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Unquillosaurus ceibali Powell, a giant maniraptoran (Dinosauria, Theropoda) from the Late Cretaceous of Argentina

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Abstract: A reviewed anatomy and phylogenetic relationships of the Late Cretaceous theropod *Unquillosaurus ceibali* is presented. This taxon is represented by an isolated pubis from Los Blanquitos Formation (Maastrichtian), from the province of Salta, NW Argentina. The size of the bone (51 cm long) originally lead to interpret this theropod as a member of the large "Carnosauria". However, the pubic anatomy of *Unquillosaurus* is more congruent with that present in metornithine coelurosaurians, a group including Alvarezsauridae, Therizinosauroidea, Oviraptorosauria, Deinonychosauria, and Aves. Derived features present in *Unquillosaurus* include: opisthopubic pelvis, pubic pedicle of ilium craniocaudally wide, ventral margin of pubic pedicle strongly concave, cranial process of pubic foot short, and length of pubic foot less than 30 percent of pubic total length. Moreover, some traits shared with early avians (e.g., pubic foot proximodistally tall and craniocaudally short), suggest that this dinosaur may be more closely related to birds than suspected. The set of autapomorphic features recognized in the pubis indicates that *Unquillosaurus* may belong to an endemic lineage of large maniraptoran theropods.

Key words: Theropoda, Maniraptora, Late Cretaceous, Argentina.

Unquillosaurus ceibali was described by Jaime Powell (1979) on the basis of an almost complete left pubis, discovered in Maastrichtian beds from Salta Province, NW Argentina (Fig.1). Powell (1979) interpreted this dinosaur as a large carnosaur of uncertain relationships. With the exception of some brief comments made by Molnar *et al.* (1990) and Bonaparte (1996), no further references to the phylogenetic relationships of this theropod are found in the literature. The fragmentary nature of *Unquillosaurus*, coupled with the limited knowledge of Gondwanan theropods available until recently, delayed the elucidation of the relationships of this dinosaur.

In the last years the fossil record of Argentine Cretaceous theropods has been favorably incremented, currently consisting of fifteen species pertaining to different lineages: Noasauridae, Abelisauridae, Carcharodontosauridae, and Coelurosauria (e.g., Bonaparte, 1991, 1996; Novas, 1997, 1998; Coria & Salgado, 1995). Other findings demonstrate that South America was inhabited by a diversity of non-avian coelurosaurian theropods, including *Santanaraptor* (Kellner, 1999), a possible oviraptorosaur (Frankfurt & Chiappe, 1999), different alvarezsaurids (Bonaparte, 1991; Novas, 1997), and the highly derived *Unenlagia comahuensis* (Novas & Puerta, 1997). This variety of dinosaurs offers valuable anatomical information that invites to reconsider the phylogenetic relationships of *Unquillosaurus*.

MATERIAL AND METHODDS

Institutional abbreviations. **AMNH**, American Museum of Natural History, New York; **HMN MB**, Humboldt Museum für Naturkunde, Berlin; **MACN**, Museo Argentino de Ciencias Naturales «B. Rivadavia», Buenos Aires; **MCZ**, Museum of Comparative Zoology, Cambridge; **PVL**, Paleontología de Vertebrados, Fundación «Miguel Lillo», San Miguel de Tucumán; **PVPH**, Paleontología Vertebrados, Museo Municipal «Carmen Funes», Plaza Huincul, Neuquén; **UA**, University of Antananarivo, Madagascar; **USNM**, United States National Museum, Washington DC; **YPM**, Yale Peabody Museum, New Haven.

Studied specimens: The following specimens have been used for this study: *Patagonykus puertai* (PVPH 37), *Albertosaurus libratus* (AMNH 5468), *Allosaurus fragilis* (AMNH 5767), *Archaeopteryx lithographica* (HMN MB 1880/81, and casts of London and Eichstatt specimens), *Carnotaurus sastrei* (MACN-CH 894), *Ceratosaurus nasicornis*

(USNM 4735), *Deinonychus antirrhopus* (AMNH 3015, MCZ 4371, YPM 5205, 5206, 5236), *Piatnitzkysaurus floresi* (MACN-CH 895), *Rahoonavis ostromi* (UA 8656), and *Unenlagia comahuensis* (PVPH 78).

