

Juvenile specimen of *Megaraptor* (Dinosauria, Theropoda) sheds light about tyrannosauroid radiation

Juan D. Porfiri^a, Fernando E. Novas^{b, c, *}, Jorge O. Calvo^a, Federico L. Agnolín^{b, d},
Martín D. Ezcurra^e, Ignacio A. Cerda^{c, f}

^a Centro Paleontológico Lago Barreales (CePaLB), Ruta Provincial 51, km. 65, Cátedra de Introducción a la Paleontología, Universidad Nacional del Comahue, Neuquén, Argentina

^b Laboratorio de Anatomía Comparada y Evolución de los Vertebrados, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Av. Ángel Gallardo 470 (C1405DJR), Buenos Aires, Argentina

^c CONICET, Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina

^d Fundación de Historia Natural “Félix de Azara”, Universidad Maimónides, Hidalgo 775 (C1405BDB), Buenos Aires, Argentina

^e School of Geography, Earth and Environmental Sciences, University of Birmingham, Birmingham, United Kingdom

^f Instituto de Investigación en Paleobiología y Geología, Universidad Nacional de Río Negro, Museo Carlos Ameghino, Belgrano 1700, Paraje Pichi Ruca (predio Marabunta), Cipolletti 8300, Río Negro, Argentina

ARTICLE INFO

Article history:

Received 26 July 2013

Accepted in revised form 9 April 2014

Available online 21 June 2014

Keywords:

Megaraptor
Coelurosauria
Tyrannosauroidae
Patagonia

ABSTRACT

Megaraptorids are a group of predatory dinosaurs that inhabited Gondwana from Cenomanian to Santonian times (Late Cretaceous). Phylogenetic relationships of megaraptorids have been matter of recent debate, being alternatively interpreted as basal coelurosaurs, carcharodontosaurian allosauroids, megalosauroids, and basal tyrannosauroids. One of the main reasons for such different interpretations is the incomplete nature of most available megaraptorid skeletons and, in particular, the scarce information about their cranial anatomy. Here we describe a partially preserved skeleton of a juvenile specimen of *Megaraptor namunhuaiquii* that provides substantial new information about the cranial morphology of this Patagonian taxon. The specimen comes from the Upper Cretaceous (Turonian–Coniacian) of the Portezuelo Formation, northwestern Patagonia, Argentina. The anatomy of the new specimen bolsters the recently proposed hypothesis that megaraptorids are nested within Coelurosauria, and possibly within Tyrannosauroidae. The most relevant features that megaraptorans share with tyrannosauroids include several foramina on the premaxillary body, extremely long and straight prenasal process of the premaxilla, incisiform premaxillary teeth with a D-shaped cross-section, and cranially expanded supratemporal fossae separated from each other by a sharp sagittal median crest on frontals, which was presumably extended caudally above the parietals (not preserved). Information gathered from the present specimen allows to make for the first time a reconstruction of the skull of *Megaraptor* and hypothesize about evolutionary trends within Tyrannosauroidae.

© 2014 Elsevier Ltd. All rights reserved.

1. Introduction

The main Cretaceous theropod dinosaur clades from South America include abelisauroids, carcharodontosaurids, alvarezsaurids and unenlagiids (Bonaparte, 1991, 1996; Novas, 1997, 2009; Martinelli et al., 2013; Novas et al., 2013). However, increasing

discoveries in the last decade demonstrate that megaraptorans constituted a diversified and relatively abundant clade of large predatory dinosaurs (Novas, 1998, 2009; Calvo et al., 2004; Benson et al., 2010; Novas et al., 2013). Basal megaraptorans are recorded from Barremian rocks of Japan (Benson et al., 2010), but more derived members of the clade (i.e., Megaraptoridae *sensu* Novas et al., 2013) are known from Cenomanian to Santonian beds of Gondwana (i.e., South America, Africa and Australia; Novas, 1998, 2009; Calvo et al., 2004; Lamanna et al., 2004; Novas et al., 2008, 2013; Sereno et al., 2008; Smith et al., 2008; Hocknull et al., 2009; Benson et al., 2012b; White et al., 2013). Megaraptorids are characterized by the formidable development of their manual claws on digits I and II and the transversely compressed and ventrally sharp

* Corresponding author. Laboratorio de Anatomía Comparada y Evolución de los Vertebrados, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Av. Ángel Gallardo 470 (C1405DJR), Buenos Aires, Argentina.

E-mail addresses: jporfiri@yahoo.com (J.D. Porfiri), fernovas@yahoo.com.ar, fedeagnolin@yahoo.com.ar (F.E. Novas), jcalvo40@yahoo.com.ar (J.O. Calvo), fedeagnolin@yahoo.com.ar (F.L. Agnolín), martindezcurra@yahoo.com.ar (M.D. Ezcurra).

ungual of the first manual digit (Calvo et al., 2004; Novas et al., 2013). Phylogenetic relationships of megaraptorans have been the focus of recent debate. Megaraptorans have been alternatively interpreted as basal coelurosaurians (Novas, 1998), basal tetanurans (Calvo et al., 2004; Smith et al., 2008), and allosauroids closely related with carcharodontosaurids (Smith et al., 2007; Benson et al., 2010; Carrano et al., 2012). However, recent evidence has been presented in favour of their inclusion within Coelurosauria, and possibly as basal members of Tyrannosauroidae (Novas et al., 2013).

We describe here a new, juvenile specimen of *Megaraptor namunhuaiquii* that is represented by a partial skull and post-cranium (MUCPv 595). This specimen offers for the first time information about the cranial anatomy of *Megaraptor* and of the snout and braincase of megaraptorans. The new discovery also amplifies the knowledge of the vertebral anatomy of megaraptorans. The skull material conforms a primary source of information for both coelurosaurian and tyrannosauroid features of Megaraptoridae, unavailable in previous studies.

Institutional abbreviations. MCF-PVPH, Museo Carmen Funes, Plaza Huincul, Neuquén, Argentina; MUCPv, Museo de la Universidad Nacional del Comahue, Paleontología de Vertebrados, Neuquén, Argentina; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China.

2. Materials and methods

2.1. Phylogenetic analysis

The cladistic analysis conducted here on theropod higher-level relationships is based on a modified version of the data matrix published by Novas et al. (2013). The resulting data matrix includes most characters traditionally used to diagnose Allosauroidae, Carcharodontosauridae, Coelurosauria, and Tyrannosauroidae. Sources of these features include the following papers: Zheng et al. (2009), Benson et al. (2010), Brusatte et al. (2010a,b), and Li et al. (2010). The original data set of Novas et al. (2013) included 287 characters, fewer than those of Benson et al. (2010) and Brusatte et al. (2010a,b), because several characters of these data matrices (focused on the relationships within Megalosauroidae, Tyrannosauridae and derived coelurosaurs) were uninformative for the taxon sampling we focused, and therefore were deleted. The data matrix of Novas et al. (2013) was enriched with the addition of new data for *Megaraptor namunhuaiquii* based on the new specimen MUCPv 595 (Appendix A). We removed from Novas et al. (2013) data matrix characters 255, 271, and 285, because they are redundant with other characters of the same data set. In addition, some character states were rescored. The data matrix we employ here was analysed under equally-weighted parsimony using TNT 1.1 (Goloboff et al., 2008). A heuristic search of 50 replications of Wagner trees (with random addition sequence) followed by TBR branch-swapping algorithm (holding 10 trees per replicate) was performed. The best trees obtained at the end of the replicates were subjected to a final round of TBR branch swapping. Zero length branches among any of the recovered MPTs were collapsed (rule 1 of Coddington and Scharff, 1994). Characters 2, 4, 6, 13, 15, 17, 27, 69, 106, 148, 155, 158, 160, 167, 169, 171, 179, 181, 194, 195, 205, 208, 217, 233, 241, 259, 267, 271 were treated as additive (=ordered). As measures of tree support, decay indices (=Bremer supports) were calculated and a bootstrap resampling analysis, with 10,000 pseudoreplicates, was performed reporting both absolute and GC (i.e. difference between the frequency that the original group and the most frequent contradictory group are recovered in the pseudoreplicates) frequencies. A second round of decay indices was calculated after the *a posteriori* pruning of the fragmentary taxa

Carcharodontosaurus iguidensis, *Orkoraptor*, *Eotyrannus*, *Chilantaisaurus*, *Kileskus*, *Eocarcharia* and *Santanaraptor*.

2.2. Palaeohistological analysis

Palaeohistological samples of the scapula and pubis were obtained to assess the ontogenetic age of MUCPv 595, MUCPv 1353, and MUCPv 341. We use girdle bones (scapula and pubis) because these are the only repeated bones in the three studied specimens (but MUCPv 1353 lacks scapulae). Samples from the scapula were obtained in the anterior portion of the scapular blade. In the case of the pubis, the sections were taken from the proximal portion of the shaft. Thin sections were prepared for each element using standard palaeohistological techniques, and examined with light microscopy (Chinsamy and Raath, 1992). Age at death was assessed from annual growth marks (annuli and/or lines of arrested growth or LAGs) (Erickson, 2005). Nomenclature and definitions of structures used in this study are derived from Francillon-Vieillot et al. (1990) and Chinsamy-Turan (2005). A detailed description of the analysis and description of the palaeohistological sections are provided in Appendix C.

3. Systematic palaeontology

Theropoda Marsh, 1881

Tetanurae Gauthier, 1986

Coelurosauria Huene, 1920

Tyrannosauroidae Osborn, 1905

Megaraptora Benson et al., 2010

Megaraptoridae Novas et al., 2013

Megaraptor namunhuaiquii Novas, 1998

3.1. Referred specimen

MUCPv 595 consists of an incomplete skeleton including premaxillae and maxillae with some teeth, nasals, left frontal, and partial braincase, articulated sequence of 9 cervicals (including axis), and dorsals 1–8 (with most of their articulated ribs), dorsals 10–12, sacals 3–5, plus four isolated proximal caudals, most of the gastral basket, both scapulae, left coracoid, both humeri, and both partial pubes.

3.2. Locality and horizon

MUCPv 595 was collected from the Baal quarry, north shore of the Barreales Lake, 15 km from Añelo, Neuquén Province, NW Patagonia, Argentina (38°32'44" S, 68°51'34" W) (Fig. 1). The fossil-bearing level belongs to the top of the Turonian–Coniacian (Late Cretaceous) Portezuelo Formation of the Neuquén Group (Calvo et al., 2007). MUCPv 595 comes from the same fossil locality and similar stratigraphic levels as specimen MUCPv 341 of *Megaraptor namunhuaiquii* (Calvo et al., 2004).

3.3. Taxonomic assignment of MUCPv 595

MUCPv 595 exhibits the following combination of characters that allow assignment to megaraptorids: *Orkoraptor*-like teeth (i.e., teeth with low and strongly distally curved crown, with unserrated mesial carina, and both sides of the tooth concave defining an 8-shaped contour in cross-section; see Novas et al., 2008), proximal end of scapular blade cranially expanded, and continuous with a proximodistally low acromial process (as in *Megaraptor* and *Aerosteon*), proximal pubis robust and showing a well developed pubic tubercle representing a convexity on the cranial margin of the bone (as in *Megaraptor* and *Aerosteon*), cervical vertebrae with strongly

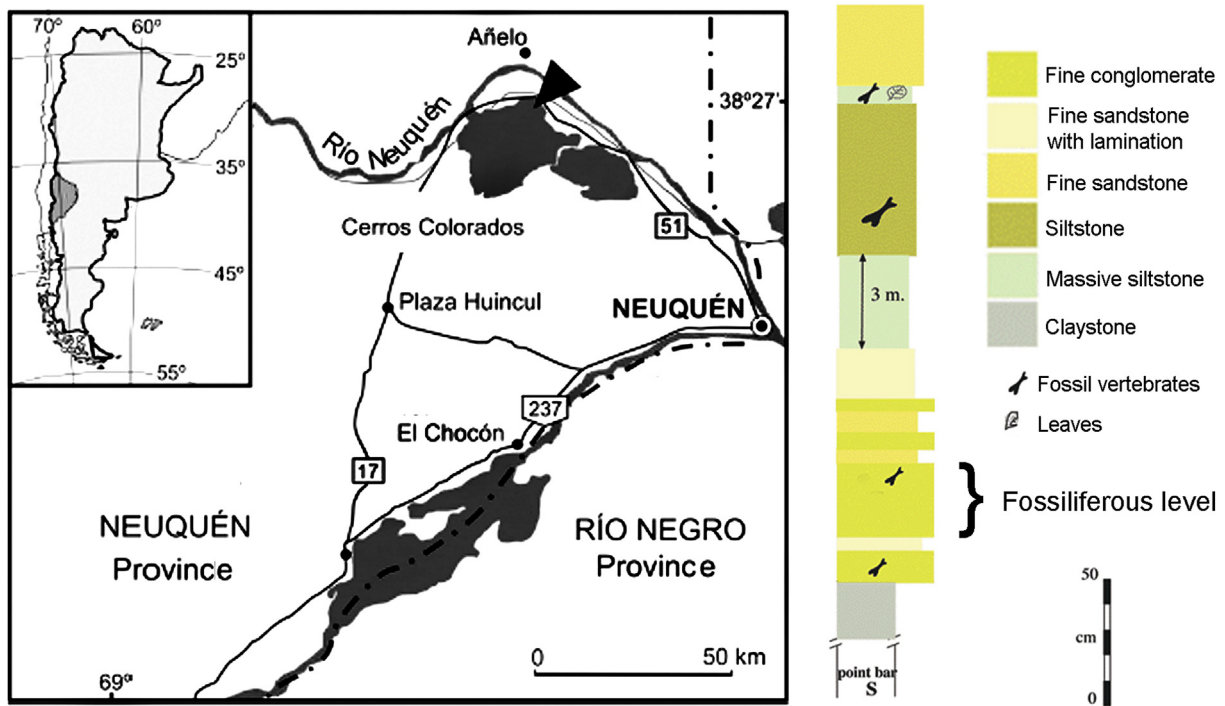


Fig. 1. Location of the fossiliferous Baar Quarry (indicated by a black arrow), and the Fossiliferous levels of the upper section of the Portezuelo Formation indicated at left (modified from Calvo et al., 2007; Passalia et al., 2008).

opisthocoelous centra, elliptical pleurocoels each divided by a transverse septum, well-developed and sharp prezygoepipophyseal laminae, and well-developed and rod-like epiphyses, resembling in all these respects *Megaraptor* (Calvo et al., 2004); cervical vertebrae 2–8 without a longitudinal keel (longitudinal keel present in *Aerosteon*; Sereno et al., 2008); dorsal vertebrae similar to *Aerosteon* in having large double pneumatic foramina, and a pneumatic canal within the transverse process (see Sereno et al., 2008) (unknown condition in *Megaraptor*). Available bone morphology of MUCPv 595 is consistent with bigger specimens of the coeval species *Megaraptor namunhuaiquii* and the latter combination of features is uniquely shared between MUCPv 595 and *Megaraptor*.

The only main difference that we note consists on body size: for example, scapula of MUCPv 595 measures 19.8 cm in total length, representing 44.6% the size of the same bone of adult *M. namunhuaiquii* MUCPv 341, which is 44.3 cm long. We estimate the whole body length of MUCPv 595 in 3 m, based on the proportions of *Allosaurus* (Madsen, 1976), contrasting with larger specimens of *Megaraptor namunhuaiquii* (e.g., MCF-PVPH 79) with an estimated body length of 9–10 m (Novas, 1998). In our view, these size distinctions mirror different ontogenetical stages for the above cited specimens of *M. namunhuaiquii*. The juvenile nature of MUCPv 595 is not only supported by its absolute size, but also for the lack of fusion of several bone elements (e.g., neural arches and their corresponding centra, scapula and coracoid, occipital condyle detached from the braincase), and by the unfinished conditions of distal extremities of both humeri and pubes, and cranial articular surfaces of cervical centra. Moreover, comparative histological analysis of MUCPv 595 with larger individuals of *M. namunhuaiquii* (i.e., MUCPv 341 and 1353) reveals that, according with its smaller size, specimen MUCPv 595 represents an earlier ontogenetic stage. The amount of secondary remodeling and number of lines of arrested growth (LAGs) present in MUCPv 595 are clearly lesser than in other examined specimens (see below). Accordingly, all this evidence leads to consider MUCPv 595 as a juvenile specimen of *Megaraptor namunhuaiquii*.

4. Description

The present description of MUCPv 595 is focused on the cranial anatomy of the specimen because a detailed description of the postcranial skeleton will be presented elsewhere (J.D. Porfiri in prep.). Skull bones of megaraptorids were unknown up to now, with exception of the postorbital, quadratojugal and possible partial coronoid of *Orkoraptor* (Novas et al., 2008), the postorbital and quadrate of *Aerosteon* (Sereno et al., 2008), and the dentary of *Australovenator* (Hocknull et al., 2009). MUCPv 595 preserves both premaxillae, maxillae, nasals, left frontal, and partial braincase and, as a result, provides substantial new information about the cranial anatomy of megaraptorids. The juvenile condition of the *Megaraptor* specimen MUCPv 595 may influence skull proportions and degree of development of cranial rugosities, as it was already recognized in other theropod dinosaurs (McNamara and Long, 2012). However, although the juvenile nature of the specimen described here, important morphological differences are noticed when it is compared with adult specimens of basal tetanurans (mainly allosauroids) and notable similarities are present with basal tyrannosauroids and, even, some basal tyrannosaurids.

