Phylogenetic status of *Megaraptor namunhuaiquii* Novas based on a new specimen from Neuquén, Patagonia, Argentina

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Abstract. A new specimen of *Megaraptor namunhuaiquii* was discovered on the north coast of the Barreales lake, Neuquén, Argentina. The material comes from the Portezuelo Formation (Upper Turonian-Lower Coniacian) of the Neuquén Group. The new specimen includes an anterior cervical vertebra, scapula, coracoids, ulna, radius, a complete hand, pubis, two caudal vertebrae with haemal arch, and metatarsal IV. This finding improves the knowledge of this species and offers more information to elucidate its phylogenetic relationships. *Megaraptor namunhuaiquii* exhibits resemblances with Carcharodontosauridae in some aspects of the cervical and caudal vertebrae, but some other similarities are seen with the basal spinosaurid *Baryonyx* in the shape of the scapula and coracoid, and pubis shape with *Torvosaurus*. However, *Megaraptor* bears several derived characters in the construction of the forelimbs that clearly distinguishes the Patagonian taxon from the theropod taxa mentioned above.

Resumen. EL ESTATUS FILOGENÉTICO DE *MEGARAPTOR NAMUNHUAIQUII* NOVAS BASADO SOBRE UN NUEVO EJEMPLAR DE NEUQUÉN, PATAGONIA, ARGENTINA. Un nuevo espécimen de *Megaraptor namunhuaiquii* fue descubierto sobre la costa norte del lago Barreales, Neuquén, Argentina. El material proviene de la Formación Portezuelo (Turoniano Superior-Coniaciano Inferior) del Grupo Neuquén. El nuevo especimen incluye una vértebra cervical anterior, escápula, coracoide, ulna, radio, una mano completa, pubis, dos vértebras caudales con arco hemal, y metatarso IV. Estos hallazgos incrementan el conocimiento de esta especie y ofrecen mayor información para dilucidar su relación filogenética. *Megaraptor namunhuaiquii* exhibe semejanzas con Carcharodontosauridae en algunos aspectos de las vértebras cervicales y caudales, pero otras similitudes son compartidas con el spinosaurido basal *Baryonyx* en la forma de la escápula y coracoide, y en la forma del pubis con *Torvosaururs*. Además *Megaraptor* muestra varios caracteres derivados en la construcción de los miembros anteriores que claramente distinguen el taxón patagónico de los taxones de terópodos mencionados anteriormente.

Key words. Theropods. Cretaceous. Patagonia.

Palabras clave. Terópodos. Cretácico. Patagonia.

Introduction

In 1998, Novas described the Cretaceous theropod *Megaraptor namunhuaiquii* on the basis of an ulna, a manual phalanx, distal end of metatarsal III, and a large ungual phalanx, interpreted as belonging to the second digit of the foot. The specimen, from the Portezuelo Formation of the Río Neuquén Group (Turonian-Santonian), was interpreted as a possible basal coelurosaurid, that convergently acquired with dromaeosaurids and troodontids the presence of a well developed trenchant claw on the foot (Novas, 1998).

In the course of paleontological exploration carried on in June 2002 by the National University of Comahue, new materials of *Megaraptor* were recovered. The specimen was found in outcrops of the Portezuelo Formation, widely exposed on the north coast of Los Barreales lake, Neuquén, where the Futalognko quarry was opened (figures 1 and 2). This quarry produced a large number of fossils in a small area of 200 square meters and 1 meter deep. The new *Megaraptor* material was found in close association with bones of large titanosaurid sauropods, iguanodontian ornithopods, several bones of a new species of *Unenlagia* (Novas and Puerta, 1997), and some fish, pterosaur, turtle and crocodile remains. Also, dinosaur eggshells and leaves of gymnosperms and angiosperms were recovered from the quarry. Because of the fossil richness of this place, it became

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the first permanent educational paleontological site in South America, named "Los Barreales Lake Paleontological Center".

The new *Megaraptor* specimen is represented by several bones (*e.g.*, vertebrae, some bones of both pectoral and pelvic girdles, and forelimb elements), some of which overlap with the holotype specimen (MCF-PVPH 79). For example, the ulna resembles that described for the holotype in sharing a blade-like olecranon process and the presence of a stout and triangular distal end (Novas, 1998). However, the most impressive and relevant element of the new specimen corresponds to an almost complete right hand, the digit 1 of which ends in a large and transversely compressed ungual phalanx, almost identical to the ungual described for the holotype specimen (Novas, 1998).

The new material allows to correct the identification of the remarkable trenchant ungual, as well as considerably amplifies our knowledge of the other parts of the anatomy of this interesting animal. This finding reveals an adaptive type not recorded before among theropods, consisting in the presence of enormous hands provided with trenchant claws on digits 1 and 2.

The purpose of the present paper is to offer descriptions of the new materials, as well as to point out resemblances and distinctions with other theropods.

Locality and geology

The Futalognko quarry (figure 1) is located 90 km NW of Neuquén city, on the north coast of Los Barreales Lake, where are exposed rocks belonging to the Río Neuquén Subgroup, the middle unit of the Neuquén Group (Albian through Campanian; Cazau and Uliana, 1973; Uliana and Dellapé, 1981; Legarreta and Gulisano, 1989; Calvo, 1991; Calvo and Salgado, 1995; Leanza, 1999). The Río Neuquén Subgroup includes two sedimentary units, predominantly composed of fluvial deposits: the underlying Portezuelo Formation, made up of yellowish sandstones, red and green claystones with a poor participation of conglomerates; and the overlying Plottier Formation, characterized by red claystones and sandstones. The age of the Portezuelo Formation has been interpreted as Turonian through Santonian on the basis of sequence stratigraphy (Leanza, 1999; Leanza and Hugo, 2001). In particular, the Portezuelo Formation comprises to deposits of meandering rivers on an almost flat region.

Fossils from the Futalognko quarry come from red claystones corresponding to the top Portezuelo Formation (figure 2). They are mostly disarticulated,
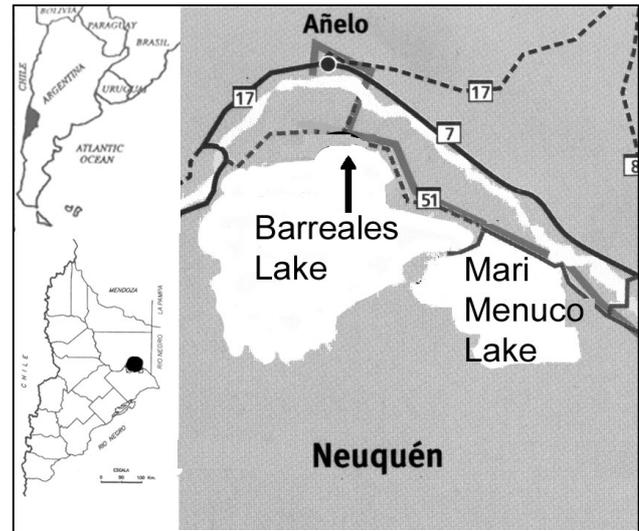
Figure 1. Map showing location of the Futalognko quarries where the material was found / *Mapa mostrando el sitio de Futalognko donde se encontraron los materiales.*

but their good preservation suggests that they have suffered little transport.