Systematic nomenclature. In this paper we are following the phylogenetic hypothesis and systematic nomenclature employed by Xu *et al.* (2002) for coelurosaurian theropods.

SYSTEMATIC PALEONTOLOGY

Theropoda Marsh, 1881
Tetanurae Gauthier, 1986
Coelurosauria Huene, 1920
Maniraptora Gauthier, 1986
Metornithes Perle, Norell, Chiappe & Clark, 1993

Genus ***Unquillosaurus*** Powell, 1979

Type species. *Unquillosaurus ceibali* Powell, 1979.

Stratigraphic distribution. Los Blanquitos Formation, Salta Group (Maastrichtian; Salfity & Marquillas, 1999).

Geographic distribution. Arroyo Morterito, Sierra de la Candelaria, Salta Province, NW Argentina.

Unquillosaurus ceibali Powell, 1979
(Fig. 1)

Emended diagnosis. The pubis of *Unquillosaurus* is proportionally long and slender. It is large (51,4 cm long; Table 1) in comparison with other basal Maniraptora (= *Ornitholestes* + Metornithes; Xu *et al.*, 2002), such as *Patagonykus puertai* PVPH 37 (25 cm), *Deinonychus antirrhopus* MCZ 4371 (38 cm), *Unenlagia comahuensis* PVPH 78 (32 cm), *Rahonavis ostromi* UA 8656 (6 cm). Its proximal end presents a thick edge defining a deep groove, which was originally interpreted by Powell (1979) as diagnostic of *Unquillosaurus ceibali*. However, this abnormal morphology (not recorded in other saurischian dinosaurs) is better explained as the broken pubic pedicle of ilium adhered to the external surface of pubis. In fact, this piece of bone resembles the pubic pedicle of the ilium of *Deinonychus* and *Unenlagia* (Ostrom, 1969; Novas & Puerta, 1997) in being craniocaudally extended, ventrally concave, and with the cranial and ventral margins forming an angle exceeding 90 degrees in side view (Fig. 1A).

The proper acetabular surface is represented by a reduced surface located caudally to the facet for the pubic pedicle of the ilium. The acetabular surface of *Unquillosaurus* is more reduced than in Ceratosauria (e.g., *Carnotaurus*, *Ceratosaurus*; Gilmore, 1920; Bonaparte *et al.*, 1990) and Tyrannosauridae (*Albertosaurus libratus* AMNH 5468). In contrast, its reduced size resembles more that of derived coelurosaurians, such as Oviraptoridae, Alvarezsauridae, Dromaeosauridae (e.g., *Unenlagia*, *Bambiraptor*; Novas & Puerta, 1997; Burnham *et al.*, 2000), and primitive birds (e.g., *Archaeopteryx*, *Rahonavis*; Wellnhofer, 1974; Forster *et al.*, 1998). On the other hand, the ischiadic facet of the pubis is dorsoventrally low, comparable to that of Dromaeosauridae, but different from the well developed one of most non-coelurosaurian theropods (e.g., *Ceratosaurus*, Abelisauridae, *Piatnitzkysaurus*, Tyrannosauridae; Gilmore, 1920; Bonaparte *et al.*, 1990; Bonaparte, 1986; Osborn, 1917). The obturator foramen is ventrally open, as it occurs in most tetanurans (Gauthier, 1986) (Fig. 2).

Table 1. Measurements of pubis of *Unquillosaurus ceibali*

Proximodistal length	514 mm
Craniocaudal diameter of proximal end	155 mm
Craniocaudal diameter of distal foot	115 mm
Greatest transverse diameter of shaft	36 mm
Lesser transverse diameter of shaft	56 mm

The intersection between the proximal margin of the pubis and the longitudinal axis of the pubic shaft describes an angle of approximately 45 degrees, reflecting an opisthopubic condition of the bone (Fig. 2). An opisthopubic pelvis is diagnostic of Metornithes (Xu *et al.*, 2002), as it is present in Alvarezsauridae (Novas, 1997), Therizinosauroidea (Barsbold, 1979), and Paraves (=Deinonychosauria + Aves; Sereno, 1997; Clark *et al.*, 2002; Xu *et al.*, 2002).