The premaxilla of *Megaraptor* (Fig. 2) is proportionally small and its external surface is pitted by several large foramina, as occurs in most tyrannosauroids (Carr and Williamson, 2010). The base of the prenarial process (=ascending process for the nasal) possesses a pair of large foramina, as it also occurs in a variety of theropods, including the allosauroids *Sinraptor*, *Neovenator*, some specimens of *Allosaurus* and *Acrocanthosaurus* (Eddy and Clarke, 2011) and tyrannosauroids such as *Kileskus*, *Raptorex*, and other tyrannosauroids (Sereno et al., 2009; Averianov et al., 2010).

The prenarial process is rod-like and extremely elongated anteroposteriorly, representing at least 300% of the length of the main body of the bone. As a result, the external naris should have been elliptical and extremely anteroposteriorly long, as also occurs in *Kileskus*, *Proceratosaurus*, *Dilong*, *Ornitholestes*, and *Guanlong* (Averianov et al., 2010; Rauhut et al., 2010; Xu et al., 2004, 2006).

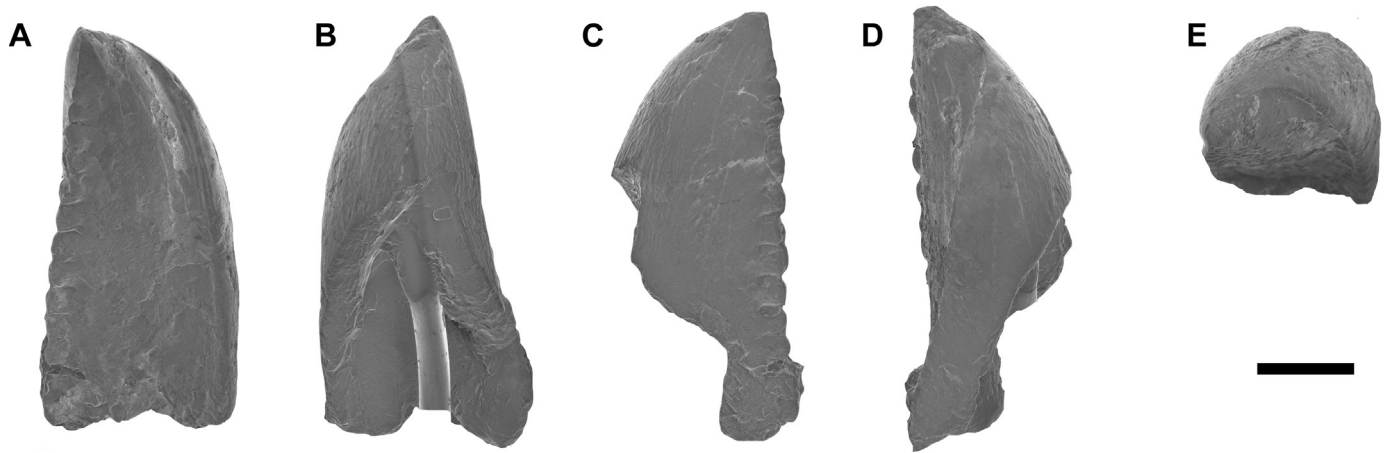


Fig. 2. Right third premaxillary tooth of *Megaraptor namunhuaiquii* (MUCPv 595) in (A) caudal, (B) rostral, (C) mesial, (D) distal, and (E) apical views. Scale bar: 1 mm.

In ventral view (Fig. 2D), both articulated premaxillae form a transversely wide and rounded arcade, different from the V-shaped and rostrally acute premaxillae of *Neovenator* (Brusatte et al., 2008) but similar to *Allosaurus* (Madsen, 1976) and *Sinraptor* (Currie and Zhao, 1993). The right premaxilla preserves the first three dental alveoli plus the rostral half of the fourth one. Notably, the third alveolus is smaller than the remaining ones, in which its diameter is half the size of the first and second alveoli. The left premaxilla preserves the walls of the first three alveoli and a portion of the fourth one. Evidence at hand supports that *Megaraptor* had four tooth positions on each premaxilla. The rostral margin of premaxilla is anterodorsally inclined. The caudal end is obliquely inclined posterodorsally, thus allowing to reconstruct a trapezoidal contour for the premaxilla in lateral view. In other words, the premaxilla is more abbreviated ventrally than on the narial margin. This trapezoidal contour resembles *Proceratosaurus*, *Guanlong*, *Dilong*, as well as some derived tyrannosaurids (e.g., *Tyrannosaurus*, *Tarbosaurus*; Tsuihiji et al., 2011). The premaxilla of *Megaraptor* differs from that of allosauroids (e.g., *Neovenator* and *Acrocanthosaurus*; Currie and Carpenter, 2000; Eddy and Clarke, 2011), because they lack a trapezoidal contour, and the rostral margin is caudodorsally inclined (Brusatte and Sereno, 2008). The premaxillary body of *Megaraptor* is proportionally small (in both dorsoventral height and rostrocaudal length) with respect to the length of the maxilla, representing approximately 0.7% the length of the maxilla. In this respect, *Megaraptor* sharply differs from allosauroids (e.g., *Sinraptor*; *Allosaurus*, *Neovenator*; *Acrocanthosaurus*; Rauhut, 2003; Brusatte et al., 2008; Currie and Carpenter, 2000) in which the premaxilla is larger, representing more than 11% the length of maxilla. The basal tyrannosauroid *Guanlong* presents a prominent and enlarged premaxilla (Xu et al., 2006), but this bone is invariably shorter in more derived members of the clade. Among tyrannosauroids, *Proceratosaurus* (Rauhut et al., 2010), *Dilong* (IVPP V14243), *Kileskus* (Averianov et al., 2010), and derived tyrannosaurids (e.g., *Tyrannosaurus*, *Tarbosaurus*; Brochu, 2002; Tsuihiji et al., 2011) possess, as in *Megaraptor*, a short premaxilla, representing 0.7–0.5% of the length of the maxilla.

The maxilla (Figs. 3 and 4) is subtriangular in side view, with a dorsoventrally low and strongly anteroposteriorly elongated rostral ramus with an almost straight dorsal margin. This condition clearly departs from basal tetanurans (e.g., megalosauroids, *Allosaurus*, *Neovenator*), basal coelurosaurids (compsognathids; but see *Sinocalliopteryx*; Ji et al., 2007), and basal tyrannosauroids (i.e., *Proceratosaurus*, *Dilong*, *Guanlong*, *Sinotyrannus*; Rauhut et al., 2010; Xu et al., 2004, 2006; Ji et al., 2009; Brusatte et al., 2012), in which

the rostral ramus is considerably shorter and the dorsal margin is deeply notched. The maxilla of *Megaraptor* resembles *Sinraptor* (Currie and Zhao, 1993) and carcharodontosaurids (e.g., *Acrocanthosaurus*, *Shaochilong*, *Carcharodontosaurus*; Currie and Carpenter, 2000; Brusatte et al., 2010a) in that the dorsal margin of maxilla is straight, but it is different from these theropods in the considerable rostrocaudal extension of the anterior ramus of maxilla. In this regard, *Megaraptor* resembles closely to ornithomimids, troodontids, unenlagiids, and tyrannosauroids more derived than *Xiongguanlong* (Li et al., 2010). The lateral surface of maxilla of *Megaraptor* lacks ornamentation, but possesses several nutrient foramina aligned with each other and situated immediately dorsal to the alveolar margin. The antorbital fossa is deep and well developed onto the lateral surfaces of both dorsal and caudal processes of maxilla, resembling the condition present in most tetanurans (Witmer, 1997), but contrasting with derived carcharodontosaurids, in which the antorbital fossa is much more reduced (Sereno et al., 1996). The length of the antorbital fossa anteriorly to the antorbital fenestra represents approximately 22% of the total length of the antorbital fossa. This ratio departs from the coelurosaurian condition, in which the value is approximately 40%, but resembles that observed in non-coelurosaurian tetanurans (see Rauhut, 2003).

The antorbital fossa is perforated by a pair of openings located at approximately the same anteroposterior level, being one above the other. Their margins are not well preserved and, as a result, their shapes cannot be confidently determined. At least the dorsal fenestra opens internally into the maxillary antrum. We assume that the dorsal one is the maxillary fenestra, and the ventral one may represent the promaxillary foramen. The disposition of these fenestrations differs from other theropods (e.g., *Acrocanthosaurus*, *Alioramus*, *Tyrannosaurus*, *Tarbosaurus*; Eddy and Clarke, 2011; Brusatte et al., 2012; Brochu, 2002; Tsuihiji et al., 2011), in which a large maxillary fenestra perforates the wall of the antorbital fossa and a smaller promaxillary fenestra is located rostrally to the former one. The basal allosauroid *Sinraptor* (Currie and Zhao, 1993) exhibits several fenestrae perforating the ascending ramus of maxilla, but the number and location of them do not agree with that described for *Megaraptor*. The unusual disposition of the pair of fenestrae in *Megaraptor* (superficially resembling that illustrated for the basal ornithomimid *Garudimimus*; Kobayashi and Barsbold, 2005), may constitutes an autapomorphic trait of the Patagonian taxon.

The medial surface of the maxilla (Figs. 3 and 4C) possesses a prominent longitudinal shelf situated adjacent to the dorsal margin of the interdental plates and ends rostrally in the palatal process.

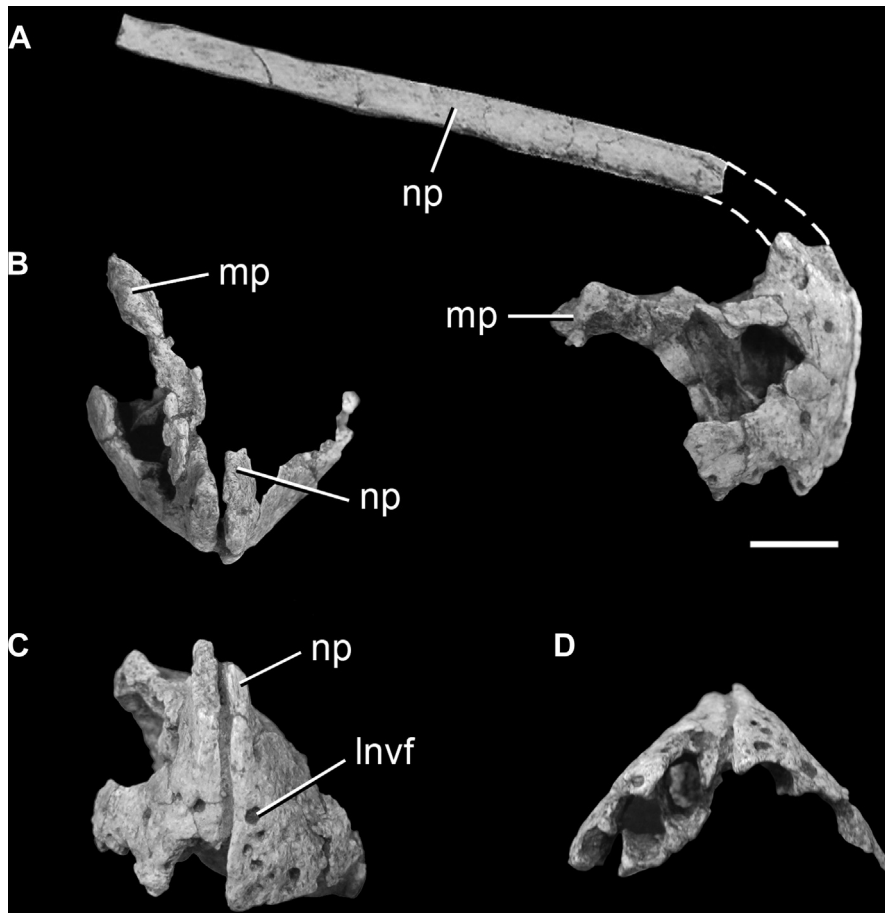


Fig. 3. Premaxillae of *Megaraptor namunhuaiquii* (MUCPv 595) in (A) right lateral, (B) dorsal, (C) anterior, and (D) ventral views. Abbreviations: Invf, large neurovascular foramen; mp, maxillary process; np, premaxillary process. Scale bar equals 1 cm.

The palatal process is slender, resembling *Alioramus* and *Kileskus* (Averianov et al., 2010; Brusatte et al., 2012), but different from the most robust condition present in *Allosaurus*, *Sinraptor*, *Mapusaurus*, and *Neovenator* (Madsen, 1976; Currie and Zhao, 1993; Coria and Currie, 2006; Brusatte et al., 2008), which may be associated with the larger and stouter premaxillae that characterize these forms. A curious aspect of the medial maxillary shelf is that it bifurcates caudally, creating a horizontal V-shaped margin that forms a deeply excavated caudal antrum, which almost surely opened rostrally into the main maxillary antrum, a condition similar to tyrannosaurids and allosauroids, such as *Sinraptor* and *Acrocanthosaurus* (Eddy and Clarke, 2011). However, a deeply incised margin of this caudal antrum seems autapomorphic for *Megaraptor*. A wide epiantral recess is present, as it occurs in *Alioramus* and other tyrannosaurids, as well as the allosauroids *Acrocanthosaurus* and *Sinraptor* (Witmer, 1997; Eddy and Clarke, 2011; Brusatte et al., 2012). The roof and the medial wall of the maxillary antrum seem to be collapsed and, as a result, no information is available about the internal fenestration of the maxilla. However, the antorbital fossa is devoid of fenestrations perforating the maxilla into the pillar to open medially, a condition resembling that of basal, non-tetanuran theropods (e.g., megalosauroids; Benson, 2010).

The portion of the maxilla that is ventral to the medial maxillary shelf is shallower than in most allosauroids, being slightly deeper than in the tyrannosauroid *Alioramus* (Brusatte et al., 2012). *Megaraptor* differs from allosauroids more derived than *Sinraptor* (Brusatte and Sereno, 2008) in that the interdental plates are unfused. The interdental plates are almost uniform in size and, most

important, proportionally small, being anteroposteriorly short and dorsoventrally tall, intermediate in size between those of *Sinraptor* and *Alioramus*. In other words, *Megaraptor* lacks the large interdental plates that characterize allosauroids more derived than *Sinraptor* (Brusatte and Sereno, 2008).

The dorsal ramus of maxilla is posterodorsally oriented and forms a sharp angle with the caudal process of maxilla. The dorsal ramus is low and slender, with a dorsal groove for the articulation with the rostral ramus of the lacrimal.

The nasals of *Megaraptor* are paired and unfused (Fig. 5E, F). They are very elongate anteroposteriorly and their transverse width is roughly uniform through their length, as in *Acrocanthosaurus*, *Carcharodontosaurus*, ornithomimids, troodontids, dromaeosaurids and birds (Rauhut, 2003). *Megaraptor* differs from *Neovenator* in that in the latter one the nasals bear a rugose dorsolateral ridge separating the dorsal and lateral surfaces, and a large pneumatopore on the antorbital fossa (Brusatte et al., 2008). The nasals of *Megaraptor* do not exhibit particular similarities with tyrannosaurids, in which they are fused in the midline, possess extensive rugosities and foramina, and are transversely wide immediately behind the external nares (Brochu, 2002; Li et al., 2010; Brusatte et al., 2012). It is worth to mention that the probably lack of fusion in the nasals may be due to the juvenile condition of the available specimen.

