Humerus of a basal abelisauroid theropod from the Late Cretaceous of Patagonia

Fernando E. NOVAS\textsuperscript{1,2}, Martín D. EZCURRA\textsuperscript{1} & Federico L. AGNOLIN\textsuperscript{1}

\begin{flushleft}
\textsuperscript{1}Laboratorio de Anatomía Comparada y Evolución de los Vertebrados, Museo Argentino de Ciencias Naturales «Bernardino Rivadavia», Av. Angel Gallardo 470, Buenos Aires (1405), Argentina. \textsuperscript{2}CONICET, email: fernovas@yahoo.com.ar.
\end{flushleft}

\textbf{Abstract:} Here we describe a partial humerus of a medium-sized theropod dinosaur from the Upper Cretaceous (Late Turonian - Early Coniacian) Portezuelo Formation, Neuquén Province, Argentina. The humerus shares with Abelisauroida and Elaphrosauridae an articular head proximally oriented, and deltopectoral crest strongly reduced. The bone is referred to Abelisauroida on the basis of the following derived features: proximal tuberosity on caudal surface of humeral shaft, and greater tubercle at level with the medial tuberosity. The gracile morphology of the humerus, as well as the poor development of its medial tuberosity, resemble more \textit{Masiakasaurus} than the condition present in abelisaurids (e.g., \textit{Carnotaurus}, \textit{Aucasaurus}), in which the humerus is more robust and the medial tuberosity is prominent. Available information demonstrates that during deposition of the Portezuelo Formation large and bulky abelisaurids (e.g., \textit{Ekrixinatosaurus}) lived together with gracile and medium-sized abelisaurids.

\textbf{Key words:} Abelisauroida, Upper Cretaceous, Patagonia, Argentina.

Abelisaurids constitute a group of predatory dinosaurs that were highly diversified and widely dispersed in Gondwana during the Cretaceous (e.g., Bonaparte, 1986; Sereno et al., 2004). Abelisauroida is usually split into two clades (Bonaparte, 1991): the small to medium-sized noasaurids, including \textit{Noasaurus}, \textit{Masiakasaurus}, \textit{Laevischus} and \textit{Deltadromeus} (Carrano et al., 2002; Sereno et al., 2004), and the medium to large-sized abelisaurids represented, among others by \textit{Rugops}, \textit{Carnotaurus}, \textit{Abelisaurus}, \textit{Ekrixinatosaurus}, and \textit{Aucasaurus} (Bonaparte, 1985; Bonaparte & Novas, 1985; Bonaparte et al., 1990; Coria et al., 2002; Calvo et al., 2004a; Sereno et al., 2004).

The theropod record of the Upper Cretaceous Portezuelo Formation (Late Turonian-Early Coniacian; Leanza et al., 2004) currently consists of the abelisaurid \textit{Ekrixinatosaurus novasi} (Calvo et al., 2004a), the basal tetanuran \textit{Megaraptor namunhuaiquii} (Novas, 1998; Calvo et al., 2004b), the maniraptoran alvarezsaurid \textit{Patagonykus puertai} (Novas, 1997), two yet undescribed coelurosaurians (Coria & Currie, 2002; Porfiri et al., 2005), and the dromaeosaurid maniraptorans \textit{Unenlagia comahuenis} (Novas & Puerta, 1997), \textit{U. paynemili} (Calvo et al., 2005), and \textit{Neuquenraptor argentinus} (Novas & Pol, 2005). Here we describe a partial humerus that constitutes the first non-abelisaurid abelisauroid recorded in the Portezuelo Formation. This new find improves our knowledge of the humeral morphology of basal abelisaurids.

\section*{MATERIAL AND METHODS}

\textbf{Institutional abbreviations. MACN-CH, Museo Argentino de Ciencias Naturales "B. Rivadavia", Colección Chubut. MCF-PVPH, Museo Carmen Funes, Paleontología de Vertebrados, Plaza Huincul, Neuquén, Argentina.}

\textbf{Systematic nomenclature.} We follow Sereno et al. (2004) and Rauhut (2003), regarding the phylogenetic relationships of Abelisauridae within Ceratosauria. Abelisauroida was defined by Holtz (1994) as a stem-based clade that includes all theropods closer to \textit{Carnotaurus sastrei} than to \textit{Ceratosaurus nasicornis}, thus \textit{Elaphrosaurus bambergi} Janensch, 1920 and the specimen described here belong to this clade.