Material

The following material was used in this study: MEF 1157, a yet undescribed carcharodontosaurid from the Albian Gorro Frigio Formation, Chubut; MUCPv-CH 1, *Giganotosaurus carolinii*; MCF-PVPH 79, *Megaraptor namunhuaiquii* Novas.
Abbreviations. MCF-PVPH, Museo Carmen Funes, Paleontología Vertebrados, Plaza Huincul; MPEF, Museo Paleontológico "E. Feruglio", Trelew; MUCPv, Museo de la Universidad Nacional del Comahue, Paleontología de Vertebrados, Neuquén.

Systematic paleontology

THEROPODA Marsh, 1881
TETANURAE Gauthier, 1986
Megaraptor namunhuaiquii Novas, 1998
Figures 3-10

Holotype. MCF-PVPH 79, right ulna, left manual phalanx1.I; ungual phalanx of manual digit I; distal half of right metatarsal III.
New material. MUCPv 341. The new specimen of *Megaraptor namunhuaiquii* was collected from a stratigraphic level no thicker than 30 centimeters. The right ulna, radius, and manus were found articulated below a sauropod femur. From the same stratigraphic level, but far from the forelimb 3 meters to the W, we-
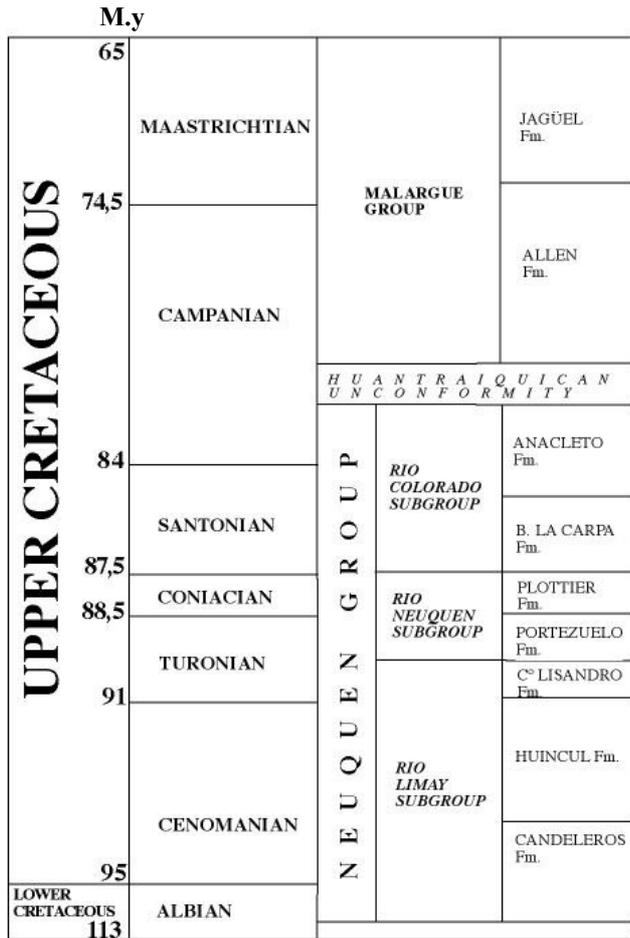
Figure 2. Stratigraphic column of the Neuquén Group. Modifief from Leanza, 1999. My: million years / *Columna estratigráfica del Grupo Neuquén. Modificado de Leanza, 1999. My: millones de años.*

re recovered an articulated left scapulocoracoid, a right pubis, a cervical vertebra, two anterior caudal vertebrae fused with one haemal arch, and two isolated hemals arches, and far from the forelimb 3.5 m to the E, a right metatarsal IV. We associate this set of bones (figure 3) with the forelimb (which bears diagnostic features of *Megaraptor namunhuaiquii*), because of their theropod nature and large size. In support of this association is the fact that no other theropod bones were found in the same area and stratigraphic level of *Megaraptor*, with the exception of *Unenlagia* (Calvo *et al.* 2003), which corresponds to a substantially smaller animal which exhibits derived characters of Maniraptora and Avialae, absent in *Megaraptor*. Besides, more than 80 teeth were collected in the excavation, ten of which may correspond to the size expected for *Megaraptor*. Such large teeth exhibit enamel wrinkles similar to those described for *Giganotosaurus* and *Carcharodontosaurus*. However, because teeth size is not always tight with large body size, we prefer to keep apart from *Megaraptor* this set of dental pieces, awaiting for cranial evidence of this animal.

Locality and horizon. Portezuelo Formation, North coast of Los Barreales lake, Neuquén, Patagonia, Argentina (figure 2).