The rostrordorsal (=premaxillary) process is broken in both nasals, but it is expected that it was anteriorly projected to contact the premaxilla. The rostroventral process bounds the posteroventral border of the external naris, forming a sharp angle with the rostrordorsal process. There are no signs of a narial fossa on the anterior

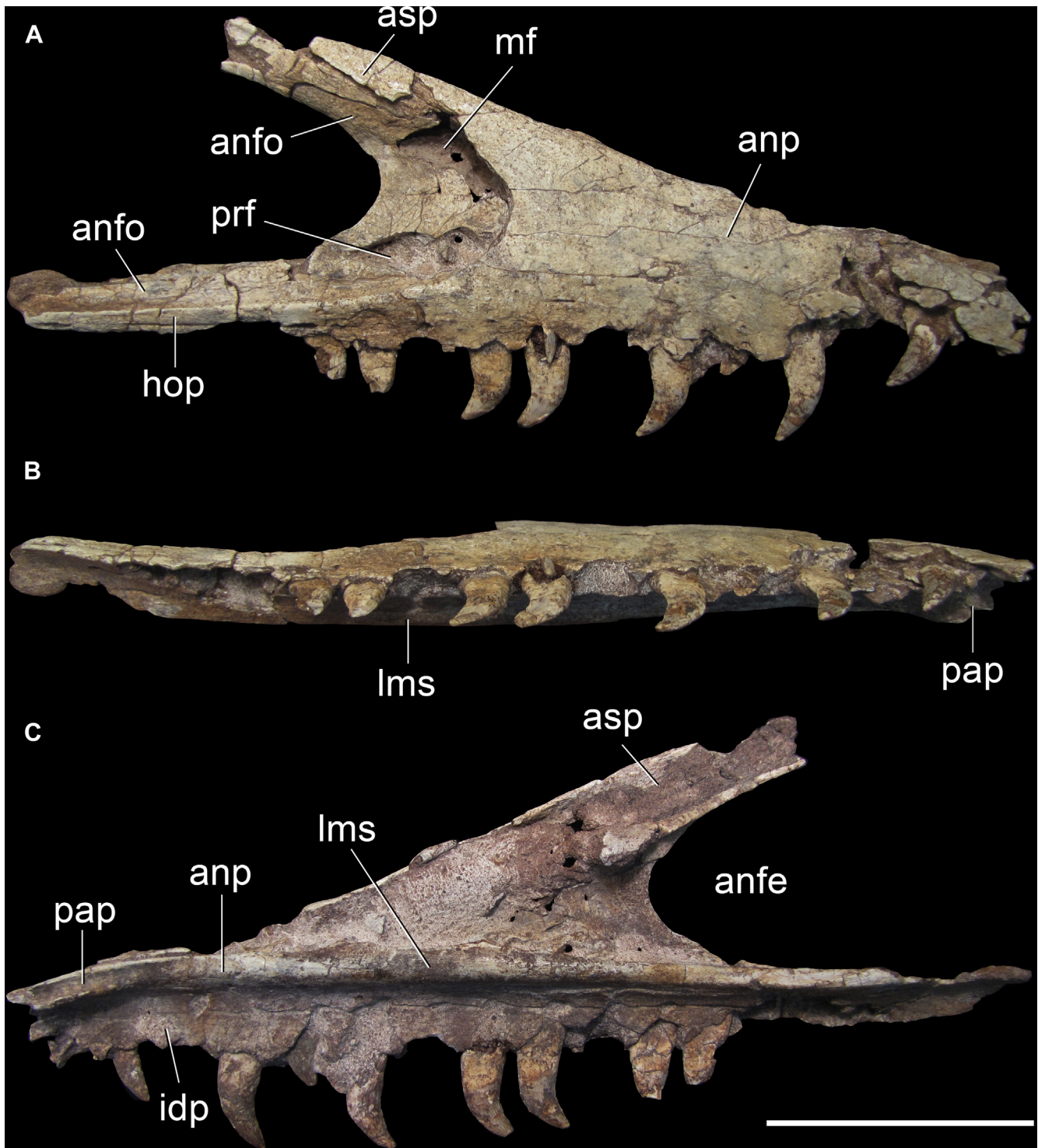


Fig. 4. Right maxilla of *Megaraptor namunhuaiquii* (MUCPv 595) in (A) lateral, (B) ventral, and (C) medial views. Abbreviations: anfe, antorbital fenestra; anfo, antorbital fossa; anp, anterior process; asp, ascending process; hop, horizontal process; idp, interdental plates; lms, longitudinal medial shelf; mf, maxillary fenestra; pap, palatal process; prf, premaxillary foramen. Scale bar equals 3 cm.

end of the nasal, contrasting with the wide and deep fossa present in basal allosauroids (e.g., *Sinraptor*, *Neovenator*, *Acrocanthosaurus*; Currie and Zhao, 1993; Brusatte et al., 2008; Eddy and Clarke, 2011). The nasals of *Megaraptor* lack the rugosities along the lateral edge of the bone that characteristically occur in allosauroids and other basal tetanurans (e.g., *Torvosaurus*, *Baryonyx*, *Allosaurus*, *Carcharodontosaurus*, *Dilong*; Holtz et al., 2004). However, it cannot be ruled out that the absence of such rugosities might be a result of

the juvenile condition of MUCPv 595. Some small foramina pierce some regions of the dorsal surface of the nasals. A triplet of small openings is present at level of the rostral end of the groove for articulation with the lacrimal. The ventral margin of the nasal does not exhibit the system of pneumatic cavities that characterize some basal tetanurans (e.g., *Monolophosaurus*, *Allosaurus*, *Sinraptor*, *Mapusaurus*; Rauhut, 2003; Coria and Currie, 2006) and basal tyrannosauroids (e.g., *Dilong*; IVPP V14243). Moreover, in

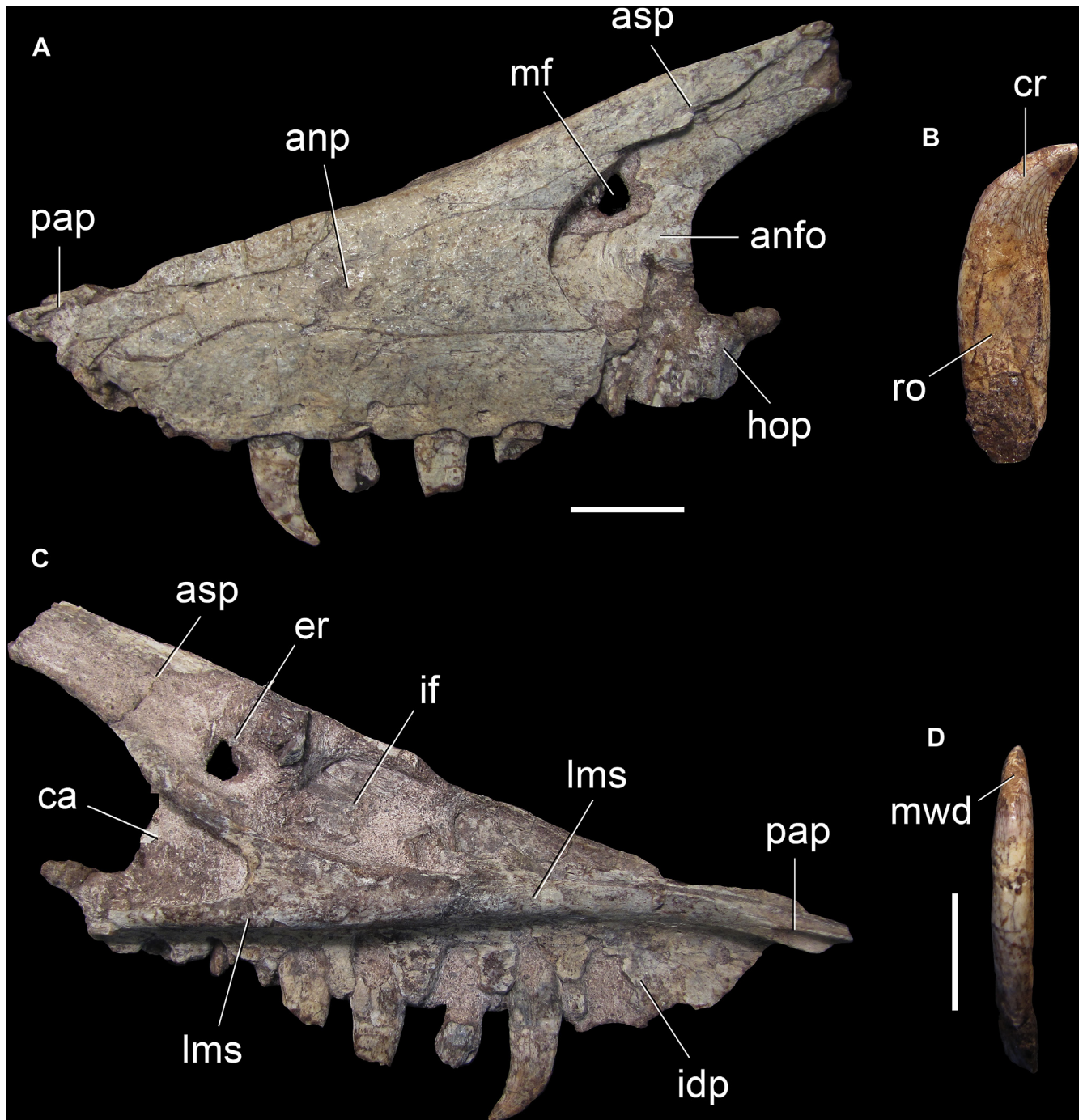


Fig. 5. Left maxilla (A, C) and isolated tooth (B, D) of *Megaraptor namunhuaiquii* (MUCPv 595) in (A) lateral, (B) side, (C) medial, and (D) mesial views. Abbreviations: anfo, antorbital fossa; anp, anterior process; asp, ascending process; ca, caudal antrum; cr, crown; er, epiantral recess; hop, horizontal process; idp, interdental plate; if, internal fenestration of maxilla; lms, longitudinal medial shelf; mwd, mesial margin without denticles; pap, palatal process; prf, promaxillary foramen; ro, root. Scale bars equal 2 cm in (A, C) and 1 cm in (B, D).

Megaraptor the antorbital fossa does not expand onto the nasals, contrasting with basal tetanurans (e.g., *Monolophosaurus*, *Sinraptor*, *Allosaurus*, *Neovenator*, *Carcharodontosaurus*; [Rauhut, 2003](#)). However, the nasal of *Megaraptor* is similar to *Acrocanthosaurus* in the lacking of a system of pneumatic cavities, and that the antorbital fossa does not extend onto the nasals ([Eddy and Clarke, 2011](#)). Lacking antorbital fossa participation in the nasals may be a generalized basal coelurosaurian feature present in *Guanlong*, *Eotyrannus*, and *Tyrannosaurus*, as for example ([Brochu, 2002](#); [Xu et al., 2006](#)).

The nasal exhibits a notch for articulation with the lacrimal on the caudolateral margin of the bone. The best fit for nasal-maxilla articulation locates the rostroventral process of the nasal immediately in front of the level of the antorbital fossa, a condition sharply different from most theropods, in which the rostral end of the nasal is close to the level of the rostral end of the maxilla. This position of the nasal with respect to the maxilla produces an extremely anteroposteriorly elongated and caudally expanded external naris. This caudal retraction of the nasal opening is in congruence with the notable caudal projection of the prenasal process of the premaxilla.

Thus, most of the ventral border of the external naris is formed by the maxilla.

The frontal (Fig. 5A–D) is quadrangular in dorsal view. The supratemporal fossa extends widely onto the dorsal surface of the frontal, being rostrally bounded by a strong and curved ridge. This ridge should have met that of the opposite frontal, forming a sagittal crest extending over the caudal half of the bones. The latter also indicates that a transversely narrow sagittal crest was present along the parietal bones (not preserved). This set of features closely resembles the condition present in tyrannosauroids (e.g., *Dilong*, *Guanlong*, *Raptorex*, *Tyrannosaurus*; IVPP V14243, V14531; Brochu, 2002; Sereno et al., 2009), and *Zuolong*, and contrast with that of allosauroids, in which the anterior extension of the supratemporal fossa onto the frontals is modest and the sagittal crest is transversely broad (e.g., *Allosaurus*, *Sinraptor*; Madsen, 1976; Currie and Zhao, 1993). Notably, the caudal half of the frontal of *Megaraptor* occupies a higher position with respect to the rostral portion of the bone, thus defining a conspicuous step on the dorsal surface of the skull roof, which separates a higher temporal region from the shallower snout in lateral profile. This condition may constitute an autapomorphy of *Megaraptor*. The ventral surface of the frontal possesses the natural moulds of the nasolacrimal duct and olfactory bulbs, which transversely duplicate the outer portion corresponding to the orbital roof. This proportion contrasts with that of allosauroids (e.g., *Sinraptor*, *Eocarcharia*; Paulina Carabajal and Currie, 2012; Sereno and Brusatte, 2008), in which the endocranial cavity is much more narrower than the orbital portion of the frontal.

A partial braincase (Fig. 6) preserves the supraoccipital, both otoccipitals (=exoccipital + opisthotic), left prootic, basioccipital and basisphenoid. The supraoccipital is strongly anterodorsally oriented, similar to that of *Alioramus* (Brusatte et al., 2012; Bever et al., 2013) and *Giganotosaurus* (Coria and Currie, 2002). A transversely thin median sagittal ridge is present on the supraoccipital and reaches the ventral margin of the bone, resembling the condition present in basal coelurosaurs, as exemplified by *Alioramus* (Bever et al., 2013). In *Giganotosaurus* the supraoccipital ridge is considerably transversely broader (Coria and Currie, 2002), and in the case of *Acrocanthosaurus* the supraoccipital bears two robust processes on its posterior surface (Eddy and Clarke, 2011). In contrast to *Megaraptor*, in allosauroids such as *Giganotosaurus* and *Acrocanthosaurus* the supraoccipital forms a robust, tall and dorsoventrally exposed surface (Eddy and Clarke, 2011). The supraoccipital forms a broad part of the dorsal border of the foramen magnum, its contribution to the opening is restricted by short dorsomedial extensions of the otoccipitals. The foramen magnum is relatively large (although its size depends on the ontogenetic stage of the individual), and deeply excavates the base of the neck of the occipital condyle. This contrast with the condition of more basal theropods in which the foramen is relatively small, and slightly (e.g., *Acrocanthosaurus*, *Sinraptor*) or do not excavates (e.g., megalosauroids) the base of the occipital neck (Bakker et al., 1992). The paraoccipital processes project posterolaterally and horizontally as occurs in most theropods (e.g., *Herrerasaurus*, *Majungasaurus*, *Tyrannosauridae*; Bakker et al., 1988; Sereno and Novas, 1993; Sampson and Witmer, 2007), and are not downturned as characteristically occurs among allosauroids (e.g., *Allosaurus*, *Acrocanthosaurus*, *Giganotosaurus*; Novas et al., 2005). The dorsal surface of the left paraoccipital process possesses a distinct facet for articulation with the caudolateral flange of the parietal (Fig. 6: paf). The crista tuberalis is subtriangular, tapering ventrally, and well ventrally extended (Fig. 6: ct). The latter structure delimits laterally the paracondylar fossa (Fig. 6: pcf), which housed the exits of the subcondylar recess, hypoglossal canal and vagal canal (Bever et al., 2013). A deep and triangular fossa is present immediately below the occipital condyle (Fig. 6: vpne) (absent in both *Allosaurus* and

Acrocanthosaurus; Madsen, 1976; Currie and Carpenter, 2000), and well developed excavations are present on both sides of the occipital condyle, bearing several pneumatic pockets of different shape and depth (Fig. 6: lpne). Pneumatic cavities also exist in the basal allosauroid *Sinraptor* (Currie and Zhao, 1993), although they are restricted to the boundaries of the occipital condyle, thus being different from the much more extended and deeper depressions present in *Megaraptor*. In this regard, *Megaraptor* resembles tyrannosauroids (e.g., “*Nanotyrannus*”, “*Gorgosaurus*”, *Daspletosaurus*, *Alioramus*; Bakker et al., 1988; Currie, 2003; Bever et al., 2013). The braincase surface below the occipital condyle is dorsoventrally low and rather simple, contrasting with the dorsoventrally deep and complex topography present in allosauroids such as *Acrocanthosaurus* (Eddy and Clarke, 2011). The basal tubera are dorsoventrally tall and connected with each other by a very tall intertuberal lamina. In side view, the basal tubera are nearly vertically oriented, a condition that contrast with the strongly posteriorly oriented tubera present in *Acrocanthosaurus* and *Sinraptor* (Paulina Carabajal and Currie, 2012; Eddy and Clarke, 2011). In posterior view, the intertuberal lamina shows a distal concavity correlated with the basisphenoidal recess, a condition shared with *Sinraptor* (Currie and Zhao, 1993), but absent in *Acrocanthosaurus* (Eddy and Clarke, 2011). The width between both basal tubera considerably exceeds that of the base of the foramen magnum. The basisphenoid contributes to the anterior portion of the basal tubera. The intertuberal lamina delimits posteriorly a very deep and funnel-shaped basisphenoid recess (Fig. 6: bsr), as it occurs in carcharodontosauroids (e.g., *Acrocanthosaurus*, *Carcharodontosaurus*; Bakker et al., 1988; Eddy and Clarke, 2011) and in tyrannosauroids (Bakker et al., 1988; Carr and Williamson, 2010). The basisphenoid recess bears a pair of slit-like excavations (Fig. 6: sle) separated from each other by a median longitudinal ridge, similar to those described for some tyrannosauroids, such as *Albertosaurus*, *Tyrannosaurus*, and some specimens of “*Gorgosaurus*”, (Bakker et al., 1988). In *Acrocanthosaurus* and *Sinraptor* the basisphenoid recess is also separated by a longitudinal ridge, but in this case, the ridge is restricted to the bottom of the recess (Paulina Carabajal and Currie, 2012; Eddy and Clarke, 2011), contrasting with the condition in *Megaraptor* and tyrannosauroids in which this lamina totally separates the recess. The basiptyergoid processes are not preserved. The caudal process of the prootic contributes to the anterior surface of the base of the paraoccipital process. The otic recess and probably the caudal tympanic recess are present immediately below the caudal process of the prootic on the very base of the anterior surface of the paraoccipital process. The prootic and laterosphenoid delimit a large, subcircular prootic fenestra for the exits of the cranial nerves V_{2/3} and VII_{pal} (Bever et al., 2013). Caudoventrally to the prootic fenestra there is a pair of openings that are interpreted as the rostral tympanic recess.