\section*{SYSTEMATIC PALEONTOLOGY}

\begin{center}
\begin{tabular}{l}
Theropoda Marsh, 1881  \\
Neotheropoda Bakker, 1986  \\
Ceratosauria Marsh, 1884  \\
Abelisauroida Bonaparte, 1991  \\
\textit{Genus et sp. indet.}
\end{tabular}
\end{center}

\textbf{Material.} MCF-PVPH 53, proximal half of a right humerus.
Fig. 1. MCF-PVPH 53 humerus. A) cranial, B) caudal, C) proximal, D) lateral, and E) medial views. Abbreviations: cd. coracobrachial depression, ct. caudal tuberosity dc. deltopectoral crest, gt. greater tubercle, hh. humeral head, mt. medial tuberosity. Scale bar 2 cm.

Fig. 3. Humeral proximal halves of several abelisauroids in caudal view. A) MCF-PVPH 53, B) *Masiakasaurus* (from Carrano et al., 2002), C) *Carnotaurus* (MACN-CH 894) and D) *Aucasaurus* (from Coria et al., 2002). Not to scale.

**Locality and horizon.** The material was collected at Sierra del Portezuelo, 20 km West from Plaza Huincul, Neuquén Province, Argentina, from levels corresponding to the Portezuelo Formation.

**Description.**

The preserved portion of humerus (Fig. 1) closely matches the morphology of the Malagasy abelisauroid *Masiakasaurus knopfleri* (Carrano et al., 2002), thus suggesting that the bone, as in this dinosaur, was long and slender when complete. On the basis of the maximum proximal width of humerus (5.1 cm), we estimate that the whole length of the bone was roughly 30 cm.

The humeral head is rounded and proximally inflated, resembling the basal ceratosaurian *Elaphrosaurus* (Galton, 1982) and the abelisauroids *Carnotaurus, Aucasaurus*, and *Masiakasaurus* (Figs. 2-4). This condition distinguishes MCF-PVPH 53 (together with the four taxa cited before) from the remaining theropods (e.g., *Syntarsus, Ceratosaurus, Allosaurus, Deinonychus*), in which the humeral head is kidned-shaped (in proximal view) and flattened (in cranial aspect). However, MCF-PVPH 53 has a humeral head that looks more plesiomorphic than *Carnotaurus and Masiakasaurus*, in being cranio-caudally more compressed than in the later two taxa (Fig. 4).

In MCF-PVPH 53 the greater tubercle is located on the proximolateral corner of humerus; it is reduced and located at level with the internal tuberosity, as it occurs in other abelisauroids (e.g., *Masiakasaurus, Aucasaurus, Carnotaurus*). This condition differs from that of basal theropods (e.g., *Syntarsus*), basal ceratosaurians (e.g., *Ceratosaurus*) and most tetanurans (e.g., *Allosaurus, Deinonychus*), in which the greater tubercle is more prominent and more proximally
located with respect to the internal tuberosity. In *Elaphrosaurus* the greater tubercle is weakly developed (as in abelisaurids), but it is located more proximally as in Theropoda ancestrally.

In MCF-PVPH 53 the internal tuberosity is highly reduced, as it occurs in *Masiakasaurus* and probably also in *Elaphrosaurus*. However, this condition is not uniformly present among abelisaurids because in abelisaurids (e.g., *Aucasaurus*, *Carnotaurus*) the internal tuberosity is prominent and conical-shaped (Fig. 2). A similar condition to that of Abelisauridae is present in most theropods, including *Herrerasaurus* (Sereno, 1993), coelophysoids (e.g., *Syntarsus*; Raath, 1977), *Dilophosaurus* (Welles, 1984), and basal tetanurans (e.g., *Allosaurus*, *Acrocanthosaurus*; Madsen, 1976; Currie & Carpenter, 2000).

