

A new clade of archaic large-bodied predatory dinosaurs (Theropoda: Allosauroidae) that survived to the latest Mesozoic

Benson RBJ, Carrano MT & Brusatte SL.

Appendix S1

(a) Institutional abbreviations.

AODF, Australian Age of Dinosaurs, Queensland, Australia; BMNH, Natural History Museum, London, UK; BYU, Brigham Young University Museum of Geology, Provo, Utah, USA; FPD, Fukui Prefectural Dinosaur Museum, Fukui, Japan; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MCNA, Museo de Ciencias Naturales y Antropológicas (J.C. Moyano) de Mendoza, Mendoza, Argentina; MCF, Museo Carmen Funes, Plaza Huinul, Argentina; MIWG, ‘Dinosaur Isle’ Museum of Isle of Wight Geology, Sandown, UK; MNN, Musée National du Niger, Niamey, Niger; MPM Museo Padre Molina, Río Gallegos, Santa Cruz, Argentina; MUCP, Museo de Geología y Paleontología, Universidad Nacional del Comahue, Neuquén, Argentina; NCSM, North Carolina State Museum, Raleigh, USA; NMV, Museum of Victoria, Melbourne, Australia; OMNH, Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma, USA; UMNH, Utah Museum of Natural History, Salt Lake City, Utah, USA; ZPAL, Institute of Palaeobiology, Polish Academy of Sciences, Warsaw, Poland.

(b) Comparisons.

We directly examined all specimens of *Chilantaisaurus*, *Megaraptor* and *Neovenator*, and inspected high-quality casts and original bones of *Aerosteon* and published images of *Australovenator* (Hocknull *et al.* 2009), *Fukuiraptor* (Azuma & Currie 2000; Currie & Azuma 2006) and *Orkoraptor* (Novas *et al.* 2008). This formed part of an ongoing review of the taxonomy and systematics of basal theropods (MTC, RBJB & S.D. Sampson unpublished data; Carrano & Sampson 2004, 2008; Brusatte & Sereno 2008; Benson in press). A summary of the comparisons made here is presented in table S1.

	Dorsal postzygapophyseal flanges	Ventral ridge in proximal caudals	Short. scapula .length:width 8.0–9.0	Precetabular shelf on ilium	Femur medial condyle projects distal	Pneumatic ilium	Tibia lateral condyle, anterolateral process curves ventrally	Postorbital, anterior process smooth and unexpanded	Atlas neural arch, pneumatic	Humerus: femur length ratio > 0.4	Humerus deltopectoral crest 0.43-0.49 humeral length	Metacarpal length: width ratio > 2.4	Manual ungual proximal height:width ratio > 2.3	Ulna, proximal crest on posterior surface	Distal tibia flat with medial ridge	Metatarsals, length:minimum width ratio > 12.5	Caudal pneumatic foramina	Prominent caudal neural arch lamina	Tall femoral lesser trochanter	Tall astragalar ascending process	Coracoid subglenoid fossa	Anteroproximal expansion of astragalar lateral condyle
Figure 1 part:	<i>b</i>	<i>e</i>	<i>d</i>			<i>i</i>	Fig. 2					<i>g, h</i>		<i>j</i>		<i>c</i>	<i>c</i>	<i>k</i>		<i>f</i>		
<i>Neovenator</i>	Y	Y	Y	Y	Y	Y	?	?	?	?	?	?	?	N	N	N	N	N	?N	N	?	
<i>Chilantaisaurus</i>	?	?	?	Y	?	?	?	?	?	Y	Y	?	Y	?	Y	N	?	?	?	?	?	
<i>Aerosteon</i>	Y	Y	Y	Y	?	Y	?	Y	Y	?	?	?	?	Y	?	Y	Y	?	Y	Y	N	
<i>Megaraptor</i>	?	?	Y	?	?	?	?	?	?	?	?	Y	Y	?	Y	Y	Y	?	?	Y	?	
<i>Orkoraptor</i>	?	?	?	?	?	?	Y	Y	?	?	?	?	?	?	?	Y	Y	?	?	?	?	
<i>Australovenator</i>	?	?	?	?	Y	Y	?	?	?	?	?	Y	Y	Y	Y	?	?	Y	Y	?	Y	
<i>Fukuiraptor</i>	?	?	?	?	Y	?	?	?	?	Y	Y	Y	Y	Y	?	?	?	Y	Y	N	Y	

Table S1. Distribution of neovenatorid synapomorphies.