The upper dental arcade is composed of at least four premaxillary and 15 (presumably 17) maxillary tooth positions. Premaxillary teeth are small (crown height 10 mm), forming an incisiform anterior row and contrasting with the higher maxillary tooth crowns (17 mm). Premaxillary teeth are conical, but with a flattened caudal surface flanked by both mesial and caudal carinae, thus conferring a D-shaped contour in cross-section, due in part to a rotated mesial carina (Fig. 7), as characteristically occurs in tyrannosauroids (Brochu, 2002; Choiniere et al., 2012). The distal carina possesses chisel-like denticles with a density of 3 denticles per mm. The denticles lack blood grooves. Interestingly, the fourth premaxillary alveolus is half the diameter of the third and second alveoli, suggesting that the fourth premaxillary tooth was smaller in size than more anterior teeth. Among coelurosaurs, premaxillary D-shaped teeth are absent in *Tanycolagreus*, *Compsognathus*, *Huaxiagnathus*, and dromaeosaurids, being present in tyrannosauroids, including *Dilong*, *Guanlong*, *Eotyrannus*, and *Tyrannosauridae* (Senter, 2007), and also the

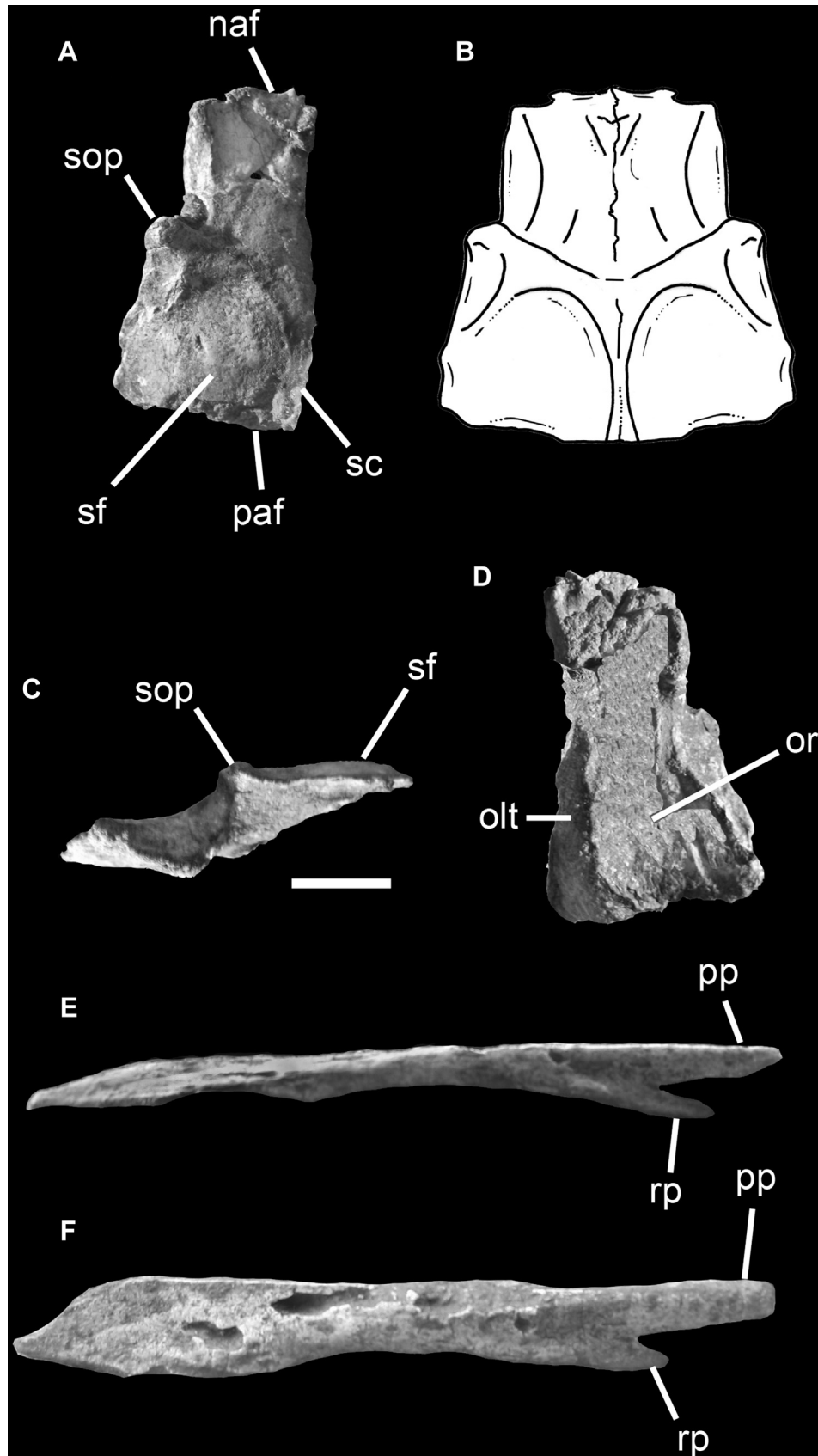


Fig. 6. Left frontal (A, C–D), reconstructed frontals (B), and right nasal (E, F) of *Megaraptor namunhuaiquii* (MUCPv 595) in (A, B, F) dorsal, (D) ventral, (C, E), and lateral views. Abbreviations: na, nasal articulation; pa, parietal articulation; pp, premaxillary process; rp, rostroventral process; sc, sagittal crest; sf, supratemporal fossa; sop, supraorbital process. Scale bar equals 2 cm.

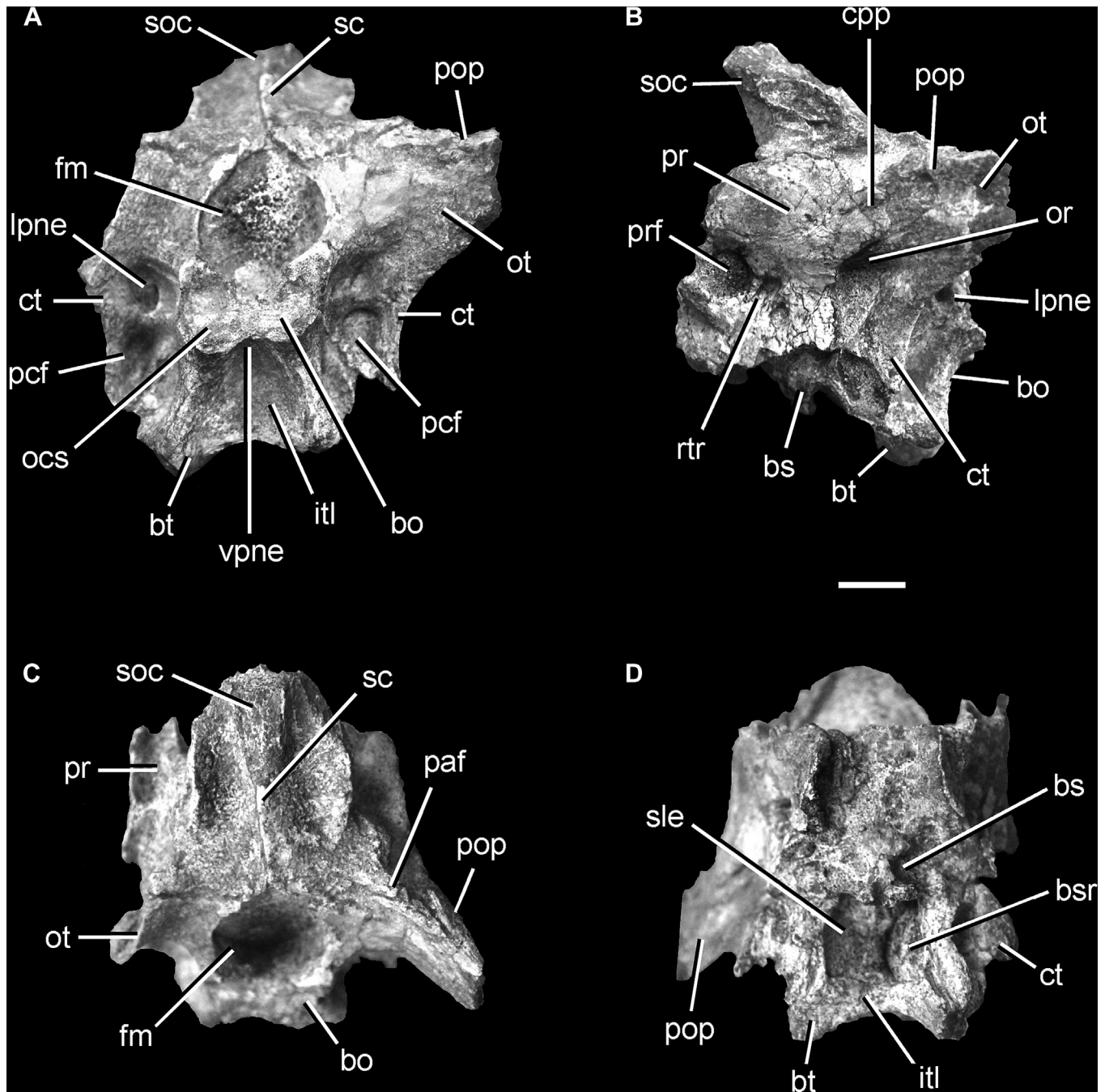


Fig. 7. Partial braincase of *Megaraptor namunhuaiquii* (MUCPv 595) in (A) posterior, (B) left lateral, (C) dorsal, and (D) ventral views. Abbreviations: bo, basioccipital; bs, basisphenoid; bsr, basisphenoid recess; bt, basal tuber; cpp, caudal process of prootic; ct, crista tuberalis; fm, foramen magnum; itl, intertubular lamina (connecting basal tubera with each other); lpne, lateral pneumatic excavation on basioccipital; ocs, occipital condyle scar; or, otic recess; ot, otoccipital; paf, parietal facet; pcf, paracondylar fossa; pop, paraoccipital process; pr, prootic; prf, prootic fossa (housing exits of CN V_{2/3} and VII_{pal}); rtr, rostral tympanic recess; sc, sagittal crest; sle, slit-like excavation; soc, supraoccipital; vpne, ventral pneumatic excavation on basioccipital. Scale bar equals 1 cm.

basal coelurosaurs *Ornitholestes* and *Zuolong* (S. Brusatte, pers. com.). Premaxillary teeth much smaller than the maxillary teeth are present in *Dilong*, *Guanlong*, *Eotyrannus*, tyrannosaurids, *Tanycolagreus*, *Huaxiagnathus*, the troodontids *Byronosaurus*, *Saurornithoides* and *Sinovenator*, and some dromaeosaurids, such as *Bambiraptor* and *Sinornithosaurus* (Holtz et al., 2004; Senter, 2007). By contrast, the premaxillary teeth are proportionately large in most other coelurosaurs, including the basal taxa *Ornitholestes*, *Sinosauropteryx* and *Compsognathus* (Senter, 2007).

The dentition of *Megaraptor* exhibits several features that depart from the dental morphology present in allosauroids. On the other

hand, the morphology present in *Megaraptor* approaches the condition of tyrannosauroids, namely heterodonty resulting from incisiform “D”-shaped premaxillary teeth much smaller than maxillary teeth, and maxillary (and dentary) teeth with curved and robust crowns associated with enlarged 8-shaped roots in cross-section. As noted elsewhere (Novas et al., 2008), the teeth of the megaraptoran *Orkoraptor* possess features resembling dromaeosaurids, as it also was recognized for *Proceratosaurus* (Rauhut et al., 2010). These taxa exhibit recurved teeth devoid of mesial denticles (see Rauhut and Werner, 1995) and 8-shaped in cross-section (Norell et al., 2006; Rauhut et al., 2010; Gianechini et al., 2011),

and the latter feature is also present in some tyrannosauroids (e.g., *Proceratosaurus*; Carr in [Rauhut et al., 2010](#)).

The neck of *Megaraptor* (Fig. 8A, B) is composed of 10 cervicals (axis plus 9 postaxial cervical vertebrae). Cervical ribs are short, only slightly overlapping the subsequent vertebra. Cervical 10 still retains an elongated and slender rib, contrasting with the extremely robust rib of D1. A pair of elliptical pleurocoels are present above the cervical parapophyses, in which the dorsal one is the largest. A similar condition is also present in adult *Megaraptor* and *Aerosteon* ([Benson et al., 2010](#)). A pair of pleurocoels separated by an oblique septum similar in position and morphology to that present in cervical vertebrae have been recorded in all of the preserved dorsals, a condition shared with *Aerosteon* ([Sereno et al., 2008](#)). Preserved sacra (probably sacra 3–5) and proximal caudals, exhibit a single but large pleurocoel, as also occurs in other megaraptorids (e.g., *Orkoraptor*, *Aerosteon*; [Novas et al., 2008](#); [Benson et al., 2010](#)). Double cervical pleurocoels is a feature that *Megaraptor* shares with *Neovenator* and carcharodontosaurids ([Brusatte et al., 2008](#); [Benson et al., 2010](#)), and pleurocoelous caudals have been also reported in carcharodontosaurids (e.g., *Acrocanthosaurus*; [Harris, 1998](#)) and oviraptorosaurs ([Rauhut, 2003](#)).

Megaraptorid pneumatic foramina in the centrum of cervical, dorsal and sacral vertebrae resembles carcharodontosaurids, such as *Giganotosaurus* and *Mapusaurus* ([Coria and Currie, 2006](#)), and coelurosaurs including tyrannosaurids, oviraptorids, therizinosauroids, and dromaeosaurids, being absent in the basal taxa *Dilong*, *Tanycolagreus*, *Coelurus*, *Ornitholestes*, *Compsognathus* and *Sino-sauropteryx* ([Senter, 2007](#); [Benson et al., 2012a,b](#)).

Cervical centra are opisthocoelous and most of them are ventrally flat, excepting for Cv9 which bears a longitudinal keel. In this respect *Megaraptor* differs from *Aerosteon riocoloradensis* (MCNA-PV-3137) in which most of the available cervicals bear a broad and flat ventral keel. The hemispherical cranial articular surface of the cervical centra resemble those of *Monolophosaurus*, *Allosaurus*, *Sinraptor*, *Acrocanthosaurus*, *Torvosaurus*, spinosaurids, and the basal coelurosaurs *Compsognathus* and *Ornitholestes* ([Rauhut, 2003](#)), whereas the cervical centra are slightly biconcave in tyrannosaurids, *Sino-sauropteryx*, *Scipionyx* and *Coelurus*, among other coelurosaurs ([Currie and Chen, 2001](#); [Dal Sasso and Maganuco, 2011](#); [Carpenter et al., 2005](#)). Hemispherical cranial articular surface of centrum is present at least up to Cv9 (the centrum of Cv10 is lost), and D1 exhibits a flat cranial articular surface. The internal structure of the cervical centra belongs to the camellate kind ([Britt, 1993](#)), although the camella vary notably in absolute size depending on the location and depth at which the sample is taken (Fig. 9). The eroded surfaces of the parapophyses, cranial articular surface of the centrum, and external rims of the caudal articular cups are made by small, thin-walls chambers. By contrast, the internal structure inside the centrum consist of a small number of larger cavities, which roughly quadruplicate the size more peripheral camellae.

The neural spine of the axis is tall, transversely narrow, and craniocaudally expanded, with a convex dorsal margin, similar to those of *Raptorex* and *Scipionyx* ([Sereno et al., 2009](#); [Dal Sasso and Maganuco, 2011](#)). By contrast, in basal tetanurans (e.g., *Monolophosaurus*, *Piatnitzkysaurus*, *Allosaurus*, *Sinraptor*) and derived

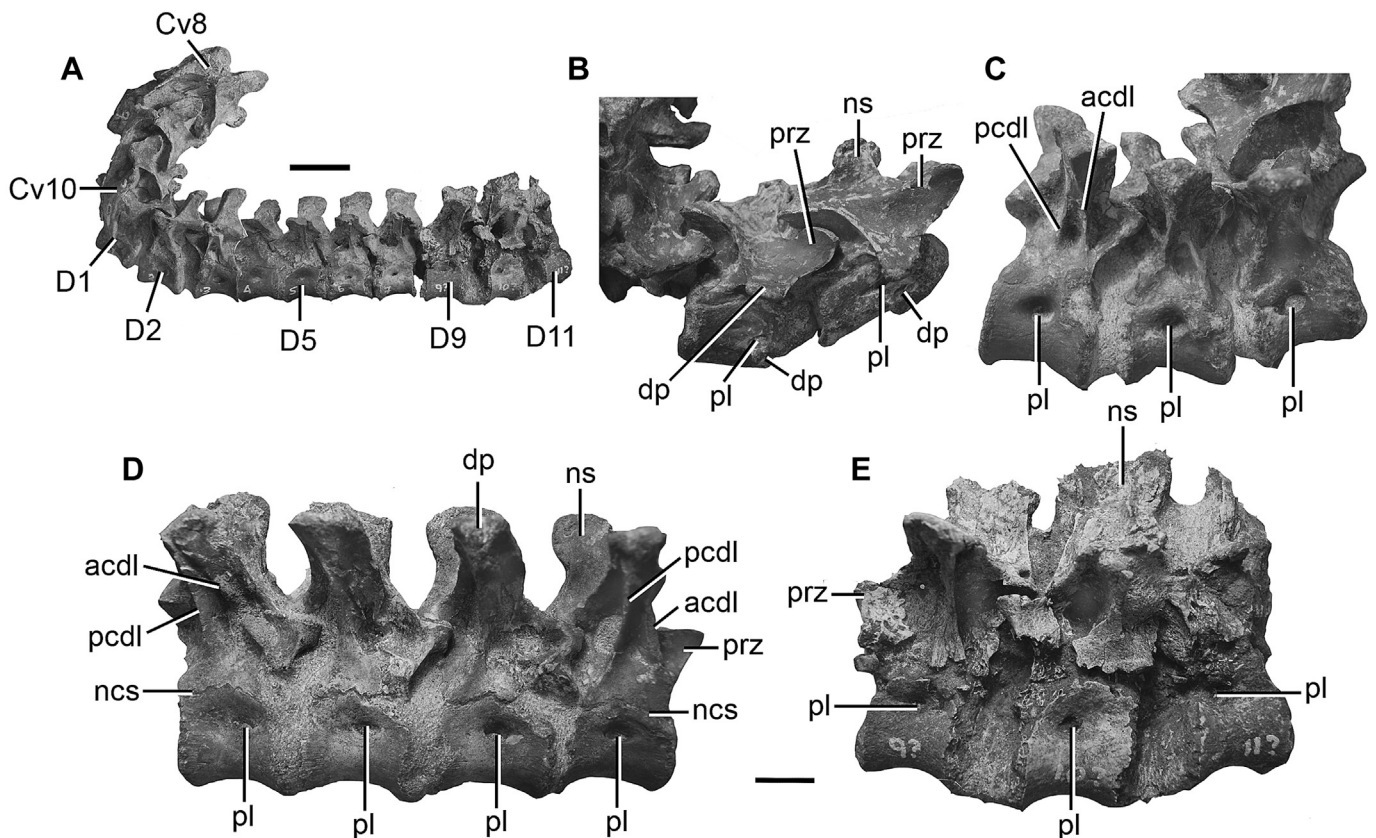


Fig. 8. Partial presacral vertebral column of *Megaraptor namunhuaiquii* (MUCPV 595). (A) Three last cervical and first to eleventh dorsal vertebrae (missing the eighth dorsal vertebra) in left lateral view; (B) two last cervical vertebrae in right lateral view; (C) first three dorsal vertebrae in right lateral view; (D) fourth to seventh dorsal vertebrae in right lateral view; (E) ninth to eleventh dorsal vertebrae in left lateral view. Abbreviations: acdl, anterior centrodiapophyseal lamina; Cv8, 10, eighth and tenth cervical vertebrae, respectively; D1, 2, 5, 9 and 11, first, second, fifth, ninth and eleventh dorsal vertebrae, respectively; dp, diapophysis; ncs, neurocentral suture; ns, neural spine; pcdl, posterior centrodiapophyseal lamina; pl, pleurocoel; prz, prezygapophysis. Scale bars equal 5 cm in (A) and 2 cm in (B–E).