Revised diagnosis. Cervical vertebrae with elongate, elliptical pleurocoels; blade-like olecranon process on proximal ulna; distal end of ulna stout and triangular in distal aspect; manual phalanx I subquadrangular in proximal view, with the dorsal portion transversely wider than the ventral one; elongate manus with enlarged and strongly transversely compressed unguals; metatarsal III with deep and wide extensor ligament pit; distal end of metatarsal IV narrower than shaft.
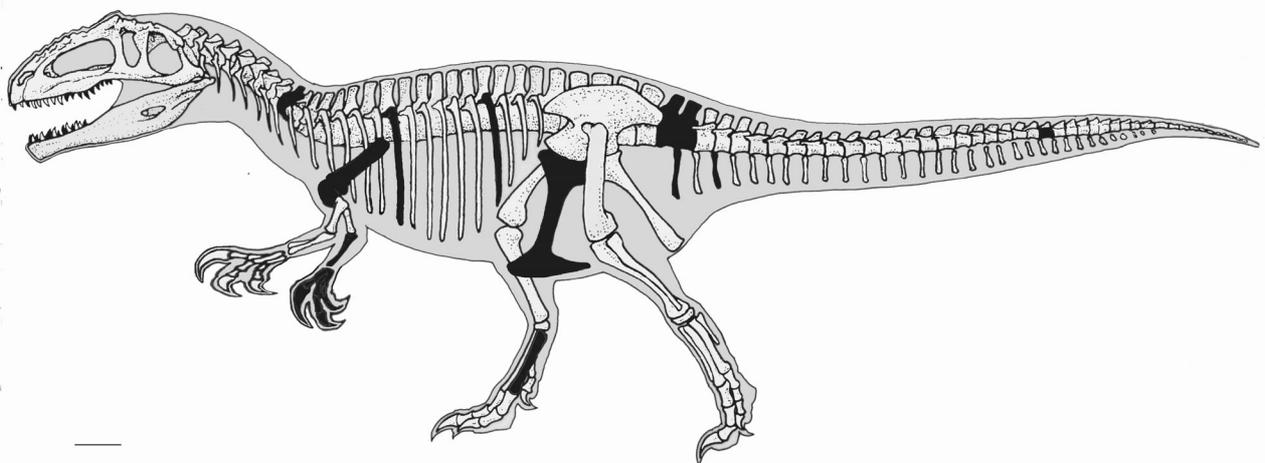
Figure 3. Hypothetical skeletal reconstruction of *Megaraptor namunhuaiquii*, including all preserved materials in black. Scale bar: 30 cm / *Reconstrucción hipotética del esqueleto de* Megaraptor namunhuaiquii, *incluyendo todos los materiales considerados. Escala: 30 cm.*
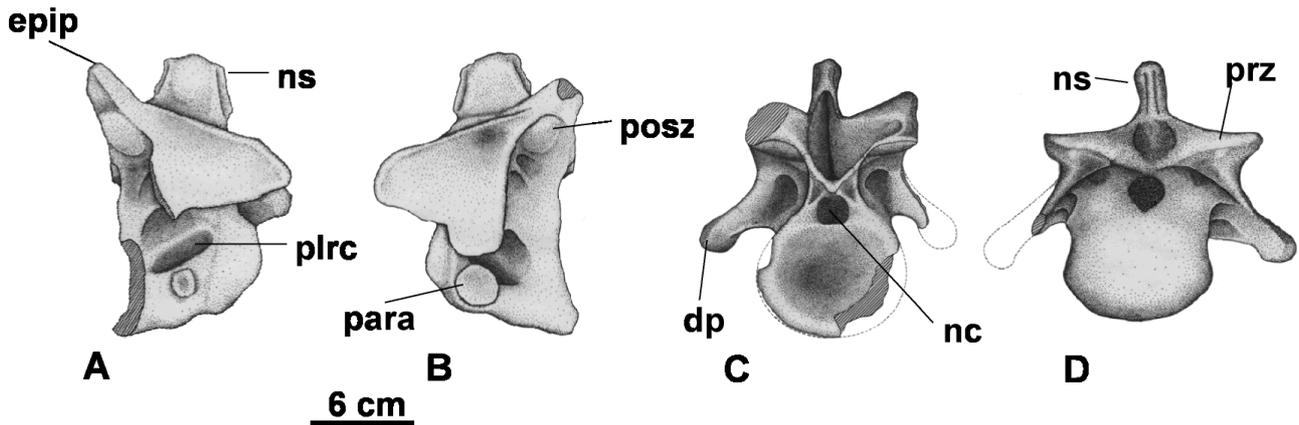
Figure 4. Cervical vertebrae of *Megaraptor namunhuaiquii*. **A-B,** lateral; **C,** anterior and **D,** posterior view. Abbreviations: dp. diapophysis; epip. epipophisis; nc. neural canal; ns, neural spine; para, parapophysis; plrc, pleurocoelous; posz, postzigapophysis; prz, prezigapophysis. *Vértebras cervicales de* Megaraptor namunhuaiquii. *Vistas **A-B**, lateral; **C**, anterior y **D**, posterior. Abreviaturas: dp, diapófisis; epip, epipófisis; nc, canal neural; ns, espina neural; para, parapófisis; plrc, pleurocelos; posz, postzigapófisis; prz, prezigapófisis.*

Description

Cervical vertebra. An almost complete mid-cervical vertebra (presumably a cervical 6) is preserved (figure 4). Cervical centra are opisthocoelous, a character interpreted as diagnostic of Tetanurae. However, the cranial articular ball is less convex than in *Baryonyx*, *Sinraptor*, *Allosaurus*, *Acrocanthosaurus*, and Carcharodontosauridae (*e.g.*, *Giganotosaurus*, MPEF 1157). As a whole, the mid-cervical of *Megaraptor* looks proportionally shorter and deeper than in these tetanurans, indicative of a thick and powerful neck for *Megaraptor*. The cranial surface of the centrum is elevated with respect to the caudal one, in contrast with the absence of this character in mid-cervical centra of carcharodontosaurids (Sereno *et al.*, 1996). A single pleurocoel, elliptical and craniocaudally elongate, is located in the middle of the centrum. It is unknown whether this kind of pleurocoel was present in the remaining cervicals of *Megaraptor*. At least, the elliptical condition of the cervical pleurocoel is not documented among other theropods, also including those in which double pleurocoels are present (*e.g.*, the spinosaurid *Spinosaurus*, the abelisaurids, and the carcharodontosaurids *Giganotosaurus* and MPEF 1157; Stromer, 1915; Novas *et al.*, in prep).

A small, bump-like process is present on the anteroventral portion of centrum. This process is absent in *Acrocanthosaurus*, *Sinraptor*, Dromaeosauridae and Abelisauria, but resembles *Ceratosaurus* where there is a keel on anterior cervicals.

The parapophyses are located at centrum midlength, and congruently the rib end of the diapophysis is caudally located. Such caudal displacement of parapophysis and diapophysis resembles the condition present in the carcharodontosaurids *Giganotosaurus* and MPEF 1157 (Novas *et al.*, in prep). The ev-

ident asymmetry that affects both parapophyses and pleurocoels of this cervical of *Megaraptor* must be pointed out: on the left side the pleurocoel is almost confluent with the excavation that is below the diapophysis, and the parapophysis is large and craniocaudally located; on the right side, instead, the pleurocoel is independent from the ventral excavation of the diapophysis, and the smaller parapophysis is located at centrum mid-length. The diapopostzygapophyseal lamina is well developed, and below it two foramina are present. The neural arch is higher than the centrum. The diapophyses are well developed, being craniocaudally wide and lateroventrally projected. A system of crests and excavations is present below the diapophyses.

The prezygapophyses are well separated from each other, and are mounted on a short pedicle that connects with the respective diapophysis. On the cranial surface of the neural arch, and ventral to each prezygapophysis, is present a shallow depression in a similar position to the deeper excavations seen in carcharodontosaurids, *Sinraptor* and abelisaurids. In dorsal view, prezygapophyses have a rounded border, except on the anteromedial one, where it shows a small concavity. In anterior view, this morphology is marked as a slightly concave surface. This character has not been seen in other theropods.

The diapophyses are triangular in side view. Notably, they are separated from the dorsal surface of the neural arch through a prominent ridge connecting the prezygapophysis with the epipophysis of the same side. Such a character is also present in abelisaurids and carcharodontosaurids.

In posterior view, a shallow pneumatic depression is present below the postzygapophyses. The epipophyses are well developed and posterodorsaly pointed, similar to MPEF 1157. A ridge connects the

prezygapophysis with the base of the epipophysis, resembling the edge present in *Sinraptor*, *Giganotosaurus*, and Abelisauroidea.

