; KELLNER, 2004). Therefore no further classification of the Neuquén material can be made at this point.

Based on comparisons with other large pterodactyloid pterosaurs, the large ulna (MUCPv-358) from the Futalognko site represents an animal with an estimated wing span of approximately six meters. A small part of this bone was taken for histological sections. According to SAYÃO *et al.* (2004), the cortex is composed of primary tissue and most of the structures, up to its subperiosteal surface, are made of reticular fibro-lamellar bone with many osteocytes lacunae. The vascular canals are numerous and small in diameter, and their orientation is longitudinal with irregular anastomoses. No evidence of bone erosion and reconstruction such as secondary osteons or lines of arrested growth were observed in this specimen.

Bone histology of pterosaur specimens have been used to define the ontogenetical stage of some animals, including a small azhdarchid pterosaur from Two Medicine Formation (PADIAN *et al.*, 1995). The histological pattern observed in the large ulna (MUCPv-358), especially in the reticular fibro-lamellar bone, is commonly reported in primary fast-growing tissue, involved in the formation of the cortex (RICQLÈS *et al.*, 2000). It differs remarkably from the condition observed in other pterosaur specimens attributed to adults in which secondary osteons (= haversian osteons) are present (PADIAN *et al.*, 1995; RICQLÈS *et al.*, 2000; SAYÃO, 2003). It should be noted that the well vascularized, reticular type of bone observed in the Neuquén specimen is very similar to the condition observed in birds (ENLOW & BROWN, 1957; RICQLÈS, 1978; CHINSAMY *et al.*, 1995), and commonly associated with rapid growth. These features indicate that the ulna (MUCPv-358) belonged to an animal that had not completed its ontogeny and was still growing at time of death. Therefore this specimen represents the largest pterosaur known from Argentina and one of the largest collected in Gondwana.

With the exception of those in the Jehol Biota (China), pterosaurs of truly terrestrial environment are rare (WANG *et al.*, 2005). Therefore the Portezuelo Formation, whose age is regarded as Upper

Cretaceous (Turonian-Early-Coniacian; LEGARRETA & GULISANO, 1989), has the potential to provide new information on pterosaurs that lived deep within the continent. To date the specimens recovered so far indicate that large pterodactyloids lived in this part of Patagonia some 90 million years ago, in an environment of meandering and anastomosing rivers with small lakes.

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REFERENCES

- BENNETT, S.C., 1993. The ontogeny of *Pteranodon* and other pterosaurs. **Paleobiology**, **19**:92-106.
- BONAPARTE, J. F., 1971. Descripción del cráneo y mandíbulas de *Pterodaustro guinazui* (Pterodactyloidea - Pterodaustriidae nov.) de la formación Lagarcito, San Luis, Argentina. **Publicaciones del Museo Municipal de Ciencias Naturales**, **1**:263-272.
- CALVO, J.O. & MORATALLA, J., 1998. First record of pterosaur tracks in Southern continents. In: ENCUESTRO ARGENTINO DE ICNOLOGIA Y REUNION DE ICNOLOGIA DEL MERCOSUR, 3., 1998. **Abstracts...** Mar del Plata. p.1-8.
- CALVO, J.O.; PORFIRI, J.D.; VERALLI, C. & POBLETE, F., 2001 a. One of the largest titanosaurid sauropods ever found, Upper Cretaceous, Neuquén, Patagonia, Argentina. **Journal of Vertebrate Paleontology**, **21**(3):37A.