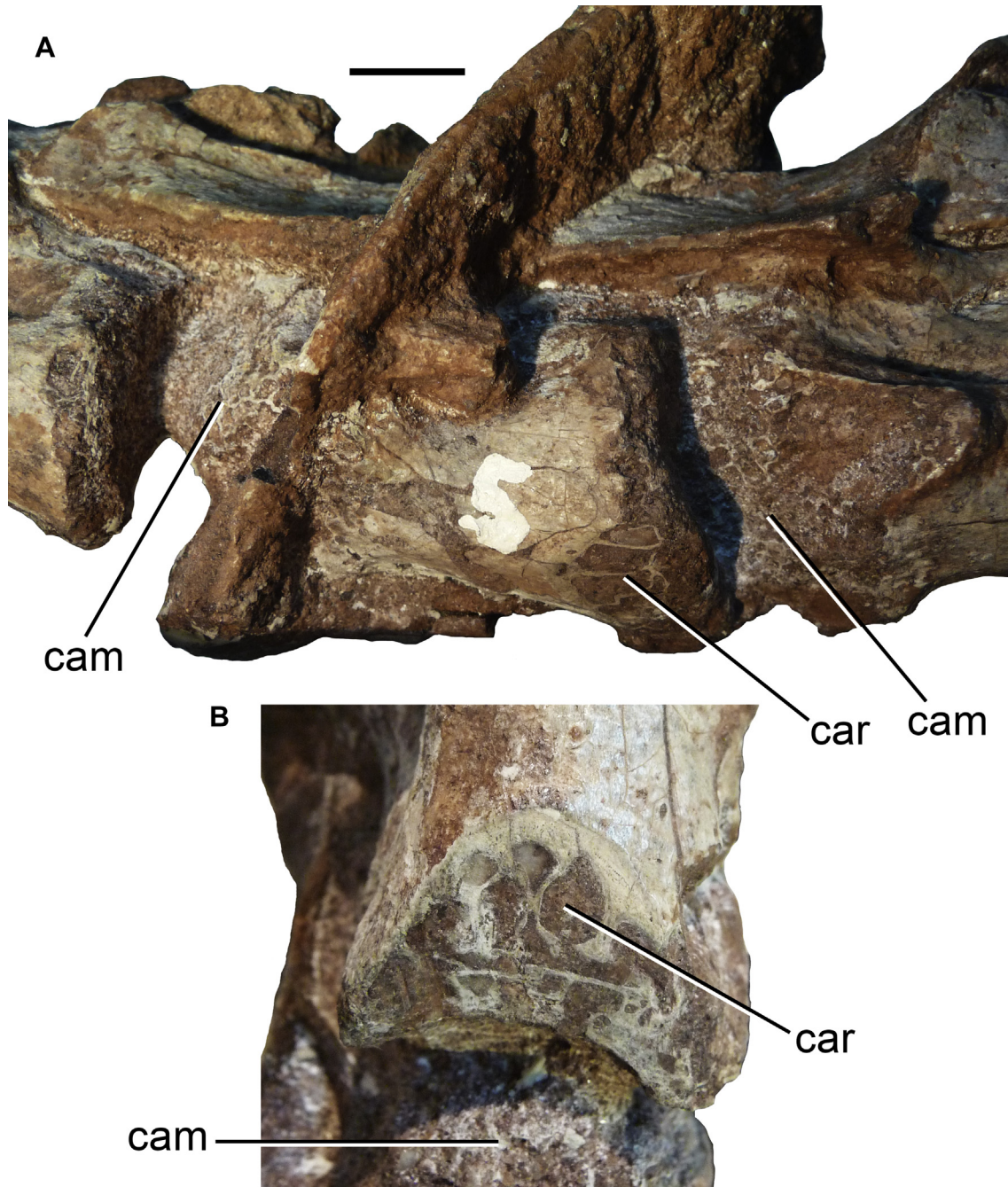


Fig. 9. Postcranial axial pneumaticity of *Megaraptor namunhuaiquii* (MUCPv 595). (A) Fifth and sixth cervical vertebrae in left lateral view and (B) posterior end of the sixth cervical centrum in ventral view. Abbreviations: car, camerate internal structure; cam, camellate internal structure. Scale bar equals 1 cm in (A) and (B) not to scale.

tyrannosaurids (e.g., *Tyrannosaurus*, *Tarbosaurus*; Maleev, 1974; Brochu, 2002) the neural spine is craniocaudally short. The depth and anteroposterior extension of the neural spine gradually decreases towards more posterior cervicals. On Cv3 the neural spine is tall and craniocaudally short (different from *Allosaurus*, which is craniocaudally extended; Madsen, 1976), cervicals 4 and 5 bear square-shaped neural spines (similar to *Allosaurus*), and cervicals 6–8 are craniocaudally short and dorsoventrally low (different from *Neovenator* and *Allosaurus*, in which they are dorsoventrally deep; Madsen, 1976; Brusatte et al., 2010a). On the contrary, in derived tyrannosaurids, such as *Tyrannosaurus* (Brochu, 2002), the

cervical neural spines are uniformly tall and craniocaudally short. Finger-like epipophyses are present on cervicals 3–5.

Dorsal vertebrae (Fig. 8C–E) increase in height from D1 to D12. The neural spines of dorsals 1–4 are craniocaudally short, sharply contrasting with the remaining dorsals, in which the neural spines are twice craniocaudally longer. Dorsal ribs in *Megaraptor* are elongate and craniocaudally wide, being deeply grooved cranially and caudally. The shafts are transversely thick, robust and externally convex, thus defining a deep and wide chest and belly, a condition also reported for tyrannosaurids (Paul, 1988). Dorsal cranial ribs bear a pneumatic foramen located at the base of the

capitulum and tubercle, as reported in *Neovenator* (Brusatte et al., 2008), *Aerosteon* (Serenó et al., 2008) and *Tyrannosaurus* (Brochu, 2002). All available caudal vertebrae possess wide and deep laminae and excavations below the transverse processes in the neural arches and bear well-developed pleurocoels in the centra. Pleurocoels are large and ovoidal in contour, they are located near the junction of the neural arch with the vertebral centrum. On its deepest point the pleurocoels shows a small strut of bone, as present in most other megaraptorids (Novas, 2009).

A series of eight gastralia is available. They correspond to both sides of the body, but they were lumped together on the midline after death of the specimen. The gastral elements are represented by several medial components that are paddle-like medially. The shape of the gastralia is very similar to those of *Australovenator* (Hocknull et al., 2009), tyrannosaurids (Claessens, 2004) and carcharodontosaurids (Brusatte and Sereno, 2008), being different from the stick-shaped condition present in compsognathids, ornithomimids, allosaurids, sinraptorids, and dromaeosaurids (Norell and Makovicky, 1997; Currie and Chen, 2001; Brusatte and Sereno, 2008). In *Sinocalliopteryx* the medial gastralia are large and similar in shape to those of *Megaraptor* (Xing et al., 2012). Most of the preserved gastral elements of *Megaraptor* are large, being a bit shorter than the available dorsal ribs, a condition resembling

that of *Tyrannosaurus* (Brochu, 2002), and probably other large theropods as well. The latter condition is clearly different from that of *Ornithomimus*, *Scipionyx* and *Huaxiagnathus* (Hwang et al., 2004), in which the gastral elements are much more delicate and smaller than the dorsal ribs. This morphology suggests the presence of a transversely wide and dorsoventrally deep belly, a condition in agreement with the dorsal rib morphology.

The scapula of *Megaraptor* has been already described for an adult individual (Calvo et al., 2004) as well as for the megaraptorid *Aerosteon* (Serenó et al., 2008; Benson et al., 2010). The scapula of MUCPv 595 possesses a morphology consistent with that of other megaraptorid specimens. The coracoid of *Megaraptor* is proximodistally deep, with a slightly developed biceps tuber. It shows a deep depression behind the glenoid, a synapomorphic condition of megaraptorids, absent in other known theropods (Benson et al., 2010). The humerus (Fig. 10) is robust and describes a sigmoid curvature in side view, as typically occurs in allosauroids and coelurosaurids. The deltopectoral crest is cranially projected, rounded, and tapers both distally and proximally. Notably, a deep longitudinal furrow is present on the caudomedial surface of humerus, as that reported in the megaraptorans *Fukuiraptor*, *Australovenator* and in tyrannosaurids (Azuma and Currie, 2000; Carpenter and Smith, 2001; White et al., 2012). By contrast, in the purported

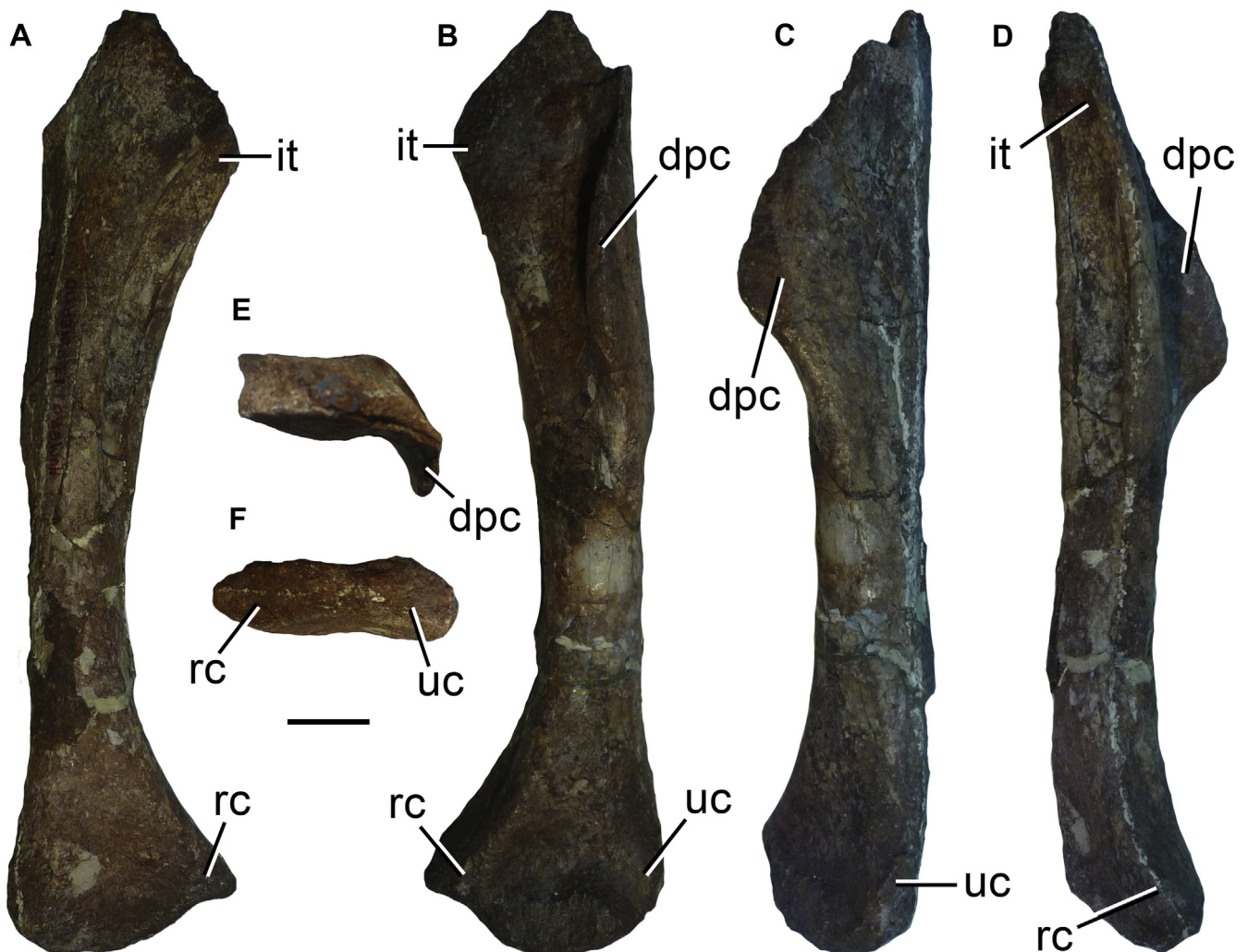


Fig. 10. Left humerus of *Megaraptor namunhuaiquii* (MUCPv 595) in (A) posterior, (B) anterior, (C) lateral, (D) medial, (E) proximal, and (F) distal views. Abbreviations: dpc, deltopectoral crest; it, internal tuberosity; rc, radial condyle; uc, ulnar condyle. Scale bar equals 2 cm.

megaraptoran *Chilantaisaurus* (Benson et al., 2010) the humerus is clearly different from that of *Megaraptor*, in having a straight shaft with a dorsoventrally short and subrectangular deltopectoral crest (Benson and Xu, 2008), a combination of characters that reinforces the exclusion of *Chilantaisaurus* from Megaraptoridae, as was recently proposed by Novas et al. (2013). The pelvic girdle of the new *Megaraptor* specimen is only represented by proximal halves of both pubes. The pubis possesses a cranial convexity that represents the insertion area of the ambiens muscle, resembling the condition present in *Aerosteon*, adult *Megaraptor* and tyrannosauroids (Benson et al., 2010; Novas et al., 2013).

5. Palaeohistology

Petrographic thin sections were made from the scapulae and pubes of specimens MUCPv 1353, MUCPv 595 and MUCPv 341. The smallest specimen (MUCPv 595) is inferred to represent a young, actively growing juvenile-to-subadult animal of six years old (Fig. 11). This interpretation is based on a combination of histological features, including predominance of well vascularized fibrolamellar bone, dense Haversian bone mostly restricted to the inner cortex, presence of few (five) growth marks (LAGs and narrow annuli), and absence of outer circumferential layer (OCL). Large longitudinally oriented vascular spaces predominate, but also radial and oblique anastomoses are observed. On the other hand, the bigger specimens MUCPv 341 and MUCPv 1353 are inferred to be older individuals, possibly mature adults, as indicated by the extensive development of secondary osteons (remains of primary bone are only preserved in some areas of the outer cortex), more numerous growth marks (at least seven and twelve in MUCPv 341 and MUCPv 1353, respectively), decrease in spacing between growth marks close to bone periphery, and more organized arrangement of the vascular spaces. Also, vascular spaces tend to be smaller and more organized than in MUCPv 595. A well-developed OCL is absent in both specimens.

6. Discussion

In a recent analysis by Benson et al. (2010) the megaraptorids, including *Megaraptor*, and *Neovenator* were included in the clade Neovenatoridae. More recently, Novas et al. (2013) conclude that *Neovenator* and megaraptorids were only distantly related, a conclusion also reached by the present analysis. In fact, *Megaraptor* exhibits sharp differences with *Neovenator* in available bones, and no synapomorphies are uniquely shared by both taxa. The premaxilla is strikingly different in *Megaraptor* and *Neovenator*. In *Megaraptor* is a very small and delicate bone, that forms a V-shaped arcade when viewed ventrally, anteroposteriorly compressed ventral margin, straight and extremely long narial process, and premaxillary body comparatively smaller (less than 0.7% total maxillary length). In *Neovenator*, on the contrary, the premaxilla is much more robust, the nasal process is shorter and curved and the premaxillary body is more than 10% maxillary length. Moreover, the morphology of the maxilla is also very different in both taxa. In *Megaraptor* the maxilla is very low and subtriangular, and the antorbital fossa is very extensive. On the contrary, in *Neovenator* the maxilla is robust and shorter, shows a very deep dorsal notch delimiting the anterior ramus, and the antorbital fossa is anteroposteriorly limited (Brusatte et al., 2008). In *Megaraptor* the nasals lack a deep narial fossa, and the antorbital fossa does not invade its lateral surface. On the other hand, in *Neovenator* nasals show a very deep and well-defined narial fossa, as well as a deep lateral concavity representing the antorbital fossa (Brusatte et al., 2008). These sharp anatomical differences between *Megaraptor* and *Neovenator*, together with other features indicated

along the text and in previous paper (Novas et al., 2013), are in agreement with the hypothesis that both taxa are only distantly related.