Neovenator. *Neovenator* was originally described as an allosaurid by Hutt *et al.* (1996) and is known by three specimens from the Wessex Formation (Barremian, Lower Cretaceous) of the Isle of Wight, UK (MIWG 6348/BMNH R10001; MIWG 5470, 6352). Almost the entire skeleton of *Neovenator* is known; only the forelimb, most phalanges and the rear two-thirds of the skull are unknown. Parts of this material were described by Naish *et al.* (2001), who noted similarities with carcharodontosaurids: the presence of pneumatic foramina in all dorsal vertebrae and an expanded ischial boot. The specimens were comprehensively re-described by Brusatte *et al.* (2008), who uncovered numerous additional skeletal features supporting allosauroid affinities and a closer relationship to carcharodontosaurids than to *Allosaurus*. These include the camellate (Britt 1993) internal structure of pneumatic vertebrae, multiple pneumatic foramina located anteriorly in some cervical vertebrae, a deeply-concave, ‘socket’-like iliac articular surface of the ischium, a pubic boot measuring anteroposteriorly more than 60% the length of the pubis, and a proximomedially inclined femoral head. Subsequent phylogenetic analyses incorporating these observations have recovered high branch support for a position of *Neovenator* at the base of the Cretaceous allosauroid radiation (Brusatte & Sereno 2008; Benson in press). Importantly, Brusatte *et al.* (2008) identified several autapomorphies of *Neovenator*, unknown in other taxa at the time of their study, which are identified here as synapomorphies of a more inclusive clade.

Aerosteon. *Aerosteon*, from the Anacleto Formation (Santonian, Late Cretaceous) of Argentina, is represented by the holotype specimen (MCNA-PV-3137), a partial skeleton, and two tentatively referred specimens: a partial hindlimb (MCNA-PV-3139) and metatarsal II (MCNA-PV-3138; although as discussed below there is no justification for referral of this specimen) found within a few kilometres of the holotype (Sereno *et al.* 2008). Although the postorbital, prefrontal, quadrate and angular are known, these do not overlap with preserved cranial material of *Neovenator*. The scapulocoracoid, pelvis and parts of the axial column and hindlimb are represented. As in *Neovenator*, the forelimb is unknown.

A brief preliminary report of the specimens proposed carcharodontosaurid affinities (Alcober *et al.* 1998). However, the first description of *Aerosteon* concluded that it was an allosauroid of uncertain affinities (Sereno *et al.* 2008). *Aerosteon* has never been included in a phylogenetic analysis but we observe that it shares several features with carcharodontosaurids and *Neovenator*, such as double cervical anterior pneumatic foramina, pneumatic foramina in all dorsal vertebrae, transversely narrow, sheet-like dorsal hyposphenes (Fig S1c–d), and a ventral longitudinal ridge on the proximal caudal vertebrae. Many of these features can be observed in the figures of Sereno *et al.* (2008) and have been found as carcharodontosaurid synapomorphies in published phylogenetic analyses (Rauhut 2003; Brusatte & Sereno 2008; Benson in press).

Aerosteon also shares several features with *Neovenator*, suggesting a close relationship between the two taxa: (1) The lateral surfaces of the anterior dorsal centra converge ventrally to form a sharp, angular ventral ridge. A low mound-like eminence, representing the hypapophysis, is present at the anterior end of this ridge (Fig. S1a–b). This arrangement was previously regarded as an autapomorphy of *Neovenator* (Brusatte *et al.* 2008). (2) Both taxa possess small, flange-like lateral extensions of the middle and posterior dorsal postzygapophyses (Fig. S1c–d). This was also proposed as an autapomorphy of *Neovenator* (Brusatte *et al.* 2008). (3) The