On the cranial surface of humeral shaft, and immediately distal to the humeral head, a shallow sulcus is present, presumably for attachment of the acrocoracohumeral ligament (Baumel & Raikow, 1993). The shallow condition of this sulcus contrasts with the deep ligament groove present in *Carnotaurus* and *Masiakasaurus*. Congruently, the caudal surface of MCF-PVPH 53 is devoid of a sulcus below the humeral head, resembling *Masiakasaurus* but contrasting with *Carnotaurus* and *Aucasaurus*, in which a deep groove is present.

In MCF-PVPH 53 the deltopectoral crest is strongly reduced and triangular in side view, being transversely thick and cranially projected. This peculiar condition is shared with other abelisaurids (e.g., *Masiakasaurus*, *Carnotaurus*), albeit at least some of these features (i.e., deltopectoral crest reduced and triangular shaped) are also present in *Elaphrosaurus*. MCF-PVPH 53 differs from *Carnotaurus* in that in the latter the deltopectoral crest is even more reduced.

On the caudal surface of the humeral shaft, MCF-PVPH 53 bears a longitudinal and conspicuous tuberosity. On the caudolateral edge of the bone, a smaller and lesser developed second tuberosity is present. Thus, the caudal surface of the humerus exhibits a double prominence located almost at level with the proximal end of the deltopectoral crest. This caudal tuberosity is documented also in *Aucasaurus* and *Carnotaurus*. In *Masiakasaurus* a prominence is visible, but its double condition can not be discerned (Carrano et al., 2002; fig. 11). The condition in *Ceratosaurus* is inconclusive (Madsen & Welles, 2000), but in coelophysoids (e.g., *Syntarsus*, *Liliensternus*) and basal tetanurans (e.g., *Baryonyx*, *Torvosaurus*, *Allosaurus*, *Deinonychus*) this caudal tuberosity is lacking.

**CONCLUSIONS**

The humerus of abelisaurid theropods is well represented by *Carnotaurus* and *Aucasaurus*. The same bone, however, remains poorly known in non-abelisaurid abelisaurids, the main source of information being currently restricted to the nosaurid *Masiakasaurus* (Carrano et al., 2002; due to the highly fragmentary condition of the holotype specimen of *Deltadromeus* agilis Sereno et al., 1996, and the few available descriptions and illustrations of the forelimb bones, we did not include this taxon in the present analysis). The humerus here described adds some new data on forelimb morphology of this group of ceratosaurian theropods.

MCF-PVPH 53 is interpreted as belonging to an abelisaurid theropod, as supported by the presence of a proximally inflated humeral head, a reduced deltopectoral crest, greater tubercle located at level with medial tuberosity, and tuberosity on caudal surface of humeral shaft (all these features are present in *Elaphrosaurus*; O. Rauhut, pers. comm.). Additionally, the humerus described here is not assigned to Abelisauridae because it retained a strongly reduced medial tuberosity that contrasts with the well developed one of *Carnotaurus* and *Aucasaurus*. The condi-
tion of the humeral head in MCF-PVPH 53 looks more primitive than in Elaphrosaurus, Masiakasaurus, Aucasaurus and Carnotaurus, because the first one lacks a rounded humeral head (in proximal aspect), a greater tubercle that is clearly offset from the humeral head (O. Rauhut, pers. comm.), and a deep cranial ligament sulcus. In this context, MCF-PVPH 53 seems to be one of the most basal abelisaurids, even more basal than the Jurassic Elaphrosaurus. MCF-PVPH 53 opens a new panorama regarding to the radiations of basal members of Abelisauridea, where stem-abelisaurids survived until late Turonian-early Coniacian times, thus depicting a currently covered radiation of basal abelisaurids from Middle Jurassic times, at least (as it is indicated by Elaphrosaurus), up to the Late Cretaceous.