- CALVO, J.O.; PORFIRI, J.D.; VERALLI, C.; POBLETE, F. & KELLNER, A.W.A. b, 2002. Futalognko Paleontological site, one of the most amazing continental Cretaceous environments of Patagonia, Argentina. In: CONGRESO LATINOAMERICANO DE PALEONTOLOGÍA DE VERTEBRADOS, 1., 2002, Santiago. **Resúmenes...** Santiago: Sociedad Paleontológica de Chile. p.19-20.
- CALVO, J.O.; PORFIRI, J.D. & KELLNER, A.W.A., 2004a. On a new maniraptoran dinosaur (Theropoda) from the Upper Cretaceous of Neuquén, Patagonia, Argentina. **Arquivos do Museu Nacional**, **62**(4):549-566
- CALVO, J.O.; PORFIRI, J.D.; VERALLI, C.; NOVAS, F. & POBLETE, F., 2004b. Phylogenetic status of *Megaraptor namunhuaikuii* Novas based on a new specimen from Neuquén, Patagonia, Argentina. **Ameghiniana**, **41**(4):565-575.
- CHIAPPE, L.M.; KELLNER, A.W.A.; RIVAROLA, D.; DAVILA, S. & FOX, M., 2000. Cranial morphology of *Pterodaustro guinazui* (Pterosauria: Pterodactyloidea) from the Lower Cretaceous of Argentina. **Natural History Museum of Los Angeles County, Contributions in Science**, **483**:1-19.
- CHINSAMY, A.; CHIAPPE, L.M. & DODSON, P., 1995. Mesozoic avian bone microstructure: physiological implications. **Paleobiology**, **21**(4):561-574.
- ENLOW, D.H. & BROWN, S.O., 1957. A comparative histological study of fossil and recent bone tissues. Part II. **Texas Journal of Sciences**, **9**:185-214.
- GALLO, V.; CALVO, J.O. & KELLNER, A.W.A., 2003. First occurrence of a teleostean fish in the Portezuelo Formation (Upper Cretaceous), Neuquén Group, Patagonia - Argentina. In: SIMPÓSIO BRASILEIRO DE PALEONTOLOGIA DE VERTEBRADOS, 3., Rio de Janeiro. **Resumo...** Rio de Janeiro: Universidade do Estado do Rio de Janeiro. p.29.
- GASPARINI, Z.; LEANZA, H. & GARATA ZUBILLIGA, J., 1987. Un pterosauria de las Calizas Litográficas Tithonianas de Area de los Catutos, Neuquén, Argentina. **Ameghiniana**, **24**(1-2):141-143.
- HOWSE, S.C.B., 1986. On the cervical vertebrae of the Pterodactyloidea (Reptilia: Archosauria). **Zoological Journal of the Linnean Society**, **88**: 307-328.
- KELLNER, A.W.A., 1994. Remarks on pterosaur taphonomy and paleoecology. **Acta Geologica Leopoldensia**, **39**(1):175-189.
- KELLNER, A.W.A., 2001. A review of the pterosaur record from Gondwana. In: TWO HUNDRED YEARS OF PTEROSAURS. **Strata, sér. 1**, **11**:51-53.
- KELLNER, A.W.A., 2003. Pterosaur phylogeny and comments on the evolutionary history of the group. In: BUFFETAUT, E. & MAZIN, J.M. (eds). **Evolution and palaeobiology of pterosaurs**. London: Geological Society. p.105-137. (Special Publication, 217.)
- KELLNER, A.W.A., 2004. New information on the Tapejaridae (Pterosauria, Pterodactyloidea) and discussion of the relationships of this clade. **Ameghiniana**, **41**(4):521-534.
- KELLNER, A.W.A., 2006. **Pterossauros - os senhores do céu do Brasil**. Rio de Janeiro: Vieira&Lent. 176p.
- KELLNER, A.W.A. & CAMPOS, D. A., 2002. The function of the cranial crest and jaws of a unique pterosaur from the Early Cretaceous of Brazil. **Science**, **297**: 389-392.
- KELLNER, A.W.A. & TOMIDA, Y., 2000. Description of a new species of Anhangueridae (Pterodactyloidea) with comments on the pterosaur fauna from the Santana Formation (Albian-Aptian), Northeastern Brazil. **National Science Museum Monographs**, Tokyo, **17**:1-135.
- KELLNER, A.W.A.; CALVO, J.O.; SAYÃO, J.M. & PORFIRI, J.D., 2004. First pterosaur from the Portezuelo Formation, Neuquén Group, Patagonia, Argentina. In: SIMPÓSIO BRASILEIRO DE PALEONTOLOGIA DE VERTEBRADOS, 4., Rio Claro. **Abstracts...** Rio Claro: UNESP. p.29-30.
- LEANZA, H.A. & HUGO, C.A., 2001. Cretaceous red beds from southern Neuquén Basin (Argentina): age, distribution and stratigraphic discontinuities. In: LEANZA, H.A. (ed.) **VII International Symposium on Mesozoic Terrestrial Ecosystems**. Buenos Aires: Asociación Paleontológica Argentina. v.7, p.117-122.
- LEGARRETA, L. & GULISANO, C., 1989. Análisis estratigráfico secuencial de la Cuenca Neuquina (Triásico superior-Terciario inferior). In: CHEBLI, G. & SPALLETI, L. (eds.) **Cuencas Sedimentarias Argentinas**. Tucumán: Universidad Nacional de Tucumán. p.221-243. (Serie Correlación Geológica, 6.)
- PADIAN, K.; RICQLÈS, A.J. & HORNER, J.R., 1995. Bone histology determinates identification of a new fossil taxon of pterosaur (Reptilia: Archosauria). **Comptes Rendus de l'Academie des Sciences de Paris**, **320**, **Ia**:77-84.
- POBLETE, J.F. & CALVO, J.O., 2003. Upper Turonian Dromaeosaurid teeth from Futalognko quarry, Barreales Lake, Neuquén, Patagonia, Argentina. In: JORNADAS ARGENTINAS DE PALEONTOLOGIA DE VERTEBRADOS, 19., Buenos Aires. **Resúmenes...** Buenos Aires. p.24.
- POBLETE, J.F. & CALVO, J.O., 2005. A crocodyliform tooth and the age of peirosaurids in Neuquén, Patagonia, Argentina. In: CONGRESO LATINOAMERICANO DE PALEONTOLOGÍA DE VERTEBRADOS, 2., Rio de Janeiro. **Abstracts...** Rio de Janeiro. p.206-207.
- PORFIRI, J. & CALVO, J.O., 2002. A new record of an ornithomimid dinosaur from the Upper Cretaceous