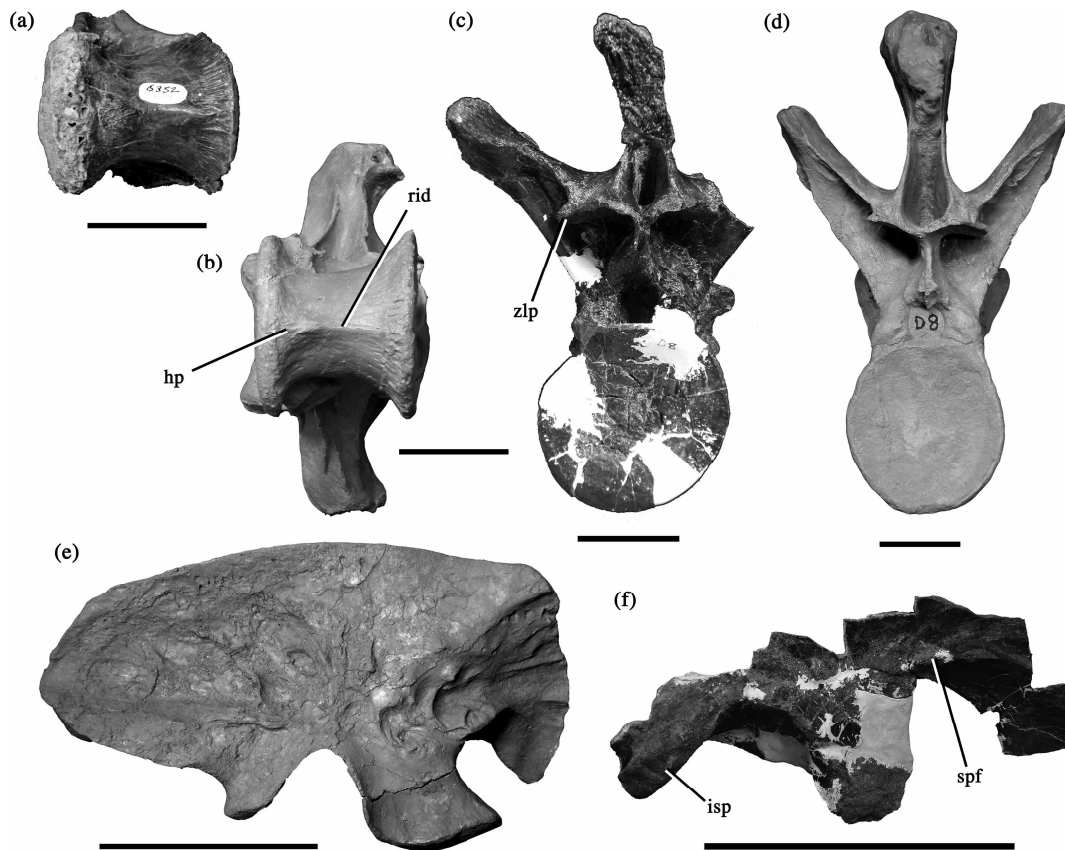


Figure S1. Vertebrae and ilium of *Neovenator* (a, MIWG 6352; c, f, holotype, BMNH R10001) and *Aerosteon* (b, d–e, holotype, MCNA-PV-3137) in ventral (a–b), posterior (c–d) and medial (e–f) views showing shared features. a, second dorsal vertebra; b, fourth dorsal vertebra; c–d, eighth dorsal vertebrae; e–f, left ilia. Abbreviations: isp, ischial peduncle; hp, hyposphene; rid, ridge; spf, preacetabular shelf; zlp, lateral process of postzygapophysis. Scale bars equal 50 mm (a–d) and 300 mm (e–f).