The neural spine is laminar and proportionally low with respect to the whole vertebral height. In contrast with *Allosaurus*, for example, the neural spine is craniocaudally wider at its base rather than at its upper end. Strong interspinous ligament scars are present on both cranial and caudal margins of the neural spine; they are uniformly developed from base to top of the neural spine, instead of being stronger towards the upper extremity of the spine, thus contrasting with *Ceratosaurus*, *Baryonyx*, *Allosaurus*, and *Acrocanthosaurus*. In this regard, the neural spine of *Megaraptor* resembles that of carcharodontosaurids, *Giganotosaurus* and MPEF 1157 in being proportionally low, triangular in side view, and with reduced ligament scars. However, *Megaraptor* differs from these large theropods in having a laminar, transversely compressed neural spine, in contrast with the block-like one of carcharodontosaurids.

Caudal vertebrae. Two articulated caudal vertebrae are preserved (figure 5), slightly laterally compressed. Their centra and the neural arches are firmly co-ossified, as well as their respective haemal arches. This fusion, not infrequent among dinosaurs, may be pathological. The available caudals correspond to the proximal portion of the tail, presumably to the region proximal to caudal 8, on the basis of centrum proportions, degree of development of prezygapophyses, and location of the transverse processes.

The centra are slightly amphicoelous and they are higher than wide. A pleurocoel (around 190 mm of maximum diameter) is present on each side of the centra, a feature that is present among non-coelurosaurian theropods such as *Carcharodontosaurus*, *Giganotosaurus*, *Acrocanthosaurus*, and *Bahariasaurus*. The neural arch is twice higher than the centra. The prezygapophyses are short and transversely thin. They surpass the anterior border of the centra. The postzygapophyses are connected with the neural spine by a spino-postzygapophyseal lamina. Both postzygapophyses are ventromedially inclined and united in the proximal portion.

The transverse processes are elongate, dorsoventrally flattened, and caudally projected. Their bases are supported from below by a pair of robust, oblique buttresses, which bound presumably pneumatic depressions. This feature is apparently absent in the remaining theropods (e.g., *Allosaurus*, *Acrocanthosaurus*, *Spinosaurus*, *Giganotosaurus*, MPEF 1157), with the probable exception of *Torvosaurus* (Britt, 1991).

The neural spines are bladelike, being dorsoventrally as deep as in *Allosaurus*, for example, albeit not reaching the exceedingly elongate proportions seen
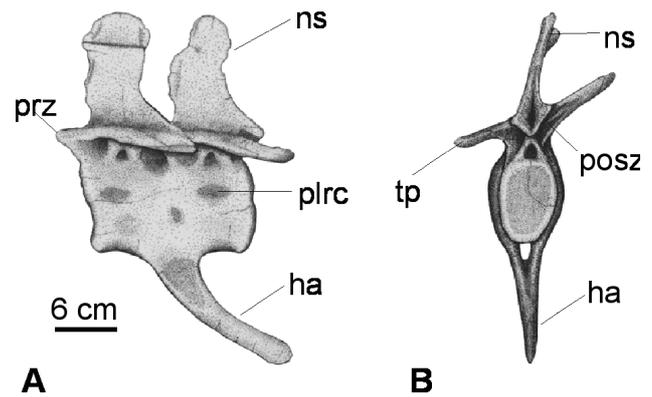
Figure 5. *Megaraptor namunhuaiqui* Caudal vertebrae fused in **A**, lateral and **B**, posterior view. Abbreviations: ha, hemal arch; ns. neural spine; plrc, pleurocoelous; prz, prezygapophysis; posz, postzygapophysis; tp, transverse process. *Vértebras caudales fusionadas en vistas* **A**, *lateral y* **B**, *posterior. Abreviaturas: ha, arco hemal; ns, espina neural; plrc, pleurocelos; prz, prezigapófisis; prz, postzigapófisis; tp, proceso transverso.*

in carcharodontosaurids (*e.g.*, *Giganotosaurus* and MPEF 1157), *Ceratosaurus* (Madsen and Welles, 2000), and spinosaurids (Stromer, 1915). The neural spines bear prominent ligament scars running along both cranial and caudal margins.

The hemal arch associated with the fused caudals described above, is elongate, slightly curved and simple in shape. It inclines approximately 45 degrees posteriorly, and its distal end is slightly expanded.

Pectoral girdle. The left scapula and coracoid were preserved in articulation (figure 6). The scapula (figure 6.A) lacks its distal end, and thus we do not known whether the blade had a distal expansion, as usual among basal theropods (Gauthier, 1986). Comparison with *Ceratosaurus* (Madsen and Welles, 2000) suggests that approximately 1/3 of the scapular blade was lost. The scapular blade looks craniocaudally wide in respect to its proximodistal length, especially in its fan-shaped proximal third. This kind of scapula resembles *Ceratosaurus* (Madsen and Welles, 2000), *Carnotaurus* (Bonaparte *et al.*, 1990), as *Baryonyx* (and possibly *Bahariasaurus*?) are tetanurans, the slender scapulae are characteristics of the more restricted group Avetheropoda (or, using Sereno's taxonomy, Neotetanurae). The cranial margin of the blade is concave while the caudal one is slightly convex. In contrast, in most theropods the blade is cranially convex, except for *Ceratosaurus* (Madsen and Welles, 2000), which exhibits a similar contour. The acromial process is proximodistally low albeit it is craniocaudally extended. The upper margin of the acromial process is notably straight, forming a strong angle with the cranial margin of the scapular blade. The subacromial depression is well
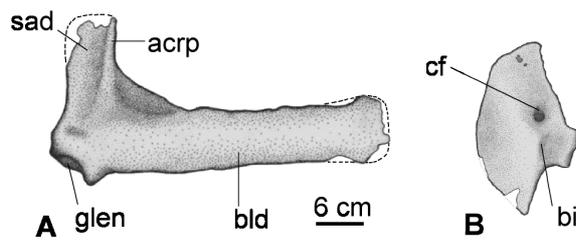
Figure 6. *Megaraptor namunhuaiquii* **A,** scapula; **B,** coracoid in lateral view. Abbreviations: acrp, acromion process; bi, biceps tubercle; bld, blade; cf, coracoid foramen; glen, glenoid; sad, subacromial depression / **A,** *escápula;* **B,** *coracoides en vista lateral. Abreviaturas: acrp, proceso acromial; bi, tubérculo biceps; bld, láminas; cf, foramen coracoideo; glen, glenoide; sad, depresion subacromial.*

developed and occupies most of the proximal region of the bone. The glenoid cavity is proportionally small. It orientates caudoventrally and has a prominent distal lip. The articular margin for the coracoid is transversely thin, and it is perpendicular to the longitudinal axis of the scapular blade.

The pectoral girdle of *Megaraptor* is distinct clearly from that of the carcharodontosaurid *Giganotosaurus*, because in the latter the scapular blade is remarkably robust, its longitudinal axis forms an acute angle with the coracoidal articular margin, and the acromial process is notably deep. The pectoral girdle is unknown in *Carcharodontosaurus* (Stromer, 1931), and that of MPEF 1157 resembles *Allosaurus*.