The proximal ¾ of the pubic shaft are craniocaudally compressed, in contrast to most theropods (e.g., *Allosaurus*, *Patagonykus*; Gilmore, 1920; Novas, 1997) in which the pubis is rod-like proximal to the pubic symphysis. The condition mentioned above for *Unquillosaurus* results in a prominent external, longitudinal ridge (named "cresta lateral" by Powell, 1979; Fig.1 A, B). The margins of the pelvic canal of *Unquillosaurus* are medially convex, differing from most theropods (e.g., *Allosaurus*, *Tyrannosaurus*, *Patagonykus*, *Velociraptor*; Gilmore, 1920; Norell & Makovicky, 1999; Novas, 1997; Osborn, 1917) in which the margins are medially concave (Fig. 3). The craniocaudal compression of the proximal pubis of *Unquillosaurus* contrasts with the craniocaudal expansion of its distal half, thus resulting in a lon-

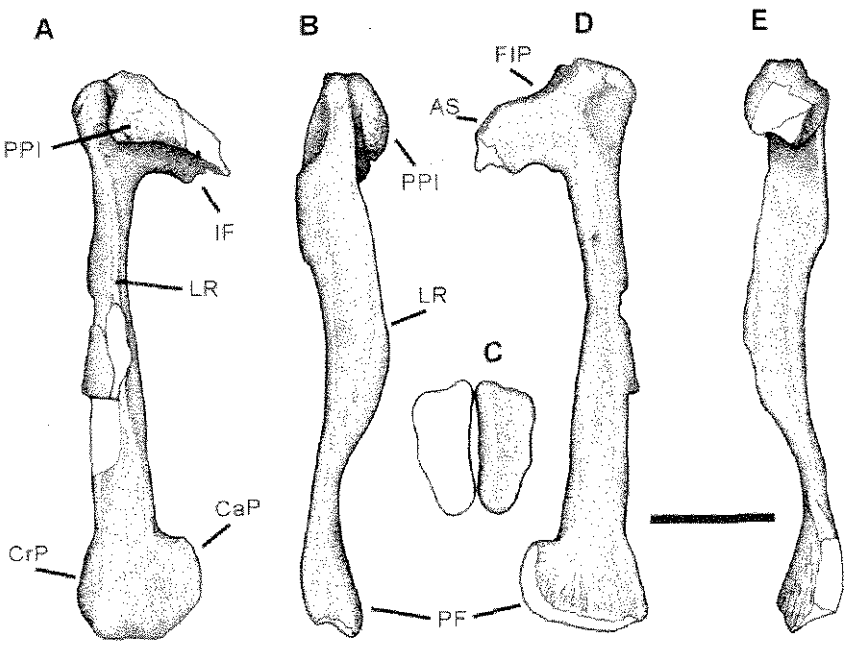

Fig. 1. *Unquillosaurus ceibali* left pubis. A) lateral, B) cranial, C) distal (restored), D) medial, and E) caudal views. AS, acetabular surface; CaP, caudal process of pubic foot; CrP, cranial process of pubic foot; FIP, facet for the iliac pedicle; LR, lateral ridge; PF pubic foot; PPI, Iliac pubic pedicel. Scale bar 10 cm.