Another two Cretaceous theropods have been interpreted as allied to Megaraptora: *Chilantaisaurus* and *Siats* (Benson et al., 2010; Zanno and Makovicky, 2013). However, both are highly fragmentary, and do not exhibit synapomorphies uniquely shared with megaraptorans. *Chilantaisaurus* is represented by a highly incomplete specimen coming from the Early Cretaceous of China (Benson and Xu, 2008), and was referred by Benson et al. (2010) to stem-Megaraptora on the basis of some features of the ilium, distal tibia, and the morphology of manual ungual phalanx. However, Novas et al. (2013) proposed that *Chilantaisaurus* was a basal coelurosaur, and was not particularly related to megaraptorids. They interpreted that the shared presence of a flat distal end of tibia and well-developed cuppedicus fossa on ilium that is medially bounded by a ridge were features that may ally *Chilantaisaurus* with Coelurosauria, but not unique to the *Chilantaisaurus* + Megaraptora clade. Although the manual ungual of *Chilantaisaurus* is considerably enlarged, similar to *Megaraptor*, it is not transversely compressed as in the later taxon, and lacks a longitudinal ventral ridge present in *Australovenator* and *Megaraptor* (Novas et al., 2013). Moreover, proportionally large manual unguals are also present in basal coelurosaurs such as compsognathids (e.g., *Sinosauropteryx*, *Juravenator*; Chiappe and Göhlich, 2010) and *Tanycolagreus* (Carpenter et al., 2005). The new specimen of *Megaraptor* indicates that the humerus was strongly different to that of *Chilantaisaurus* in gross morphology, proportions, and general characters (see above). Thus, anatomical differences between megaraptorids and *Chilantaisaurus* are in agreement with the hypothesis proposing that both taxa are only distantly related.

Regarding *Siats*, the holotype consists on an incomplete and distorted skeleton coming from the Cenomanian (Late Cretaceous) of United States of America (Zanno and Makovicky, 2013). Its referral to Megaraptora was based on the presence of pronounced centrodiapophyseal laminae bracketed by deep infradiapophyseal fossa on the caudal neural arches. However, the fossae are much deeper and wider and are bounded by distally extended laminae in *Megaraptor* (Calvo et al., 2004), being different from the condition of *Siats*. The most complete dorsal vertebra of *Siats* described by Zanno and Makovicky (2013) has been described as the 5th, but the cranial inclination of the neural spine and the lack of parapophysis on centrum (and even on the neural arch) suggest that it belong to the posterior portion of the dorsal series (probably dorsal 13th). Comparing this dorsal with posterior dorsals of *Aerosteon*, *Siats* clearly differs in having very low and craniocaudally extended neural spine, craniocaudally longer centrum, smaller and undivided pleurocoel, and different disposition and extension of infradiapophyseal laminae. Furthermore, the ilium of *Siats* is not particularly similar to the megaraptorid *Aerosteon*. In *Siats* the postacetabular blade is low and the medial wall of the brevis fossa is laterally exposed, a condition similar to that of basal tetanurans (e.g., *Torvosaurus*, *Eustreptospondylus*; Rauhut, 2003), being sharply different from the deep postacetabular blade of *Aerosteon* that laterally hidden the brevis fossa. Besides, the horizontal ridge interpreted as the external margin of a cuppedicus fossa in *Siats*, is located in an unusually high position compared with those theropods in which the cuppedicus fossa is undoubtedly preserved (e.g., *Aerosteon*, *Tyrannosaurus*). Moreover, in *Siats* the fibula is very short and robust, and does not shows a strong narrowing of the shaft at the level of the fibular tubercle, a plesiomorphic condition that differs from the thinner fibular shaft present in coelurosaurs, including *Megaraptor* (Novas et al., 2013). In conclusion, *Siats* lacks clear derived characters linking it with Megaraptora, and even Coelurosauria.

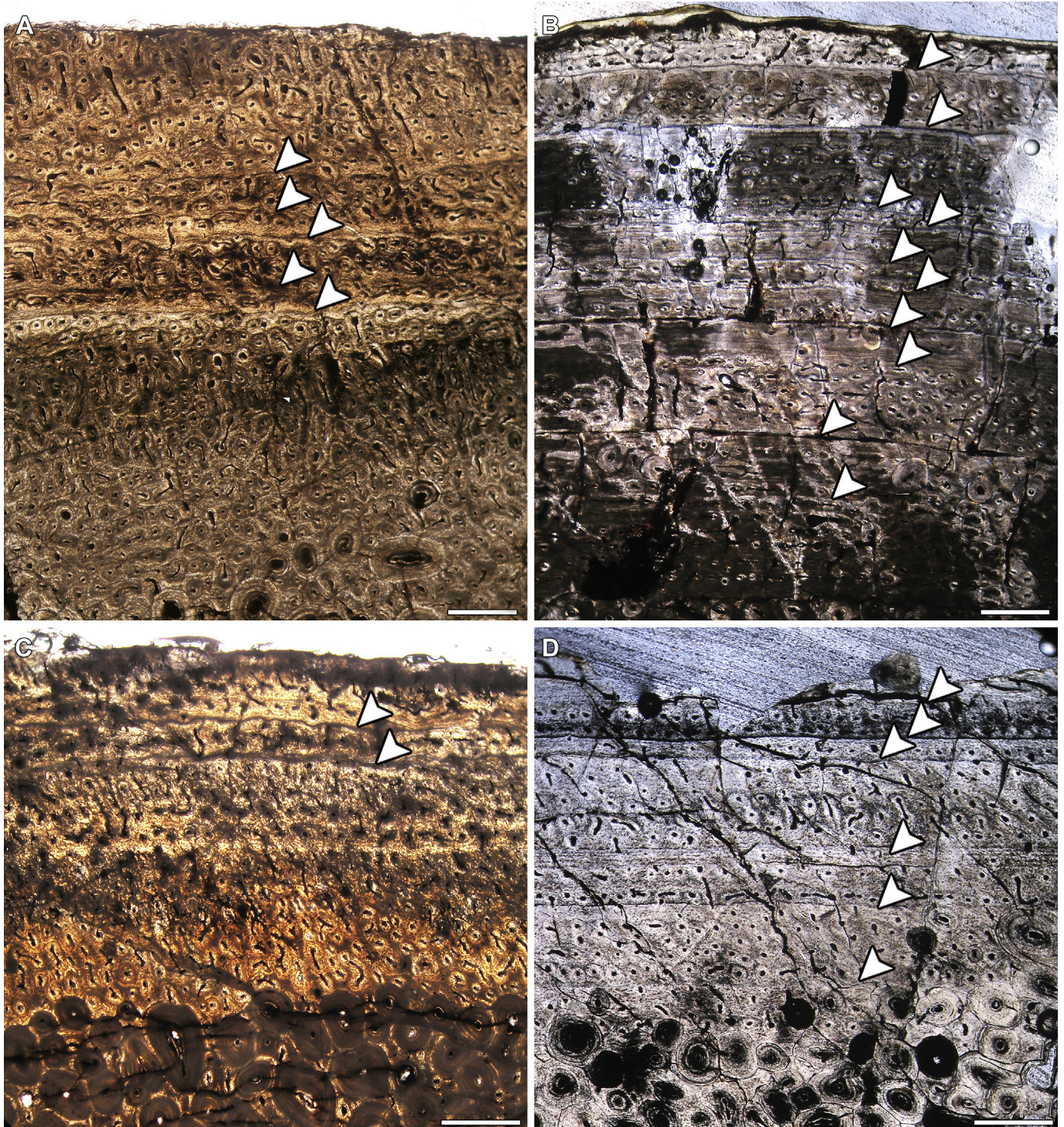


Fig. 11. Bone histology of *Megaraptor namunhuaiquii*. (A) Pubis from MUCPv 595, (B) pubis from MUCPv 1353, (C) scapula from MUCPv 595, and (D) scapula from MUCPv 341. The external surface is towards the top of the figure. Arrowheads indicate the presence of growth marks (annuli and/or LAGs) in the samples. Note the minor number of growth marks in the samples from MUCPv 595 compared with the other specimens. Scale bars equal 500 microns.

Megaraptor and its kin have been alternatively interpreted as belonging to different theropod lineages (Calvo et al., 2004; Smith et al., 2007, 2008; Benson et al., 2010; see Introduction). More recently, Novas et al. (2013) analyzed these previous proposals, and found *Megaraptor* and related taxa as deeply nested within Coelurosauria, notably as the sister group of *Xiongguanlong* + Tyrannosauridae. Novas et al. (2013) data set was re-analyzed after including the new information gathered from the specimen

of *Megaraptor* described here. The phylogenetic analysis (best scores were found in all the replications) recovered 54 most parsimonious trees (MPTs) of 919 steps, with a consistency index of 0.376 and a retention index of 0.669 (Fig. 12). The result of the present analysis expanded the list of derived characters supporting the position of megaraptorans within Coelurosauria and Tyrannosauroidae (Appendix B). Apomorphies shared by megaraptorans and coelurosaurs include: 1) ilium with a deep cuppedicus fossa

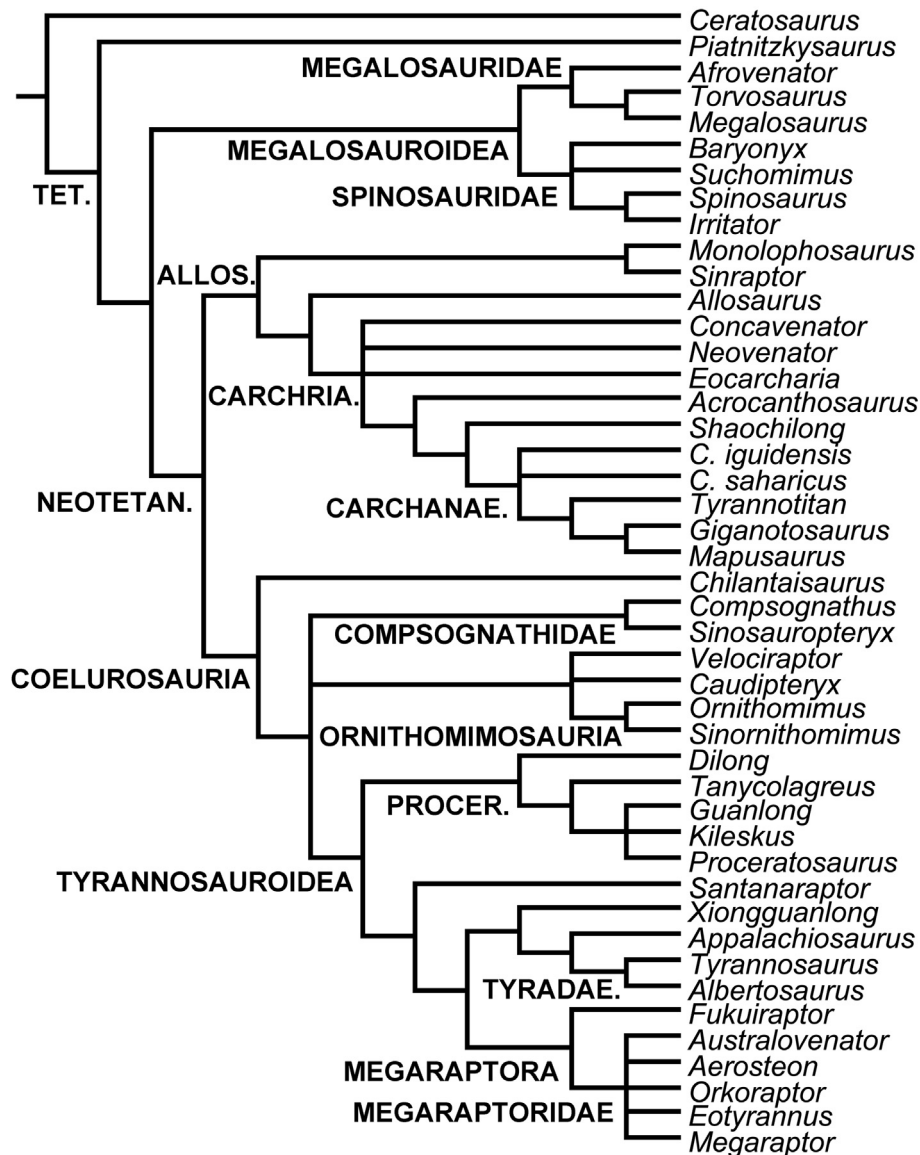


Fig. 12. Strict consensus tree of all the recovered MPTs of the present phylogenetic analysis. Abbreviations: ALLOS, Allosauroidae; CARCHANAE, Carcharodontosaurinae; CARCHRIA, Carcharodontosauria; NEOTETAN, Neotetanurae; PROCER, Proceratosauridae; TET, Tetanurae; TYRADAЕ, Tyrannosauridae.

bounded dorsomedially by a prominent shelf (also present in the allosauroid *Neovenator*; Brusatte et al., 2008); 2) femur with a squared lateral border of the head, being more than half of the maximum anteroposterior length of the femoral head (variably present in specimens of the basal megaraptoran *Fukuiraptor*; Currie & Azuma 2006); 3) femur with a proximally projected greater trochanter at level with the proximal surface of the head; 4) tibial length more than 12 times its anteroposterior width at mid-length; 5) tibia with an anterior surface of the distal end flat; and 6) metatarsal III length more than 10 times its minimum width. The position of megaraptorans within Coelurosauria is well supported, with a Bremer support of 4 (Fig. 13) and absolute and GC bootstrap frequencies of 70% and 69%, respectively. In particular, when fragmentary tetanurans were pruned *a posteriori* the Bremer support of the node raised to 8 (Fig. 13).

Megaraptorans share the following synapomorphies with tyrannosauroids: 1) premaxilla with incisiform; 2) “D”-shaped teeth (Fig. 7); 3) premaxilla with very large, circular foramina on the lateral surface of the body (also present in some allosauroids);

4) external naris major axis length more than three times its maximum dorsoventral height (ambiguous optimization at the base of Tyrannosauroidae) (Fig. 14); 5) dentary first alveolus substantially smaller than the more posterior ones; 6) parietals with a median sagittal crest and thus, skull table between supratemporal fossae extremely reduced in width (sagittal crest or crests pinched between opposing fossae; also present in the carcharodontosaurid *Shaochilong*; Brusatte et al., 2010a); 7) caudal vertebrae with a flat ventral surface; 8) humerus with a medial condyle expanded further medially than the lateral condyle is laterally; 9) metacarpal III <0.75 length of metacarpal II; 10) ilium with preacetabular blade anterodorsally notched; 11) pubis with a well developed ambiens tubercle; 12) pubic symphysis interrupted distally by a large median fenestra (also present in allosauroids; Benson et al., 2010); 13) pubic boot $\geq 60\%$ length of the bone (also present in allosauroids; Benson et al., 2010); and 14) tibia with a large medial malleolus. In particular, the new *Megaraptor* specimen allowed to recognize tyrannosauroid synapomorphies 1–4, 6, and 10. Bremer support of Tyrannosauroidae is 2 (Fig. 13) and the bootstrap frequencies are

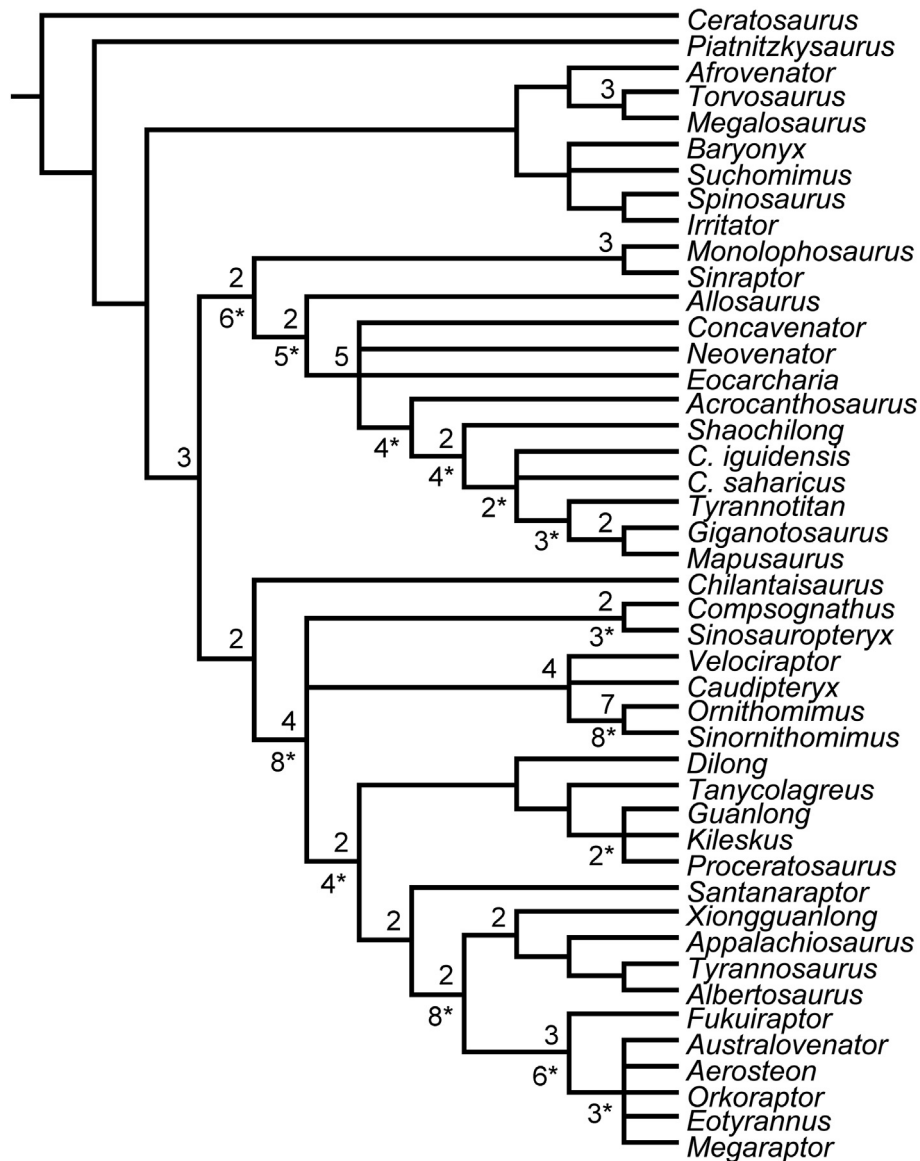


Fig. 13. Strict consensus tree of all the recovered MPTs of the present phylogenetic analysis showing Bremer supports higher than 1. Values with asterisks below the nodes are Bremer supports recovered after a *posteriori* pruning of some fragmentary taxa (see [Introduction](#)).

below 50%. However, after pruning of fragmentary taxa the Bremer support of Tyrannosauridae raised to 4 (Fig. 13).