The coracoid (figure 6.B) is an almost flat, elliptical plate, with its longest axis craniocaudally directed. Its external surface is smooth and devoid of a prominent biceps tubercle. The posterior process is well developed, with a widely concave caudal notch, as is usual among tetanurans. The coracoid is proximodistally deeper than in *Allosaurus*, resembling more the coracoid of the spinosaurid *Baryonyx* (Charig and Milner, 1997). As in the latter taxon, the distal margin of the coracoid of *Megaraptor* describes a wide convexity. In *Giganotosaurus* the coracoid is unusual in being robust and craniocaudally short. The bone is pierced by a large coracoid foramen; caudal to it there is a slightly marked biceps tubercle, represented by an elongate and low pyramidal ridge, similar to that of *Allosaurus*.

Forearm. An almost complete articulated right forearm (including ulna, radius and manus) was recovered in the field (figures 7-9). The articulated bones measure 93.8 cm from the proximal end of radius to the distal tip of the ungual phalanx of digit I. The hand alone reaches 70 cm in maximum length. The material, impressive for its preservation and enor-

mous trenchant unguals, is decisive in identifying it as corresponding to *Megaraptor namunhuaiquii*, because it preserves bones that overlap with the holotype specimen (*e.g.,* ulna, phalanx 1 of digit 1, and a large ungual).

The ulna (figure 7.A-C) is almost identical to that of the holotype specimen of *Megaraptor* (Novas, 1998), although some minor variations are evident: in the new specimen the shaft is more curved (caudally convex), and the distal end is more quadrangular (in distal aspect) than in the holotype specimen. However, in both specimens the ulna is a stout bone with a prominent and transversely compressed olecranon process, triangular-shaped in proximal view. As in the holotype, the distal end of the ulna is medially bowed, as seen in cranial aspect. The peculiar condition of the olecranon process contrasts with the more rounded and blunted ones of *Torvosaurus*, *Allosaurus*, *Acrocanthosaurus*, and *Tyrannosaurus*. The blade-like olecranon of *Megaraptor* superficially resembles that of the spinosaurid *Baryonyx* (Charig and Milner, 1997), but strong differences are seen in the rest of the bone.

The right radius (figure 7.D-F) is nearly straight and slender. It is proximally expanded and slightly rounded. It is subtriangular-shaped in proximal view. Notably, the proximal end is convex in contrast to the concave proximal end present in other theropods. The distal end of the radius is expanded, but at an angle of nearly 90 degrees with respect to the proximal end. Thus, the ulna is twisted along its longitudinal axis. In distal view, the radius is oval-shaped, as in *Allosaurus*.

Manus. The hand of *Megaraptor* (figure 9) is characterized by the presence of enlarged ungual phalanges on digits I and II. Manual unguals are strongly compressed from side to side, and the flexor tubercles are prominent. Digits I, II and III are well developed, with a phalangeal formulae of 2-3-4, as is usual for tetanurine theropods. However, a rudimentary fourth metacarpal is present, albeit lacking phalanges. Digits I-III terminate in laterally compressed, sharply curved, trenchant unguals, of which those corresponding to digits I and II are the larger.

Carpal elements are partially complete (figure 8). Carpals I and II are fused; they are in contact with Mc I and Mc II. In dorsal view it probably had a pulley shapes in palmar view it has a semilunate shape. A thin sheet of bone is a remnant of the ulnare. This shape is similar to the carpals of tetanuran theropods, such as *Allosaurus* and more derived forms.

Metacarpal I (figure 8.A-B, table 1) is short, massive, and with its distal half deflected medially. Distal condyles are asymmetrical and separated by a shallow sulcus. This asymmetrical structure allowed

Table 1. Measurements in cm of metacarpals and phalanges of *Megaraptor namunhuaiquii* / *Medidas en centímetros de metacarpales y falanges de* Megaraptor namunhuaiquii.

Metacarpal	Length (cm.)	Proximal end	Distal end	Transverse diameter
I	10.6	6.4	6.3	3.9
II	17	8	3.7	3.3
III	11.9	2.9	0.8	1.2
IV	4			
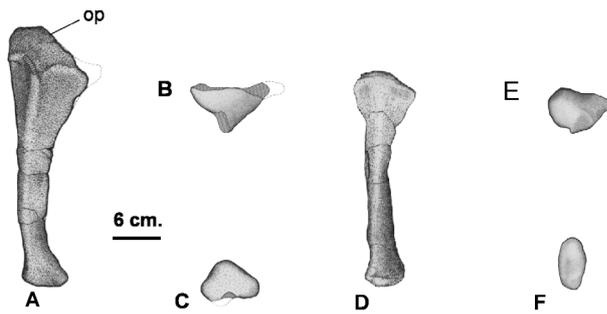
Figure 7. *Megaraptor namunhuaiquii.* **A-C,** ulna in **A,** lateral; **B,** proximal and **C,** distal views; **D-F,** radio in **D,** lateral; **E,** proximal and **F,** distal views; op, olecranon process / **A-C,** *ulna en vistas: A, lateral; B, proximal y C, distal; D-F, radio en vistas: D, lateral; E, proximal; F, distal; op, proceso del olecranon.*

Megaraptor to have a lateromedial rotation of digit I during flexion. Metacarpal II is robust and it is the longest of the hand (17 cm). The articular distal condyles are symmetrically developed. Metacarpal II is parallelogram-shaped in proximal view. Thus, metacarpal II partially overlaps metacarpal I in dorsal view. Metacarpal III (figure 8. C-E) is shorter than metacarpal II. As in other Tetanurae the shaft diameter of metacarpal III is 50 % or less than metacarpal II (Sereno *et al.*, 1996). It is straight, laterally compressed at the distal end and wider at the proximal end. The proximal end is triangular in shape. The distal end of metacarpal III articulates on the palmar surface of the distal end of metacarpal II. Metacarpal IV is reduced, representing less than half the length of metacarpal II. The presence of such a bone resembles *Sinraptor* among neotetanurans, and may be interpreted as less derived than *Allosaurus, Acrocanthosaurus*, and Coelurosauria.

Phalanx 1 of digit I (figure 9.A) is the longest of the hand. Its morphology fits well with the same manual phalanx of the holotype specimen, and no description is required here. Its correspondent ungual phalanx is 35 cm long as preserved. This impressive bone is almost identical to the same phalanx of the holotype specimen (originally thought by Novas, 1998, as corresponding to the ungual phalanx of pedal digit II). Notably, this ungual is the sharpest of the manual unguals, especially because its cutting edge is strongly compressed transversely. Also, this phalanx is the largest ungual of the hand, as usual among saurischian dinosaurs (Gauthier, 1986). As occurs in the holotype specimen, the ungual of digit I exhibits both lateral and medial grooves, with the internal furrow occupying a higher position than the external, a character absent in manual unguals of

most theropods (e.g., *Baryonyx, Allosaurus, Deinonychus, Fukuiraptor*), but present in the specialized trenchant unguals of digit II of maniraptoran coelurosaurs (*e.g.,* Dromaeosauridae and Troodontidae). However, as Novas pointed out (1998), such a large ungual of *Megaraptor* lacks two features that are usually found in the specialized pedal unguals of maniraptorans: tendon pit for the inside of the flexor tubercle, and flexor tubercle poorly developed.