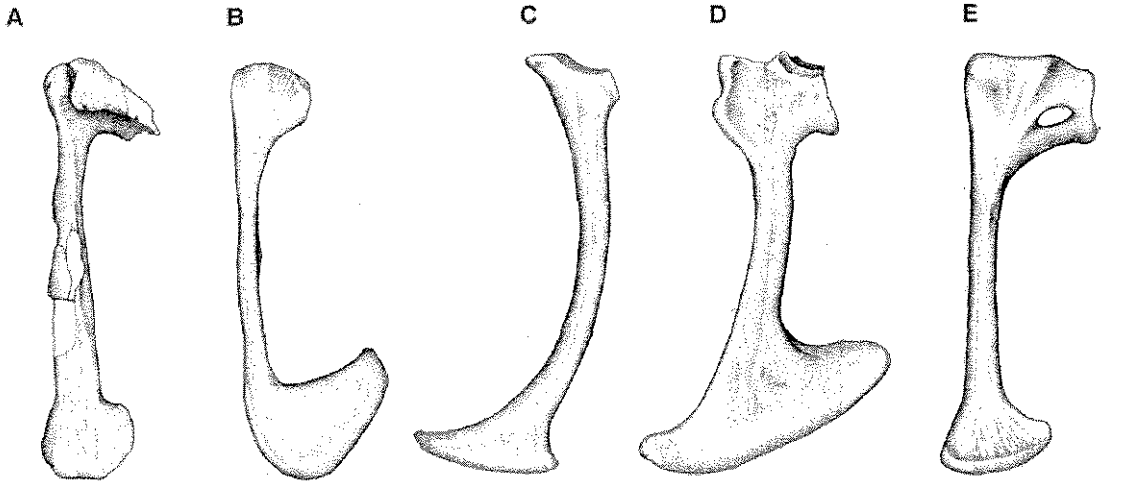

Fig. 2. Pubis of several theropods in lateral view. Not to scale. A) *Unquillosaurus*, B) *Unenlagia*, C) *Oviraptor*, D) *Tyrannosaurus*, E) *Piatnitzkysaurus*.

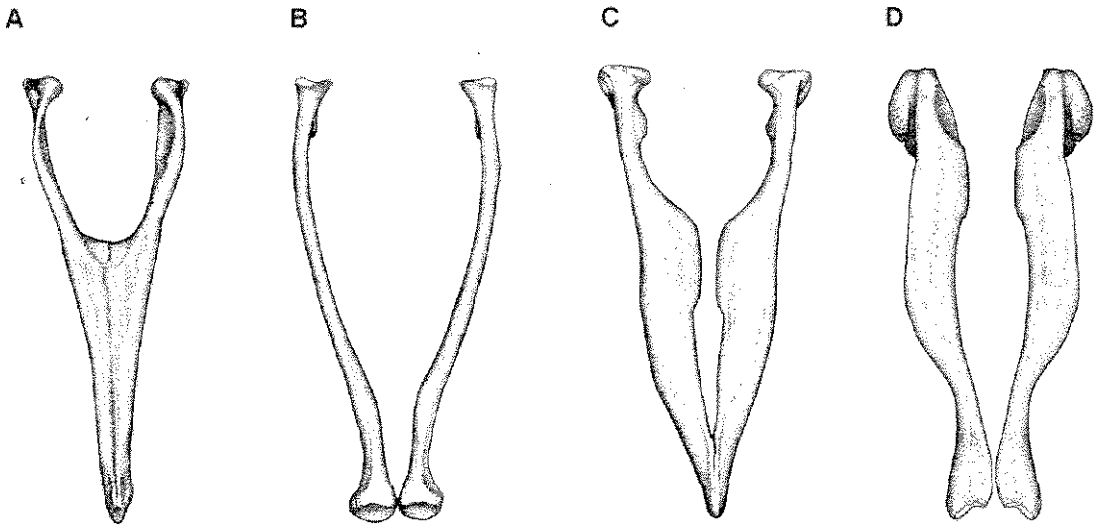

Fig. 3. Reconstructed pubises of several theropods in cranial view. Not to scale. A) *Ornithomimus*, B) *Patagonykus*, C) *Unenlagia*, D) *Unquillosaurus* (without the pubic pedicle of ilium).

gitudinal "twisting" of the bone (Fig. 1). In most theropods, instead, the cranial and caudal margins of the pubic shaft are nearly parallel (Fig. 2).