Megaraptorans, *Santanaraptor* and the tyrannosaurid lineage (i.e., *Xiongguanlong*, *Appalachiosaurus* and Tyrannosauridae) share the apomorphies previously described by Novas et al. (2013) (see [Appendix C](#)). The Bremer support of these nodes was relatively low, but after pruning of fragmentary taxa the decay index of the megaraptoran + tyrannosaurid lineage raised to 8. The relationships and apomorphies found at Megaraptora and Megaraptoridae are the same previously recovered by Novas et al. (2013) (see [Appendix C](#)). However, a clearly distinct result of this new analysis is the position of the Early Cretaceous European *Eotyrannus* within Megaraptoridae. The position of this taxon within Megaraptora is supported by: 1) cervical centra strongly opisthocelous and 2) presence of pleurocoels in dorsal vertebrae. This result implies an European-Gondwanan distribution for Megaraptoridae, a palaeobiogeographic pattern in agreement with that proposed by Ezcurra and Agnolín (2012). However, the position of *Eotyrannus* within Tyrannosauroidae should be currently taken with caution

and more detail analyses focused mostly in this issue should test this hypothesis in the future.

Under suboptimal topologies, we need 37 additional steps to force the monophyly of Neovenatoridae *sensu* Benson et al. (2010) (i.e., *Neovenator* + Megaraptora), with the inclusion or not of *Chilantaisaurus* within the clade. In addition, 18 additional steps are necessary to force the position of Megaraptora as the sister-taxon of the clade that includes Tyrannosauroidae, Compsognathidae and maniraptorans. 10 additional steps are necessary to situate megaraptorans at the base of Tyrannosauroidae. Finally, 26 extra steps are necessary to move *Neovenator* as the sister-taxon of Megaraptora within Tyrannosauroidae. Accordingly, the analysis of alternative positions under suboptimal topologies strongly supports the position of Megaraptora within Tyrannosauroidae.

In addition, the cranial and dental morphology of *Megaraptor* (as well as *Orkoraptor*, *Aerosteon*, and *Australovenator*) sharply differ from those of allosauroids in general, and carcharodontosaurids in particular. Main distinctions are the long and low skull (as

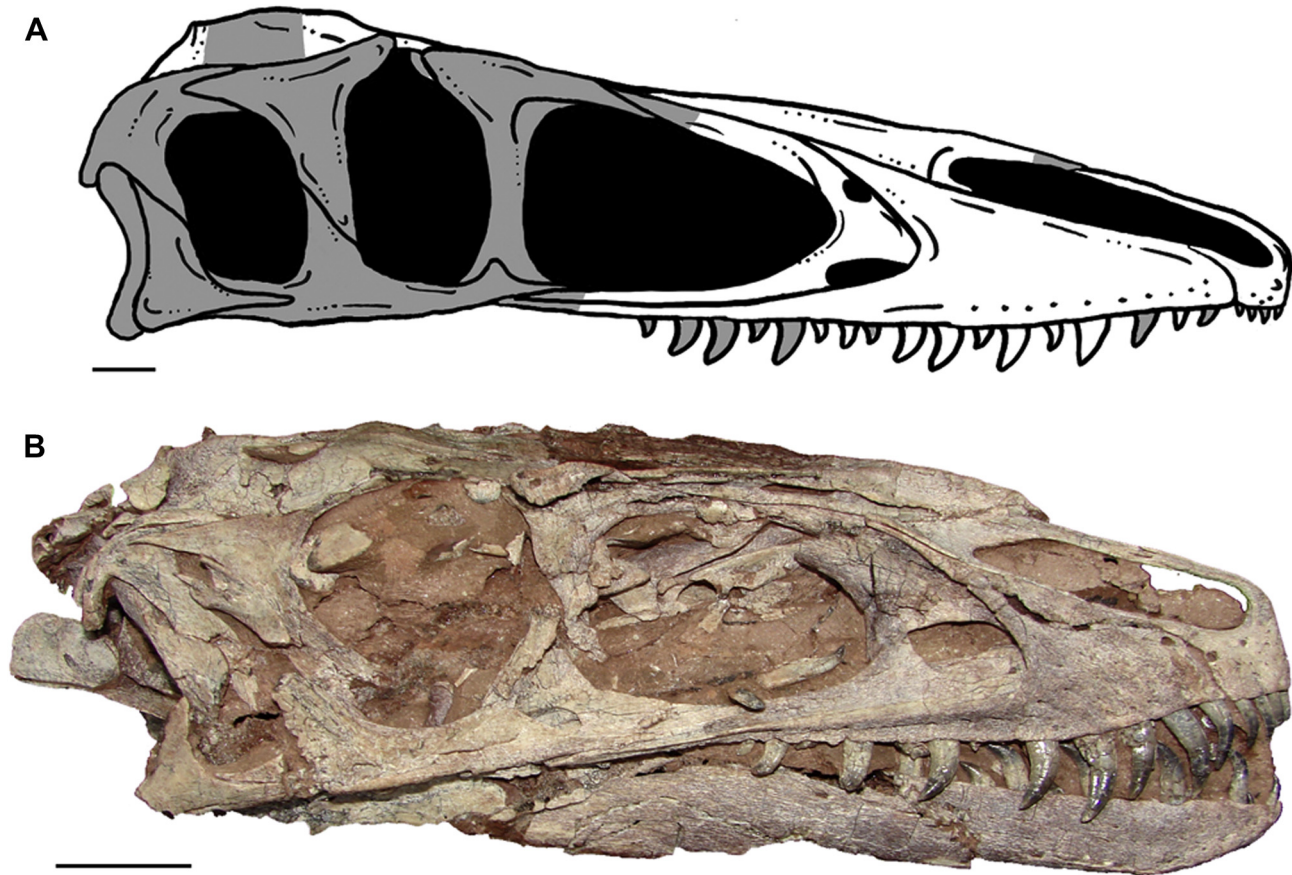


Fig. 14. (A) Cranial reconstruction of *Megaraptor namunhauquii* based on MUCPv 595 and (B) skull of *Dilong paradoxus* (IVPP V14243) in right lateral view. Grey tones indicate missing bones in MUCPv 595. Postorbital and quadratojugal partially based on *Orkoraptor burkei* (Novas et al., 2008). Scale bars equal 2 cm.

suggested by the low and rostrally extended maxillary body, flattened and almost straight nasals of *Megaraptor*, and the slender and elongated dentary of *Australovenator*; anteroposteriorly enlarged external naris; proportionally small premaxilla with a very elongated, rod-like premaxillary process; heterodont dentition (represented by the small and D-shaped premaxillary teeth, compared with the larger maxillary tooth); upturned anterior process of the postorbital bone; and lateral pneumatic excavation dorsoventrally extended on basioccipital. The skull roof possesses rostrally expanded supratemporal fossae, which are separated by a narrow and sharp sagittal crest in the posterior end of the frontals (and probably on the parietals), contrasting with the short supratemporal fossae and transversely thick sagittal crest present in basal theropods (including allosauroids, and particularly carcharodontosaurids, excepting for *Shaochilong*).

In spite of the phylogenetic hypothesis recovered here, there are several cranial and postcranial similarities shared by *Megaraptor* and carcharodontosaurid allosauroids (e.g., *Acrocanthosaurus*, *Mapusaurus*, *Giganotosaurus*; Coria and Salgado, 1995; Harris, 1998; Currie and Carpenter, 2000; Coria and Currie, 2006; Smith et al., 2007), including a straight dorsal margin of the anterior ramus of the maxilla, subrectangular nasals, cervical vertebrae with prominent and centrally positioned parapophyses and reduced neural spines, pleurocoels in caudal vertebrae, and craniocaudally expanded distal pubic boot. On the basis of the phylogenetic analysis performed here, we interpret these features as convergences acquired independently by megaraptorid tyrannosauroids and carcharodontosaurid allosauroids.

We demonstrate here that the pneumatic condition of the outer portion of the vertebrae is not uniformly present in the rest of the bone. Thus, studies on the internal structure of theropod vertebrae need to take into account this variation in the degree of pneumaticity, avoiding observations based on localized portions of the bone. We highly recommend to recover internal structure information on equivalent regions of homologous vertebral segments.

Based on the combined information of known specimens of *Orkoraptor*, *Aerosteon*, *Australovenator* and *Megaraptor*, but specially on the basis of the present juvenile individual of *Megaraptor* we are able to make a reliable reconstruction of megaraptorid skeleton. Megaraptorids possess an elongated skull, with a gracile snout bearing small teeth (Fig. 14). The neck was also gracile and shows a very deep and well-developed “S”-shaped cervical series. The thorax was very wide and deep, with thick and extended dorsal ribs and gastralia, the latter similar in size to the dorsal ribs. The pectoral girdle was robust, supporting elongated and robust forelimbs, with manual digits I and II ending in enlarged and sharp unguals. The hindlimbs were gracile and slender. Information of anterior caudals suggests a rather robust and deep tail.

At the *Megaraptora*-Tyrannosauridae node we document a departure of two forelimb evolutionary trends: while in megaraptorids the forelimbs became powerful and with large-clawed hands (Calvo et al., 2004), in tyrannosaurids, instead, the overall trend was towards forelimb reduction (Brusatte et al., 2010b). Nevertheless, both evolutionary trends present a common pattern that is the reduction of the third manual digit. Accordingly, the results of our analysis indicate that megaraptorids represented the

counterpart of the tyrant-reptile evolution in the southern territories of Gondwana.

7. Concluding remarks

The present paper describes in detail the anatomy of the most complete megaraptorid skeleton known so far. The specimen sheds new light on the phylogenetic relationships of megaraptorans, and sustain their position as basal coelurosaurids nearly related to tyrannosaurids. Present phylogeny indicates that megaraptorans share with tyrannosaurids very small premaxillary body with extremely long premaxillary process, incisiform D-shaped premaxillary teeth, and supratemporal fossae separated by a sharp sagittal median crest on frontals.

The new finding also supports that the possible megaraptorans *Chilantaisaurus* and *Siats*, coming from the Lower Cretaceous of China and upper Lower Cretaceous of the United States, respectively, do not exhibit synapomorphies uniquely shared with megaraptorans. The phylogenetic position of these two genera within theropods is still not well understood.

Information gathered from the present specimen allows to make for the first time a reconstruction of the skull and body of megaraptorids. Megaraptorids possessed an elongated skull, with a gracile snout bearing small teeth, a gracile S-shaped neck, and a very wide and deep thorax, with gastralia similar in size to dorsal ribs. The pectoral girdle supported elongate and robust forelimbs, with large and sharp unguals on digits I and II. On the contrary, hindlimbs were rather gracile and slender. This unique body plan is not shared by any other known theropod.

The results of our analysis also indicate that megaraptorids represented a peculiar and still poorly known radiation of tyrant-reptiles in the territories that were once part of Gondwana.

Acknowledgements

We thank J.I. Canale for comments and sharing information on carcharodontosaurid anatomy. We also thank Clara Abal, Scott Hocknull, Xu Xing and Rodolfo Coria for allowing the study of specimens under their care. Ignacio Canudo and Prebiterio Pacheco participated actively in the field excavation of the juvenile specimen of *Megaraptor*. Steve Brusatte and an anonymous reviewer made clever observations that improved the quality of the present paper. JDP is supported by a grant of the Agencia Nacional de Promoción Científica y Tecnológica (FONCYT PICT-2011-2591). FEN is supported by Agencia Nacional de Promoción Científica y Tecnológica (FONCYT PICT-2010-066). MDE is supported by a grant of the DFG Emmy Noether Programme to Richard Butler (BU 2587/3-1).

References

- Averianov, A.O., Krasnolutskii, S.A., Ivantsov, S.V., 2010. A new basal coelurosaur (Dinosauria: Theropoda) from the Middle Jurassic of Siberia. *Proceedings of the Zoological Institute* 314, 42–57.
- Azuma, Y., Currie, P.J., 2000. A new carnosaur (Dinosauria: Theropoda) from the Lower Cretaceous of Japan. *Canadian Journal of Earth Sciences* 37, 1735–1753.
- Bakker, R.T., Williams, M., Currie, P.J., 1988. *Nanotyrannus*, a new genus of pygmy tyrannosaur, from the latest Cretaceous of Montana. *Hunteria* 1, 1–30.
- Bakker, R.T., Siegwark, J., Kralis, D., Filla, J., 1992. *Edmarka rex*, a new, gigantic theropod dinosaur from the Middle Morrison Formation, Late Jurassic of Como Bluff outcrop region. *Hunteria* 2, 9–24.
- Benson, R.B.J., 2010. A description of *Megalosaurus bucklandii* (Dinosauria: Theropoda) from the Bathonian of the UK and the relationships of Middle Jurassic theropods. *Zoological Journal of the Linnean Society of London* 158, 882–935.
- Benson, R.B.J., Xu, X., 2008. The anatomy and systematic position of the theropod dinosaur *Chilantaisaurus tashuikouensis* Hu, 1964 from the Early Cretaceous of Alanshan, People's Republic of China. *Geological Magazine* 145, 778–789.
- Benson, R.B.J., Carrano, M.T., Brusatte, S.L., 2010. A new clade of archaic large-bodied predatory dinosaurs (Theropoda: Allosauroidae) that survived to the latest Mesozoic. *Naturwissenschaften* 97, 71–78.
- Benson, R.B.J., Butler, R.J., Carrano, M.T., O'Connor, P.M., 2012a. Air-filled postcranial bones in theropod dinosaurs: physiological implications and the reptile–bird transition. *Biological Reviews* 97, 168–193.
- Benson, R.B.J., Rich, T.H., Vickers-Rich, P., Hall, M., 2012b. Theropod Fauna from southern Australia indicates high polar diversity and climate-driven dinosaur provinciality. *PLOS ONE* 7 (5), e37122.
- Bever, G.S., Brusatte, S., Carr, T.D., Xu, X., Balanoff, A.M., Norell, M., 2013. The braincase anatomy of the late Cretaceous dinosaur *Alioramus* (Theropoda, Tyrannosauroidae). *Bulletin of the American Museum of Natural History* 376, 1–32.
- Bonaparte, J.F., 1991. The Gondwanan theropod families Abelisauridae and Noasauridae. *Historical Biology* 5, 1–25.
- Bonaparte, J.F., 1996. Cretaceous tetrapods of Argentina. *Münchner Geowissenschaftliche Abhandlungen* 30, 73–130.
- Britt, B.B., 1993. Pneumatic postcranial bones in dinosaurs and other archosaurs. PhD Thesis. University of Calgary.
- Brochu, C.A., 2002. Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. *Society of Vertebrate Paleontology Memoir* 7, 1–138.
- Brusatte, S.L., Benson, R.B.J., Hutt, S., 2008. The osteology of *Neovenator salerii* (Dinosauria: Theropoda) from the Wealden Group (Barremian) of the Isle of Wight. *Paleontological Society Monographs* 162, 1–75.
- Brusatte, S.L., Carr, T.D., Norell, M.A., 2012. The osteology of *Alioramus*, a gracile and long-snouted tyrannosaurid (Dinosauria: Theropoda) from the Late Cretaceous of Mongolia. *Bulletin of the American Museum of Natural History* 366, 1–197.
- Brusatte, S., Chure, D., Benson, R., Xu, X., 2010a. The osteology of *Shaochilong maotuisensis*, a carcharodontosaurid (Dinosauria: Theropoda) from the Late Cretaceous of Asia. *Zootaxa* 2334, 1–46.
- Brusatte, S.L., Norell, M.A., Carr, T.D., Erickson, G.M., Hutchinson, J.R., Balanoff, A.M., Bever, G.S., Choiniere, J.N., Makovicky, P.J., Xu, X., 2010b. Tyrannosaur paleobiology: new research on ancient exemplar organisms. *Science* 329, 1481–1485.
- Brusatte, S.L., Sereno, P.C., 2008. Phylogeny of Allosauroidae (Dinosauria: Theropoda): comparative analysis and resolution. *Journal of Systematic Paleontology* 6, 155–182.
- Calvo, J.O., Porfiri, J.D., González Riga, B.J., Kellner, A.W.A., 2007. A new Cretaceous terrestrial ecosystem from Gondwana with the description of a new sauropod dinosaur. *Anais da Academia Brasileira de Ciências* 79, 529–541.
- Calvo, J.O., Porfiri, J.D., Veralli, C., Novas, F.E., Poblete, F., 2004. Phylogenetic status of *Megaraptor namunhuaiquii* Novas based on a new specimen from Neuquén, Patagonia, Argentina. *Ameghiniana* 41, 565–575.
- Carpenter, K., Smith, M., 2001. Forelimb Osteology and Biomechanics of *Tyrannosaurus rex*. In: Tanke, D., Carpenter, K. (Eds.), *Mesozoic vertebrate life*. Indiana University Press, Bloomington, pp. 90–116.
- Carpenter, K., Miles, C., Cloward, K., 2005. New small theropod from the Upper Jurassic Morrison Formation of Wyoming. In: Carpenter, K. (Ed.), *The Carnivorous Dinosaurs*. Indiana University Press, Bloomington, pp. 23–48.
- Carr, T.D., Williamson, T.E., 2010. *Bistahieversor sealeyi*, gen. et sp. nov., a new tyrannosauroid from New Mexico and the origin of deep snouts in Tyrannosauroidae. *Journal of Vertebrate Paleontology* 30, 1–16.
- Carrano, M.T., Benson, R.B.J., Sampson, S.D., 2012. The phylogeny of Tetanurae (Dinosauria: Theropoda). *Journal of Systematic Palaeontology* 10, 211–300.
- Chinsamy, A., Raath, M.A., 1992. Preparation of fossil bone for histological examination. *Paleontologia Africana* 29, 39–44.
- Chinsamy-Turan, A., 2005. The microstructure of dinosaur bone. *Johns Hopkins University Press*, Baltimore.
- Choiniere, J.N., Forster, C.A., De Klerk, W.J., 2012. New information on *Nqwebasaurus thwazi*, a coelurosaurian theropod from the Early Cretaceous (Hauterivian?) Kirkwood Formation in South Africa. *Journal of African Earth Sciences*. <http://dx.doi.org/10.1016/j.jafrearsci.2012.05.005>.
- Claessens, L.P.A.M., 2004. Dinosaur gastralia: origin, morphology, and function. *Journal of Vertebrate Paleontology* 24, 89–106.
- Coddington, J.A., Scharff, N., 1994. Problems with Zero-Length Branches. *Cladistics* 10, 415–423.
- Coria, R.A., Salgado, L., 1995. A new giant carnivorous dinosaur from the Cretaceous of Patagonia. *Nature* 377, 224–226.
- Coria, R.A., Currie, P.J., 2002. The braincase of *Giganotosaurus carolinii*, (Dinosauria: Theropoda) from the Upper Cretaceous of Argentina. *Journal of Vertebrate Paleontology* 4, 802–811.
- Coria, R.A., Currie, P.J., 2006. A new carcharodontosaurid (Dinosauria, Theropoda) from the Upper Cretaceous of Argentina. *Geodiversitas* 28, 71–118.
- Currie, P.J., Azuma, Y., 2006. New specimens, including a growth series, of *Fukuiraptor* (Dinosauria, Theropoda) from the Lower Cretaceous Kitadani Quarry of Japan. *Journal of the Paleontological Society of Korea* 22, 173–193.
- Currie, P.J., Zhao, X., 1993. A new carnosaur (Dinosauria, Theropoda) from the Jurassic of Xinjiang, People's Republic of China. *Canadian Journal of Earth Sciences* 30, 2037–2081.
- Currie, P.J., 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., 2003. Cranial anatomy of tyrannosaurid dinosaurs from the Late Cretaceous of Alberta, Canada. *Acta Palaeontologica Polonica* 48 (2), 191–226.