- of Neuquén, Patagonia, Argentina. In: CONGRESO LATINOAMERICANO DE PALEONTOLOGÍA DE VERTEBRADOS, 1., Santiago. **Resúmenes...** Santiago. p.45.
- PRÁMPARO, M.B.; PASSALIA, M.G.; HEREDIA, S. & CALVO, J.O., 2003. Hallazgo de una macroflora en el cretácico superior del Grupo Neuquén, Lago Barreales, Neuquén. In: REUNIÓN ANUAL DE COMUNICACIONES DE LA ASOCIACIÓN PALEONTOLÓGICA ARGENTINA Y SIMPOSIO DE TAFONOMÍA Y PALEOECOLOGÍA, Santa Rosa. **Resúmenes...** Santa Rosa. p.18.
- RICQLÈS, A.J., 1978. Recherches paléohistologiques sur les os longs des tétrapodes, VII, sur la classification fonctionnelle et l'histoire des tissue osseux des tétrapodes: Troisième partie, fin. **Annales de Paléontologie (Vertébrés)**, **64**(2):153-176.
- RICQLÈS, A.J.; PADIAN, K.; HORNER, J. R. & FRANCILLON-VIEILLOT, H., 2000. Paleohistology of the bones of pterosaurs (Reptilia: Archosauria): anatomy, ontogeny, and biomechanical implications. **Zoological Journal of the Linnean Society**, **129**:349-385.
- SAYÃO, J.M., 2003. Histovariability in bones of two pterodactyloid pterosaurs from the Santana Formation, Araripe Basin, Brazil: preliminary results. In: BUFFETAUT, E. & MAZIN, J.M. (eds). **Evolution and Palaeobiology of Pterosaurs**. London: Geological Society. p.335-342. (Special Publication, 217.)
- SAYÃO, J.; KELLNER, A.; CALVO, J. & PORFIRI, J., 2004. Bone histology of a large pterosaur from the Portezuelo Formation, Neuquen Group, Patagonia, Argentina. **Journal of Vertebrate Paleontology**, **24**(suppl. to 3):109A-110A.
- VERALLI, C. & CALVO, J.O., 2003. New findings of carcharodontosaurid teeth (Upper Turonian) on Futalogno quarry, North Barreales Lake, Neuquén, Argentina. In: JORNADAS ARGENTINAS DE PALEONTOLOGÍA DE VERTEBRADOS, 19., Buenos Aires. **Resúmenes...** Buenos Aires. p.31.
- WANG, X.; KELLNER, A.W.A.; ZHOU, Z. & CAMPOS, D.A., 2005. Pterosaur diversity and faunal turnover in Cretaceous terrestrial ecosystems in China. **Nature**, **437**:875-879.
- WELLNHOFER, P., 1991. **The illustrated encyclopedia of Pterosaurs**. London: Salamander Books. 192p.