The pubic shaft lacks an apron, and the medial symphysis is absent (Figs. 1, 3), unlike most theropods (e.g., *Allosaurus, Carnotaurus, Ornithomimus, Velociraptor, Unenlagia, Rahonavis, Archaeopteryx*; Gilmore, 1920; Bonaparte *et al.*, 1990; Osborn, 1917; Norell & Makovicky, 1999; Novas & Puerta, 1997; Forster *et al.*, 1998; Wellnhofer, 1974) in which the apron is transversely wide and a relatively extended symphysis is present. In this sense, *Unquillosaurus* resembles alvarezsaurids (e.g., *Patagonykus*; Novas, 1997) and basal pygostilian birds (e.g., *Confusiusornis, Changchengornis, Concornis*; Chiappe, 2001) in having a pubic symphysis reduced to the distal extremity of the bones. Notably, the distal end of the the pubis of *Unquillosaurus* is medially flattened, and lacks marks for the articulation with the opposite bone (Fig. 1D).

The pubic foot is craniocaudally short and proximodistally deep. The cranial projection of the boot is more reduced than in *Deinonychus* (Ostrom, 1975), *Achillobator* (Perle *et al.*, 1999), and *Velociraptor* (Norell & Macovicky, 1999) thus resembling the smaller proportions present in *Bambiraptor* (Burnham *et al.*, 2000), *Unenlagia* (Novas & Puerta, 1997), and birds (Chiappe, 2001). Also, the caudal process of the pubic foot is strongly reduced as in primitive birds such as *Rahonavis* and *Archaeopteryx* (Wellnhofer, 1974; Forster *et al.*, 1998) but differing from some basal paravians (e.g., *Unenlagia, Bambiraptor*; Novas & Puerta, 1997; Burnham *et al.*, 2000) in which it is well developed. However, in *Unquillosaurus* the apex of the caudal process is dorsally curved, condition absent in the remaining theropods (Fig.2).

DISCUSSION

The pubis of *Unquillosaurus* clearly indicates that this genus is not a member of Abelisauroidea (=Noasauridae + Abelisauridae; Novas, 1992; Carrano *et al.*, 2002). In the later ones the pubis retained plesiomorphic features absent in *Unquillosaurus*, such as: obturator foramen enclosed by bone, ischiadic facet proximodistally deep, extended pubic symphysis, and pubic boot enlarged and dorsoventrally depressed. Besides, the pubic foot of *Unquillosaurus* lacks the lateral inset described in *Carnotaurus* and *Masiakasaurus* (Carrano *et al.*, 2002). *Unquillosaurus* may not belong to Carnosauria (=Allosauroidea + Carcharodontosauridae; Padian *et al.*, 1999) because carnosaurs retained a pubic symphysis and developed very large pubic boots. Both conditions are absent in *Unquillosaurus*.

On the contrary, the pubic anatomy of *Unquillosaurus* is more congruent with that present in theropods more derived than Carnosauria (e.g., Coelurosauria, a group including theropods more closely related to birds; Gauthier, 1986). The following apomorphic trait supports the inclusion of *Unquillosaurus* within Metornithes (=Alvarezsauridae + ((Therizinosauroidea + Oviraptorosauria) + Paraves); Xu *et al.*, 2002): 1) opisthopubic pelvis (but see Chiappe, 2001, for al-

ternative interpretation on this character). The following features of *Unquillosaurus* are present in Paraves (=Deinonychosauria + Aves; Sereno, 1997): 1) pubic pedicle of ilium craniocaudally wide; 2) ventral margin of pubic pedicle strongly concave; 3) cranial process of pubic foot short; 4) length of pubic foot less than 30 percent of pubic total length. Notably, *Unquillosaurus* shares with basal birds (e.g., *Rahonavis*, *Archaeopteryx*; Wellnhofer, 1974; Forster *et al.*, 1998) a proximodistally tall and craniocaudally short pubic foot, even shorter than in *Deinonychus, Velociraptor,* and *Unenlagia*. Besides, the highly reduced pubic symphysis of *Unquillosaurus* resembles that of alvarezsaurids (Novas, 1997) and birds more derived than *Archaeopteryx* (Chiappe, 2001).