Digit II (figure 9.B) comprises of three robust phalanges. Phalanx 2 has two subcircular ligament fossae on the lateral surface of its distal end. The ungual phalanx is smaller but more curved than ungual of digit I. When complete it may have reached 24 cm. Another distinction with the largest ungual is that the ungual of digit II is symmetric, with both lateral and medial furrows located almost at the same level as that present in *Fukuiraptor kitadaniensis* (Azuma and Currie, 2000).

Digit III is the shorter of the hand, distally reaching the level of the distal end of phalanx 2 of digit II. As its correspondent metacarpal, digit III is transversely narrow. Phalanges 1 and 2 present a ventral expansion on their proximal articulations. Phalanx 2 is the shortest element of the hand; however, because it is dorsoventrally deep, this bone acquires a blunt aspect, different from the slender proportions seen in *Allosaurus* (Madsen, 1976), but similar to that of *Acro-*

Table 2. Measurements of phalanges of *Megaraps namunhuaiquii* / *Medidas de las falanges de* Megaraptor namunhuaiquii.

Phalanx	Length (cm.)	Proximal end height	Distal end height	Transverse diameter
1.I	18.2	5.3	5.0	3.3
1. U	35 curved	9,5	– – – –-	
2. I	10.8	5.6	3.7	2.3
2. II	10.4	3.5	3.7	2.5
2. U	23.5 curved	6.5	– – – –-	
3.I	5.6	– –-	2.5	
3.II	4.1	2.1	2.1	
3.III	5.6	2.2	2.4	
3.U	6.5 curved	3.5	– – –	
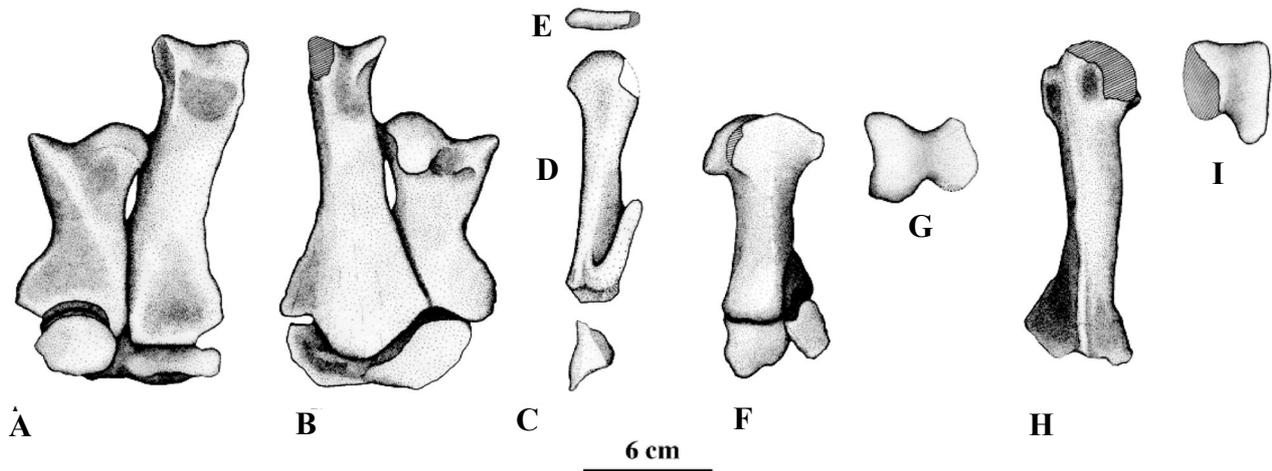
Figure 8. A-B, Metacarpal I and II: **A,** in dorsal and **B,** in palmar view; **C-E,** metacarpal III: **C,** in proximal; **D,** in lateral and **E,** in distal views; **F-G,** metacarpal I: **F,** in medial and **G,** in distal view; **H-I,** metacarpal II: **H,** in lateral and **I,** in distal view / *A-B, Metacarpos I y II: A, vista dorsal y B, vista palmar; C-E, Metacarpo III: C, vista proximal; D, vista lateral y E, vista distal; F-G, Metacarpo I: F, en vista medial y G, en vista distal; H-I, Metacarpo II: H, en vista lateral e I, en vista distal.*

canthosaurus (Currie and Carpenter, 2000 see table 3 here). On the dorsal surface of digit 2 there is a spine-like process that may have restricted the upward flexion of phalanx 1. Phalanx 3 is more normal in morphology. The ungual phalanx of digit III is incomplete, but the preserved proximal portion (3.5 cm deep) reveals that it was a small bone (the preserved

Table 3. Comparative measurements of manual bones of *Acrocanthosaurus athokensis* (Currie and Carpenter, 2000) and *Megaraptor namunhuaiquii* (MUCPv 341) / *Medidas comparativas de huesos de la mano de* Acrocanthosaurus athokensis *(Currie y Carpenter, 2000) y* Megaraptor namunhuaiquii *(MUCPv 341).*

Rigth hand	*Acrocanthosaurus*	*Megaraptor*
Digit I		
Ungual phalanx I		35, 42*
Phalanx 1.I	14.5	18.2
Mc I	6.2	10.6
Total		70.8
Digit II		
Ungual phalanx II		24*
Phalanx 1.II	13.5	10.8
Phalanx 2.II	10.5	10.4
Mc II	11.6	17
Total	35.5	62.2
Digit III		
Ungual phalanx III		7.5*
Phalanx 1.III	8.5	7*
Phalanx 2.III	6	4.6
Phalanx 3.III	7	5.7
Mc III	8.9	12.3
Total	30.4	37.1

* estimated size when complete

length along its dorsal length is 6.5 cm). In contrast with the unguals of the internal digits, this one is devoid of a groove on its lateral surface.

Pubis. Most of a right pubis is available, although its distal foot is broken. As preserved, the bone measures 49 cm long on its cranial margin. The proximal extremity of the pubis is dorsoventrally deep and craniocaudally expanded, thus giving the aspect of a stout bone. The articular surface for the ilium is elliptical, longer anteroposteriorly than lateromedially, suggesting that the pubic pedicle of ilium was craniocaudally expanded, as in *Allosaurus* for example. In relation with this, the acetabular portion is reduced. The ischial articulation, instead, is notably high, revealing the same condition for the proximal end of the ischium. This condition resembles that present in basal tetanurans (e.g., *Torvosaurus, Piatnitzkysaurus*; Galton and Jensen, 1979; Bonaparte, 1986), thus contrasting with that of more derived tetanurans (e.g., *Allosaurus, Giganotosaurus, Bahariasaurus,* coelurosaurs) in which the pubis is proximodistally low. Curiously, the pubis of *Megaraptor* has a fully open obturator foramen, in contrast with the more primitive condition seen in coelophysids, *Ceratosaurus,* Abelisauridae, *Torvosaurus,* and *Piatnitzkysaurus,* for example.