Among Abelisauridea two different kinds of humeri can be recognized: a plesiomorphic, gracile and elongate morphotype represented by Masiakasaurus and MCF-PVPH 53, and a shorter and stouter kind of humerus as present in abelisaurids (e.g., Aucasaurus and Carnotaurus). Curiously, they are reminiscent of the humerus of ornithimimosaurs and tyranosaurids, respectively, in which the deltopectoral crest is proxi-modistally reduced and subtriangular in side view (e.g., Gauthier, 1986; Rauhut, 2003). Moreover, in Tyrannosaurus (Brochu, 2002) the humeral head is also proximally inflated, resembling the condition present in abelisaurids.

The non-abelisaur abelisauroid condition of MCF-PVPH 53 indicates that during the deposition of the Portezuelo Formation two kinds of abelisaurid theropods co-existed. On the one hand, the large-sized and bulky abelisaurid Ekrixinatosaurus; on the other hand, a smaller and gracile basal abelisaurid (MCF-PVPH 53). Thus, the abelisaurid faunistic component of Portezuelo Formation resembles to that of other Cretaceous Gondwanan outcrops (e.g., India, Madagascar), which shows the simultaneous presence of large-sized abelisaurids (Indosuchus, India; Majungatholus, Madagascar) and smaller non-abelisaur abelisauroid theropods (Laevisuchus, India; Masiakasaurus, Madagascar).

ACKNOWLEDGEMENTS

The comments provided by O. Rauhut and S. Archangelsky are greatly appreciated, which improved the quality of the manuscript. Agustina Lecuona took some of the photographs that composed the figures of the present contribution. Rodolfo A. Coria lended the material under his care for study.

BIBLIOGRAPHY


Holtz, T. R. 1994. The phylogenetic position of the
Tyrannosauridae: implications for theropod systems-
- 2000. A new phylogeny of the carnivorous dino-
Janensch, W 1920. Ueber Elaphrosaurus bambergi und
die Megalosaurier aus den Tendaguru-Schichten
in: 225-235.
Leanza, H. A., S. Apesteguia, F. E. Novas & M. S. de la
Puente. 2004. Cretaceous terrestrial beds from the
Neuquén Basin (Argentina) and their tetrapod as-
osteology. Utah Geol. Min. Surv. Bull. 109: 1-
163.
(Dinosauria, Theropoda) a Revised Osteology. Mis-
cellaneous Pub. 00-2 Utah Geol. Surv.: 1-80.
(Theropoda, Avialae, Alvarezsauridae), from the
17: 137-166.
- 1998. Megaraptor namunhuaiquii gen. et. sp. nov.,
a large-clawed, Late Cretaceous Theropod from
Novas, F. E. & P Puerta. 1997. New evidence concern-
ing avian origins from the Late Cretaceous of

Novas, F. E. & D. Pol. 2005. New evidence of de-
inonychosaurian dinosaurs from Late Cretaceous
de un nuevo Theropodo del Cretácico Tardío en
Lago Barreales, Neuquén, Patagonia, Argentina.
Rauth, M. A. 1977. The anatomy of the Triassic theropods
Syntarsus rhodensiensis (Saurischia: Podokesauridae)
and a consideration of its biology. Ph. D. dissertation,
Rhodes University, Salisbury; 233 pp.
Rauhut, O. W. M. 2003. The interrelationships and ev-
olution of basal theropod dinosaurs. Special papers
Sereno, P. C. 1993. The pectoral girdle and forelimb of
the basal theropod Herrerasaurus ischigual-
Sereno, P. C., D. B. Dutheil, M. Iarochene, H. C. E.
Larsson, G. H. Lyon, P. M. Magwene, C. A. Sidor,
D. J. Varricchio & J. A. Wilson. 1996. Predatory di-
nosaur from the Sahara and Late Cretaceous
dinosaurs link landmasses in the Mid-Cretaceous.
Welles, S. P. 1984. Dilophosaurus wetherilli (Dinosauria,
Theropoda): osteology and comparisons. Palaeon-
tagraphica Abteilung A 185: 85-180.

Recibido: 30-IX-2005
Aceptado: 15-VI-2006