In sum, available information supports *Unquillosaurus* as a member of Metornithes (*sensu* Xu *et al.*, 2002). Its large size (comparable to *Achillobator*; Perle *et al.*, 1999) makes *Unquillosaurus* one of the largest known maniraptorans. *Unquillosaurus* adds to the list of bird-like theropods discovered in Gondwana, such as *Unenlagia* and *Rahonavis*, but constituting a giant member of the group. We interpret that a radiation of large-sized maniraptorans occurred in South America during the Late Cretaceous, probably including other recent discoveries (e.g., Coria *et al.*, 2001; Novas *et al.*, 2003). The unique pubic features also prompt to the conclusion that *Unquillosaurus* was part of a lineage of predatory dinosaurs endemic from South America.

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BIBLIOGRAPHY

Barsbold, R. 1979. Opisthopubic pelvis in the carnivorous dinosaurs. *Nature* 279: 792-793.

Bonaparte, J.F. 1986. Les dinosaures (carnosaures, allosauridés, sauropodes, cetiosauridés) du Jurassique Moyen de Cerro Cóndor (Chubut, Argentine). *Ann. Paleont. (Vert.-Invert.)* 72(3-4): 247-386.

- 1991. Los vertebrados fósiles de la Formación Río Colorado, de la Ciudad de Neuquén y cercanías, Cretácico superior, Argentina. *Rev. Mus. Arg. Cienc. Nat. "Bernardino Rivadavia", Paleontología* IV (3): 17-123.
- 1996. Cretaceous tetrapods of Argentina. *Munchner Geowissen. Abhandl.* 30 (A): 73-130.

Bonaparte, J.F., Novas, F.E. & R.A. Coria. 1990. *Carnotaurus sastrei* Bonaparte, the horned, lightly built carnosaur from the Middle Cretaceous of Patagonia. *Nat. Hist. Mus. Los Angeles County, Contrib. Sci.* 416: 1-42.

Burnham, D., K. Derstler, P. Currie, R. Bakker, Z. Zhou & J. Ostrom. 2000. Remarkable new Birdlike dinosaur (Theropoda: Maniraptora) from the upper Cretaceous of Montana. *Paleontol. Contrib. Univ.Kansas* 13: 1-14.

Carrano, M.T., S.D. Sampson, & C.A. Forster. 2002. The osteology of *Masiakasaurus knopfleri*, a small abelisauroid (Dinosauria: Theropoda) from the Late Cretaceous of Madagascar. *Jour. Vert. Paleont.* 22(3): 510-534.

Chiappe L. 2001. Phylogenetic relationships among basal birds. *In*: Gauthier, J. & G. Gall eds., *New perspectives on the origin and early evolution of birds: Proceedings of the International Symposium in Honor of John H. Ostrom*. Pp. 125-139. Peabody Museum of Natural History Yale University.

Clark, J.M. , M.A. Norell & P.J. Makovicky. 2002. Cladistic approaches to the relaitonships of birds to other theropod dinosaurs. *In*: L.M. Chiappe & L. Witmer, eds., *Mesozoic birds. Above the head of dinosaurs*. Pp. 31-61, University of California Press.

Coria, R., P. Currie, D. Eberth, A. Garrido & E. Koppelhus. 2001. Nuevos vertebrados fósiles del Cretácico Superior de Neuquén. *Ameghiniana* 38(4) suppl.: 6R.

Coria, R. & L. Salgado. 1995. A new giant carnivorous dinosaur from the Cretaceous of Patagonia. *Nature* 377: 224-226.

Forster, C., S. Sampson , L. Chiappe & D. Krause. 1998. The Theropod ancestry of birds: new evidence from the Late Cretaceous of Madagascar. *Science* 279: 1915-1919.

Frankfurt, N. & L. Chiappe. 1999. A possible oviraptorosaur from the Late Cretaceous of Northwestern Argentina. *Jour. Vert. Paleont.* 19 (1): 101-105.