The pubic shaft is twisted along its length, so that it meets with the opposite bone forming a pubic apron at mid length. The contact of both pubes is restricted to the mid portion of the shaft. There are indications that a pubic foot was present, but we do not know its size and shape.

Metatarsal IV. This is the only preserved hind limb bone. It is complete and belongs to the right foot (figure 10). The shaft is gently curved outwards, as in

Figure 9. *Megaraptor namunhuaiquii* Digits; A, Digit I: a, ungual phalanx in medial view. Phalanx I in: b, medial; c, proximal, d, palmar; e, lateral and f, distal views. Ungual phalanx: g, in lateral view. B, Digit II in: a, dorsal and b, lateral view; C, Digit III in lateral view. *A, Dígito I: a, falange ungueal en vista medial. Falange I en: b, vista medial; c, vista proximal; d, vista palmar; e, vista lateral y f, vista distal. Falange ungueal: g, vista lateral. B, Dígito II en : a, vista dorsal y b, vista lateral. C, Dígito III en vista lateral.*

in side view) than in other theropods, and the external condylid of the distal end does not form the wing-shaped process seen in metatarsal IV of *Allosaurus* and *Sinraptor*, for example.

Discussion

Teeth recovered in the quarry correspond to different kinds based on size and shape. Referral of any of these teeth to the rest of the new specimen of *Megaraptor* is risky. Such teeth can be interpreted in various ways: 1) to demonstrate that carcharodontosaurids, aside from *Megaraptor* and *Unenlagia*, were also members of the Portezuelo theropod fauna; 2) that *Megaraptor* had teeth of the carcharodontosaurid kind, thus constituting evidence in favor of the carcharodontosaurid affiliation of this animal; or 3) that *Megaraptor* had Carcharodontosaurid-like teeth, but that they were convergently acquired with carcharodontosaurids. Obviously, to check these hypotheses it is necessary to consider all the anatomical evidence yielded by *Megaraptor* in the context of a parsimony character analysis.

The finding of new and more complete material of *Megaraptor namunhuaiquii* clarifies the nature of the

Sinraptor and *Torvosaurus* (Britt, 1991), but not to the degree present in *Dilophosaurus* (Welles, 1984), *Allosaurus*, and *Deinonychus* (Ostrom, 1969), for example. Its proximal end is subtriangular, but with its ventral (plantar) portion thicker than in *Torvosaurus* (Britt, 1991), *Sinraptor* (Currie and Zhao, 1993), and *Allosaurus* (Madsen, 1976). In this regard, metatarsal IV of *Megaraptor* resembles more the thicker proximal end of *Acrocanthosaurus* (Currie and Carpenter, 2000) as well as a metatarsal IV belonging to an indeterminable African species illustrated by Stromer (1934, pl. III, fig. 18B). The metatarsal is robust as seen in dorsal view. Notably, its shaft tends to become transversely narrower towards the distal end, to end in an articular condyle that is transversely narrower than the rest of the bone. This represents an unusual condition not present in other theropods (*e.g.*, *Allosaurus*, *Sinraptor*, *Torvosaurus*) in which the distal end of metatarsal IV tends to exceed the transverse diameter of the central part of the bone. Moreover, the distal articular surface looks more rounded (*e.g.*, convex

Figure 10. *Megaraptor namunhuaiquii* Metatarsal IV: A, anterior; B, proximal; C, distal view / *Metatarso IV: A, vista anterior; B, vista proximal; C, vista distal.*

holotype specimen, and also helps to understand better its phylogenetic relationships. The new evidence indicates that *Megaraptor* is not a member of Coelurosauria, as originally suspected by Novas (1998). Moreover, it seems clear that *Megaraptor* is not closely related to Abelisauroidea, and that there are no diagnostic features that unequivocally refer this taxon to either Carcharodontosauridae or Spinosauridae.

Cervical vertebrae of *Megaraptor* exhibit some features (e.g., parapophyses located at centrum mid-length; presence of a prominent ridge connecting prezygapophysis with epipophysis; epipophyses posterodorsaly pointed; low neural spine, craniocaudally wider at its base rather than on its upper end) resembling carcharodontosaurid allosauroids, but the rest of the neural arch and centrum anatomy does not respond to the kind of cervical vertebrae present in carcharodontosaurids (*e.g.*, *Giganotosaurus*, MPEF 1157). Caudal vertebrae also resemble those of *Carcharodontosaurus* (Stromer, 1931) in having a proportionally large pleurocoel, but it must be emphasized that distribution of this character is not uniform among carcharodontosaurids (Novas *et al.*, com. pers.) and their claimed sister groups (*Acrocanthosaurus*), and caution must be exercised when this character is considered alone.

The scapula of *Megaraptor* retained some primitive features (*e.g.*, scapular blade craniocaudally wide in respect to its proximodistal length, and proximal third fan-shaped) present in *Ceratosaurus* and basal tetanurines (*e.g.*, *Baryonyx* and possibly *Bahariasaurus*?). On the other hand, the slender scapulae are characteristics of the more restricted group Avetheropoda (or, using Sereno's taxonomy, Neotetanurae) no present in the Patagonian taxon. In other words, *Megaraptor* does not exhibit the tetanuran condition for the scapula (*e.g.*, strap-like scapular blade, long and slender, being at least four times longer than mid-shaft width). Besides, the coracoid exhibits tetanuran features such as the presence of a well developed posterior process, with a widely concave caudal notch.

The presence of a metacarpal IV indicates features more primitive than in derived tetanurans (*e.g.*, *Allosaurus*, coelurosaurs). Also the pubis, provided with a notably expanded proximal end, looks more primitive than in neotetanurans.

The suite of characters present in *Megaraptor* suggests that it separated from the main tetanuran clade before the origin of Neotetanurae (= Allosauroidea + Coelurosauria, *sensu* Sereno, 1999). The absence of features of the main theropod lineages (*e.g.*, Abelisauridae, Spinosauridae, Carcharodontosauridae, Allosauridae) emphasizes that it is representative of a theropod clade not identified before, which exhibits

a particularly interesting combination of a bulky construction of the body (as suggested by cervical vertebrae, proportions of scapulocoracoid, hands, pubis, metatarsal IV) with exceptional raptorial abilities in the hands.

No other predatory dinosaur other than *Megaraptor* was discovered to date showing elongate but powerful hands ending in enlarged and strongly compressed, trenchant claws. In this regard, spinosaurids may compete with the Patagonian taxon in the presence of powerful arms and developed ungual phalanges, but even in these theropods their hands are not enlarged to the extreme of *Megaraptor*.

Acknowledgments

References

Azuma, Y. and Currie, P.J. 2000. A new carnosaur (Dinosauria: Theropoda) from the Lower Cretaceous of Japan. *Canadian Journal of Earth Sciences* 37: 1735-1753.