- Currie, P.J., Chen, P.J., 2001. Anatomy of *Sinosauropteryx prima* from Liaoning, northeastern China. *Canadian Journal of Earth Sciences* 38, 705–727.
- Dal Sasso, C., Maganuco, S., 2011. *Scipionyx samniticus* (Theropoda: Compsognathidae) from the Lower Cretaceous of Italy – Osteology, ontogenetic assessment, phylogeny, soft tissue anatomy, taphonomy and palaeobiology. *Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano* 37, 1–281.
- Eddy, D., Clarke, J., 2011. New Information on the Cranial Anatomy of *Acrocanthosaurus atokensis* and Its Implications for the Phylogeny of Allosauroidae (Dinosauria: Theropoda). *PLoS ONE* 6, e17932.
- Erickson, G.M., 2005. Assessing dinosaur growth patterns: a microscopic revolution. *Trends in Ecology and Evolution* 20, 677–684.
- Ezcurra, M.D., Agnolin, F.L., 2012. A new global palaeobiogeographical model for the late Mesozoic and early Tertiary. *Systematic Biology* 61, 553–566.
- Francillon-Vieillot, H., de Buffrénil, V., Castanet, J., Géraudie, J., Meunier, F.J., Sire, J.Y., Zylberberg, L., de Ricqlès, A.J., 1990. Skeletal biomineralization: Patterns, Processes and Evolutionary Trends. In: Carter, J.G. (Ed.), *Microstructure and mineralization of vertebrate skeletal tissues*. Van Nostrand Reinhold, pp. 471–548.
- Gauthier, J.A., 1986. Saurischian monophyly and the origin of birds. In: Padian, K. (Ed.), *The Origin of Birds and the Evolution of Flight*. *Memoirs of the California Academy of Sciences*, 8, pp. 1–55.
- Gianechini, F.A., Lio, G.L., Apesteguía, S., 2011. Isolated archosaurian teeth from “La Bonita” locality (Late Cretaceous, Santonian–Campanian), Río Negro province, Argentina. *Historia Natural* 1, 5–16.
- Chiappe, L.M., Göhlich, U.B., 2010. Anatomy of *Juravenator starki* (Theropoda: Coelurosauria) from the Late Jurassic of Germany. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen* 258, 257–296.
- Goloboff, P.A., Farris, J.S., Nixon, K.C., 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24, 774–786.
- Harris, J.D., 1998. A reanalysis of *Acrocanthosaurus atokensis*, its phylogenetic status and paleobiogeographic implications, based on a new specimen from Texas. *Bulletin New Mexico Museum of Natural History and Science* 13, 1–75.
- Hocknull, S.A., White, M.A., Tischler, T.R., Cook, A.G., Calleja, N.D., Sloan, T., Elliott, D.A., 2009. New Mid-Cretaceous (Latest Albian) Dinosaurs from Winton, Queensland, Australia. *PLoS ONE* 4, e6190.
- Holtz, T.R., Molnar, R.E., Currie, P.J., 2004. Basal Tetanurae. In: Weishampel, D.B., Dodson, P., Osmolska, H. (Eds.), *The Dinosauria*, second ed. California University Press, pp. 71–110.
- Huene, F., 1920. Bemerkungen zur Systematik und Stammesgeschichte einiger Reptilien. *Zeitschrift für induktive Abstammungs- und Vererbungslehre* 24, 162–166.
- Hwang, S.H., Norell, M.A., Ji, Q., Gao, K., 2004. A large compsognathid from the Early Cretaceous Yixian Formation of China. *Journal of Systematic Palaeontology* 2, 13–30.
- Ji, S., Ji, Q., Lu, J., Yuan, C., 2007. A new giant compsognathid dinosaur with long filamentous integuments from Lower Cretaceous of Northeastern China. *Acta Geologica Sinica* 81, 8–15.
- Ji, Q., Ji, S.A., Zhang, L.J., 2009. First large tyrannosauroid theropod from the Early Cretaceous Jehol Biota in northeastern China. *Geological Bulletin of China* 28, 1369–1374.
- Kobayashi, Y., Barsbold, R., 2005. Reexamination of a primitive ornithomimosaur, *Garudimimus brevipes* Barsbold, 1981 (Dinosauria: Theropoda), from the Late Cretaceous of Mongolia. *Canadian Journal of Earth Sciences* 42, 1501–1521.
- Lamanna, M., Martinez, R., Luna, M., Casal, G., Ibiricu, L., Ivany, E., 2004. New specimens of the problematic large theropod dinosaur *Megaraptor* from the Late Cretaceous of central Patagonia. *Journal of Vertebrate Paleontology* 64, 252A.
- Li, D., Norell, M.A., Gao, K.Q., Smith, N.D., Makovicky, P.J., 2010. A longirostre tyrannosauroid from the Early Cretaceous of China. *Proceedings of the Royal Society B* 277, 183–190.
- Madsen Jr., J.H., 1976. *Allosaurus fragilis*: a revised osteology. *Utah Geological and Mineralogical Survey Bulletin* 109, 3–163.
- Maleev, E.A., 1974. Gigantic carnosaurus of the family Tyrannosauridae. The Joint Soviet–Mongolian Paleontological Expedition Transactions 1, 132–191 (in Russian).
- Marsh, O.C., 1881. Principal characters of American Jurassic dinosaurs. Part V. *American Journal of Sciences* 3 (21), 417–423.
- Martinelli, A.G., Ribeiro, L.C.B., Neto, F.M., Méndez, A.H., Cavellani, C.L., Felix, E., Ferraz, M.L.F., Teixeira, V.P.A., 2013. Insight on the theropod fauna from the Uberaba Formation (Bauru Group), Minas Gerais State: new megaraptoran specimen from the Late Cretaceous of Brazil. *Rivista Italiana di Paleontologia e Stratigrafia* 119, 205–214.
- McNamara, K.J., Long, J.A., 2012. The Role of Heterochrony in Dinosaur Evolution. In: Brett-Surman, M.K., Holtz, T.R., Farlow, J.O. (Eds.), *The complete dinosaur. Life of the Past*. Indiana University press, Indiana, pp. 761–784.
- Norell, M.A., Makovicky, P.J., 1997. Important features of the dromaeosaur skeleton: information from a new specimen. *American Museum Novitates* 3215, 1–28.
- Norell, M.A., Clark, J.M., Turner, A.H., Makovicky, P.J., Barsbold, R., Rowe, T., 2006. A new dromaeosaurid theropod from Ukhaa Tolgod (Ömnögovi, Mongolia). *American Museum Novitates* 3545, 1–51.
- Novas, F.E., 1997. Anatomy of *Patagonykus puertai* (Theropoda, Avialae, Alvarezsauridae), from the Late Cretaceous of Patagonia. *Journal of Vertebrate Paleontology* 17, 137–166.
- Novas, F.E., 1998. *Megaraptor namunhauquii* gen. et. sp. nov., a large-clawed, Late Cretaceous Theropod from Argentina. *Journal of Vertebrate Paleontology* 18, 4–9.
- Novas, F.E., 2009. The Age of Dinosaurs in South America. Indiana University Press, Bloomington, pp. 1–536.
- Novas, F.E., de Valais, S., Vickers-Rich, P., Rich, T., 2005. A large Cretaceous theropod from Patagonia, Argentina, and the evolution of carcharodontosaurids. *Naturwissenschaften* 92, 226–230.
- Novas, F.E., Ezcurra, M.D., Lecuona, A., 2008. *Orkoraptor burkei* nov. gen. et sp., a large theropod from the Maastrichtian Pari Aike Formation, Southern Patagonia, Argentina. *Cretaceous Research* 29, 468–480.
- Novas, F.E., Agnolin, F.L., Ezcurra, M.D., Porfiri, J., Canale, J.L., 2013. Evolution of the carnivorous dinosaurs during the Cretaceous: the evidence from Patagonia. *Cretaceous Research* 45, 174–215.
- Passalia, M.G., Prámparo, M.B., Calvo, J.O., Heredia, S., 2008. Primer registro de hojas de angiospermas en el Grupo Neuquén (Turoniano tardío–Coniaciano temprano), Lago Barreales, Argentina. *Ameghiniana* 45, 125–129.
- Paul, G.S., 1988. *Predatory Dinosaurs of the World: A Complete Illustrated Guide*. Simon & Schuster, New York, pp. 1–464.
- Paulina Carabajal, A., Currie, P.J., 2012. New information of the braincase of *Sinraptor dongi* (Theropoda: Allosauridae): Ethmoidal region, endocranial anatomy, and pneumaticity. *Vertebrata Palasiatica* 2012, 85–101.
- Rauhut, O.W.M., 2003. Interrelationships and evolution of basal theropod dinosaurs. *Special Papers in Palaeontology* 69, 1–215.
- Rauhut, O.W.M., Werner, C., 1995. First record of the family Dromaeosauridae (Dinosauria: Theropoda) in the Cretaceous of Gondwana (Wadi Milk Formation, northern Sudan). *Paläontologische Zeitschrift* 69, 475–489.
- Rauhut, O.W.M., Milner, A.C., Moore-Fay, S., 2010. Cranial osteology and phylogenetic position of the theropod dinosaur *Proceratosaurus bradleyi* (Woodward, 1910) from the Middle Jurassic of England. *Zoological Journal of the Linnean Society* 158, 155–195.
- Sampson, S.D., Witmer, L.M., 2007. Craniofacial anatomy of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. In: Sampson, S.D., Krause, D.W. (Eds.), *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. *Society of Vertebrate Paleontology Memoir* 8, pp. 32–102.
- Sender, P., 2007. A new look at the phylogeny of Coelurosauria (Dinosauria: Theropoda). *Journal of Systematic Palaeontology* 5, 429–463.
- Sereno, P.C., Brusatte, S.L., 2008. Basal abelisaurid and carcharodontosaurid theropods from the Lower Cretaceous Elrhaz Formation (Aptian–Albian) of Niger. *Acta Palaeontologica Polonica* 53, 15–46.
- Sereno, P.C., Novas, F.E., 1993. The skull and neck of the basal theropod *Herrerasaurus ischigualastensis*. *Journal of Vertebrate Paleontology* 13, 451–476.
- Sereno, P.C., Dutheil, D.B., Iarochene, M., Larsson, H.C.E., Lyon, G.H., Hagwene, P.M., Sidor, C.A., Varricchio, D.J., Wilson, J.A., 1996. Predatory dinosaurs from the Sahara and Late Cretaceous faunal differentiation. *Science* 272, 986–991.
- Sereno, P.C., Martinez, R.N., Wilson, J.A., Varricchio, D.J., Alcober, O.A., 2008. Evidence for Avian Intrathoracic Air Sacs in a New Predatory Dinosaur from Argentina. *PLoS ONE* 3, e3303.
- Sereno, P.C., Tan, L., Brusatte, S.L., Kiegestein, H.J., Zhao, X., Cloward, K., 2009. Tyrannosaurid skeleton design first evolved at small body size. *Science* 326, 418–422.
- Smith, N.D., Makovicky, P.J., Hammer, W.R., Currie, P.J., 2007. Osteology of *Cryolophosaurus ellioti* (Dinosauria: Theropoda) from the Early Jurassic of Antarctica and implications for early theropod evolution. *Zoological Journal of the Linnean Society* 151, 377–421.
- Smith, N.D., Makovicky, P.J., Agnolin, F.L., Ezcurra, M.D., Pais, D.F., Salisbury, S.W., 2008. A *Megaraptor*-like theropod (Dinosauria: Tetanurae) in Australia: support for faunal exchange across eastern and western Gondwana in the Mid-Cretaceous. *Proceedings of the Royal Society of London* 275, 2085–2090.
- Tsuihiji, T., Watabe, M., Togtbaatar, K., Tsubamoto, T., Barsbold, R., Suzuki, S., Lee, A.H., Ridgely, R.C., Kawahara, Y., Witmer, L.M., 2011. Cranial osteology of a juvenile specimen of *Tarbosaurus bataar* (Theropoda, Tyrannosauridae) from the Nemegt Formation (Upper Cretaceous) of Bugin Tsav, Mongolia. *Journal of Vertebrate Paleontology* 31, 1–21.
- White, M.A., Cook, A.G., Hocknull, S.A., Sloan, T., Sinapius, G.H.K., Elliott, D.A., 2012. New Forearm Elements Discovered of Holotype Specimen *Australovenator wintonensis* from Winton, Queensland, Australia. *Plos One* 7 (6), e39364.
- White, M.A., Falkingham, P.L., Cook, A.G., Hocknull, S.A., Elliott, D.A., 2013. Morphological comparisons of metacarpal I for *Australovenator wintonensis* and *Raptor ornitholestoides*: implications for their taxonomic relationships. *Alcheringa* 37, 1–7.
- Witmer, L.M., 1997. The evolution of the antorbital cavity of archosaurs: A study in soft-tissue reconstruction in the fossil record with an analysis of the function of pneumaticity. *Memoirs of the Society of Vertebrate Paleontology* 3, 1–73.
- Xing, L., Bell, P.R., Persons, W.S., Ji, S., Miyashita, T., Burns, M.E., Ji, Q., Currie, P.J., 2012. Abdominal Contents from Two Large Early Cretaceous Compsognathids (Dinosauria: Theropoda) Demonstrate Feeding on Confuciusornithids and Dromaeosaurids. *Plos One* 7 (8), e44012.
- Xu, X., Norell, M.A., Kuang, X., Wang, X., Zhao, Q., Jia, C., 2004. Basal tyrannosauroids from China and evidence for protofeathers in tyrannosauroids. *Nature* 431, 680–684.
- Xu, X., Clark, J.M., Forster, C.A., Norell, M.A., Erickson, G.M., Eberth, D.A., Ji, A.C., Zhao, Q., 2006. A basal tyrannosauroid dinosaur from the Late Jurassic of China. *Nature* 439, 715–718.

- Zanno, L.E., Makovicky, P.J., 2013. Neovenatorid theropods are apex predators in the Late Cretaceous of North America. *Nature Communications* 3827, 1–9.
- Zheng, X., Xu, X., You, H., Zhao, Q., Dong, Z., 2009. A short-armed dromaeosaurid from the Jehol Group of China with implications for early dromaeosaurid evolution. *Proceedings of the Royal Society of London B* 277, 211–217.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.cretres.2014.04.007>.