Gilmore, C.W. 1920. Osteology of the carnivorous Dinosauria in the United States National Museum, with special reference to the genera *Antrodemus* (*Allosaurus*) and *Ceratosaurus*. *Bull. U.S. Natl. Mus.* 110: 1-159.

Gauthier, J.A. 1986. Saurischian monophyly and the origin of birds. *In* K.Padian (ed.), *The Origin of Birds and the Evolution of Flight*. California Academy of Sciences, Memoire 8:1-55.

Kellner, A. 1999. Short note on a new dinosaur (Theropoda, Coelurosauria) from the Santana Formation (Romualdo Member, Albian), Northeastern Brasil. *Bol. Mus. Nac. Geol.* 49: 1-8.

Molnar, R., S. Kurzanov & Z. Dong. 1990. Carnosauria. *In:* Weishampel D., Dodson P. & Osmólska (eds.), *The Dinosauria*, pp. 169-209. University of California Press.

Norell, M. A. & P. J. Makovicky. 1999. Important features of the dromaeosaurid skeleton II: informa-

tion from newly collected specimens of *Velociraptor mongoliensis*. *Am. Mus. Nov.*, 3282:1-45.

Novas, F. 1992. La evolución de los dinosaurios carnívoros. *In:* J. Sanz and R. Buscalioni (eds.): *Los dinosaurios y su entorno biótico*. Pp. 125-163.

- 1997. Anatomy of *Patagonykus puertai* (Theropoda, Avialae, Alvarezsauridae), from the Late Cretaceous of Patagonia. *Jour. Vert. Paleont.* 17(1): 137-166.
- 1998. *Megaraptor namunhuaiquii* gen. et. sp. nov., a large-clawed, Late Cretaceous Theropod from Argentina. *Jour. Vert. Paleont.*18 (1): 4-9.

Novas, F., J.I. Canale & M.P. Isasi. 2003. Un terópodo maniraptor del Campaniano-Maastrichtiano del norte patagónico. *Ameghiniana*, 40(4) suppl.: 63R.

Novas, F. & P. Puerta. 1997. New evidence concerning avian origins from the Late Cretaceous of Patagonia. *Nature* 387: 390-392.

Osborn, H.F. 1917. Skeletal adaptations of *Ornitholestes, Struthiomimus, Tyrannosaurus*. *Bull. Amer. Mus. Nat. Hist.*, 35: 733-771.

Ostrom, J.H. 1969. Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. *Bull. Peabody Mus. Nat. Hist.*, 30:1-165.

- 1975. On new specimen of the Lower Cretaceous theropod dinosaur *Deinonychus antirrhopus*. *Breviora*, 439:1-21.

Padian, K., J. Hutchinson & T. Holtz. 1999. Phylogenetic definitions and nomenclature of the major taxonomic categories of the carnivorous Dinosauria (Theropoda). *Jour. Vert. Paleont.* 19 (1): 69-80.

Perle, A., M. Norell, & J. Clark. 1999. A new maniraptoran theropod –*Achillobator giganticus* (Dromaeosauridae), from the Upper Cretaceous of Burkhant, Mongolia. *Nat. Univ. Mongolia*, Pp. 1-106.

Powell, J. 1979. Sobre una asociación de dinosaurios y otras evidencias de vertebrados del Cretácico superior de la región de la Candelaria, prov. de Salta, Argentina. *Ameghiniana* XVI (1-2): 191-204.

Salfity, J.A. & R. Marquillas, 1999. La cuenca cretácico-terciaria del norte argentino. *Instit. Geol. Rec. Min., Geología Argentina* 29(19): 613-626.

Sereno, P.C. 1997. The origin and evolution of dinosaurs. *Ann. Rev. Earth Planet. Sci.*, 25:435-489.

Wellnhofer, P. 1974. Das funfte Skelettexemplar von *Archaeopteryx lithographica*. *Palaeontographica* (A) 147:169-216.

Xu, X., M. A. Norell, X. Wang, P. Makovicky & X. Wu. 2002. A basal troodontid from the Early Cretaceous of China. *Nature* 415: 780-784.

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