Bonaparte, J.F. 1986. Les dinosaures (Carnosaures, Allosauridés, Sauropodes, Cétiosauridés) du Jurassique Moyen de Cerro Cóndor (Chubut, Argentine). *Annales de Paléontologie* (*Vert.-Invert.*) 72: 247-289.

Bonaparte, J.F.; Novas, F.E. and Coria, R. 1990. *Carnotaurus sastrei* Bonaparte, the horned, ligthly built carnosaur from the Middle Cretaceous of Patagonia. *Contribution in Science* 416: 1-41.

Britt, B.B. 1991. Theropods of Dry Mesa Quarry (Morrison Formation, Late Jurassic), Colorado, with emphasis on the osteology of *Torvosaurus tanneri*. *Brigham Young Geological Studies* 37: 1-72.

Calvo, J.O. 1991. Huellas de dinosaurios en la Formación Río Limay (Albiano-Cenomaniano), Picún Leufú, provincia del Neuquén, Argentina (Ornithischia-Saurischia-Sauropoda-Theropoda). *Ameghiniana* 28: 241-258.

Calvo, J. O. and Salgado, L. 1995. *Rebbachisaurus tessonei* sp. nov. A new Sauropoda from the Albian-Cenomanian of Argentina; new evidence on the origin of Diplodocidae. *Gaia* 11: 13-33.

Calvo, J.O., Porfiri, J.D. and Kellner, A.W.A. 2003. A close relative of *Unenlagia comahuense* (Theropoda, Maniraptora) from the Upper Cretaceous of Neuquén, Patagonia, Argentina. 18° Congreso Brasileiro de Paleontología (Brasilia, 2003): 82-83.

Cazau, L.B. and Uliana, M.A 1973. El Cretácico superior continental de la Cuenca Neuquina. *5° Congreso Geológico Argentino* (Villa Carlos Paz, 1972), *Actas* 3: 131-163.

Charig, A.J. and Milner, A.C. 1997. *Baryonyx walkieri*, a fish- eating dinosaur from the Wealden of Surrey. *Bulletin of the Natural History Museum*, *Geol. Ser.* 53: 11-70

Colbert, E.H. and Russell, D.A. 1969. The small Cretaceous dinosaur *Dromaeosaurus*. *American Museum Novitates* 2380: 1-19.

Currie, P.J. and Carpenter, K. 2000. A new specimen of *Acrocanthosaurus atokensis* (Theropoda, Dinosauria) from the Lower Cretaceous Antlers Formation (Lower Cretaceous, Aptian) of Oklahoma, USA. *Geodiversitas* 22 : 207-246.

Currie, P.J. and Zhao, X.-J. 1993. A new carnosaur (Dinosauria, Theropoda) from the Jurassic of Xinjiang, People´s Republic of China. *Canadian Journal of Earth Sciences* 30: 2037-2081.

Galton, P.M. and Jensen, J.A. 1979. A new large theropod dinosaur from the Upper Jurassic of Colorado. *Bringham Young Geological Studies.* 26: 1-12.

Gauthier, J. 1986. Saurischian monophyly and the origin of birds. In: K. Padian, (ed.), The origin of birds and the evolution of flight. *Memoirs of the California Academy of Sciences* 8: 1-55.

Harris, J.D. 1998. An analysis of *Acrocanthosaurus atokensis*, its phylogenetic status, and paleobiogeographic implications, based on a new specimen from Texas. New Mexico Museum of Natural History and Science, *Bulletin* 13: 1-75.

Leanza, H.A. 1999. The Jurassic and Cretaceous terrestrial beds from southern Neuquén Basin, Argentina. *Instituto Superior de Correlación Geológica, Miscelánea.* 4: 1-30.

Leanza, H.A. and Hugo, C.A. 2001. Cretaceous red beds from southern Neuquén Basin (Argentina): age, distribution and stratigraphic discontinuities. Asociación Paleontológica Argentina, Publicación Especial 7: 117-122.

Legarreta, L. and Gulisano, C. 1989. Análisis estratigráfico secuencial de la Cuenca Neuquina (Triásico Superior-Terciario Inferior). In: G. Chebli and L. Spalletti (eds.), Cuencas Sedimentarias Argentinas. *Universidad Nacional de Tucumán, Serie de Correlacion Geológica* 6: 221-243.

Madsen, J.H.Jr. 1976. *Allosaurus fragilis*: a revised Osteology. Utah *Geol. Survey Bull.* 109: 1-163.

Madsen, J.H. and Welles, S.P. 2000. Ceratosaurus (Dinosauria, Theropoda) a revised osteology. *Utah Geological Survey Miscellaneous Publication* 2: 1-80.

Marsh, O.C. 1881. Classification of the Dinosauria. *American Journal of Sciences* 23: 81-86.

Novas, F. 1998. *Megaraptor namunhuaiquii,* gen. et sp. nov., a large-clawed, late cretaceous theropod from Patagonia. *Journal of Vertebrate Paleontology* 18: 4-9.

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

Ostrom, J.H. 1969. Osteology of *Deinonychus antirrhopus*, an unusual theropod from the lower Cretaceous of Montana. *Peabody Museum of Natural History Bulletin* 30: 1-165.

Sereno, P.M. 1999. The evolution of dinosaurs. *Science* 284: 2137-2147.

Sereno, P.C., Duthiel, D.B., Larochene, M., Larsson, H.C.E., Lyon, G.H., Magwenw, P.M., Sidor, C.A., Varrichio, D.J., and Wilson, J.A. 1996. Predatory dinosaurs from the Sahara and the Later Cretaceous faunal differentiation. *Science* 272: 986-991.

Stromer, E. 1915. Wirbeltier- Reste der Baharije-Stufe (unterstes Cenoman). 3. Das Original Theropoden *Spinosaurus aegypticus* nov. gen. nov. esp. *Abhandlungen der Bayerischen Akademie der Wissenschaften,KI.* 28: 1-32.

Stromer, E. 1931. Ein skelett-Rest von *Carcharodontosaurus*. *Abhandlungen der Bayerischen Akademie der Wissenschaften*, N.F. 9: 1-23.

Stromer, E. 1934. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wusten Agyptens. II. Wirbeltierreste der Baharije-Stufe (unterstes Cenoman). 13. Dinosauria. *Abhandlungen der Bayerischen Akademie der Wissenschaften*, N.F 22: 5-79.

Uliana, M.A. y Dellapé, D.A. 1981. Estratigrafía y evolución paleoambiental de la sucesión Maastrichtiano-Eoterciaria del Engolfamiento Neuquino (Patagonia Septentrional). *8º Congreso Geológico Argentino* (San Luis, 1981), *Actas* 3: 673-711.

Welles, S.P. 1984. Dilophosaurus wetherilli (Dinosauria, Theropoda) osteology and comparisons. *Palaeontographica* A, 185: 85-180.