medial ridge bounding the preacetabular fossa of the ilium is hypertrophied to form a prominent shelf (Fig. 1e–f), possibly to strengthen the articulation with the anterior sacral ribs. This morphology is also found in tyrannosauroids (Holtz 2001), but is not present in other allosauroids or basal coelurosaurids (e.g., ornithomimosaurids: *Gallimimus*: ZPAL MgD-I/1, I/94). (4) Sereno *et al.* (2008) drew attention to evidence for appendicular pneumaticity in *Aerosteon*, including pneumatopores in the ilium, proposed as unique among non-maniraptoran theropods. However, the broken ilia of *Neovenator* contain internal spaces lined by finished bone surface, suggesting a similar pattern of pneumaticity (Brusatte *et al.* 2008). (5) In *Aerosteon* and *Neovenator* the scapular blade has a low ratio of length to minimum dorsoventral thickness (8.0–9.0; Fig. S2b) relative to those of other derived allosauroids such as *Allosaurus* (13.8; Fig. S2a) and *Acrocanthosaurus* (11.5; NCSM 14345).

There are also numerous general similarities between *Aerosteon* and *Neovenator*, many of which reflect the position of both taxa as allosauroids more derived than Sinraptoridae. One striking similarity is the proportions of the vertebrae (Fig. 1a–d), which are also similar to those in *Allosaurus*, but unlike the high-spined elements of sinraptorids and carcharodontosaurids. Gross similarity is also observed among appendicular bones, congruent with their allosauroid affiliation; for instance, the puboischiadic membrane is poorly ossified, and the pubic distal expansion ('boot') is anteroposteriorly expanded to over half the pubic shaft length;

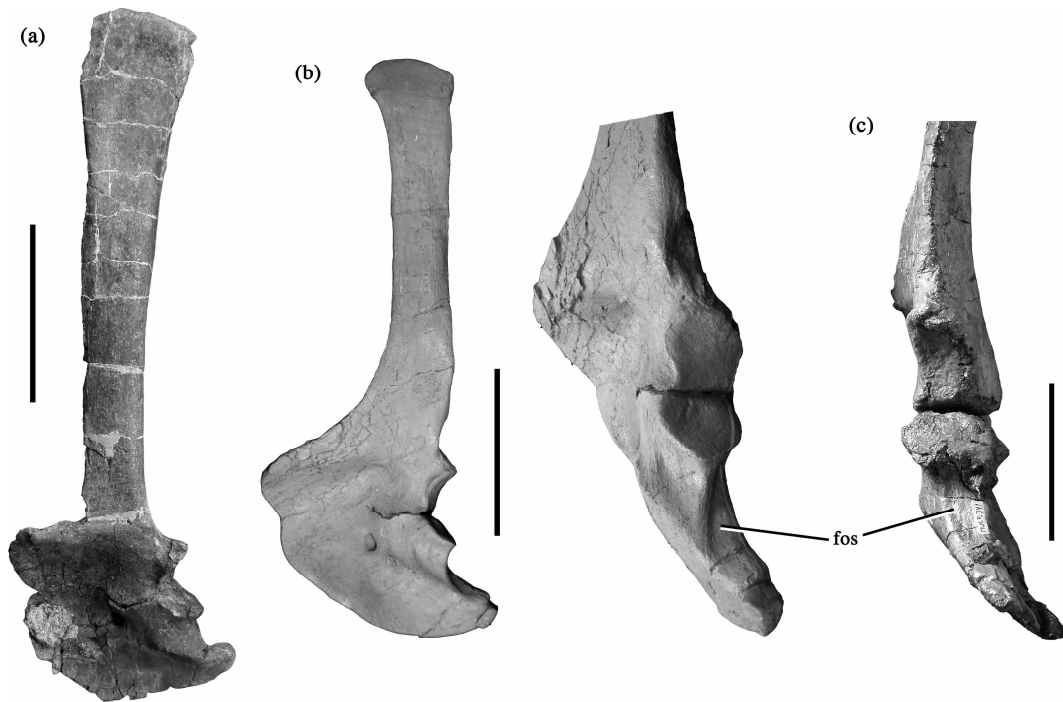


Figure S2: Allosauroid scapuloacoracoids: (a) right scapuloacoracoid of *Allosaurus fragilis* (reversed; BYU 8895) in lateral view; (b) left scapuloacoracoid of *Aerosteon* (MCNA-PV-3137) in lateral (right) and ventrolateral (left) views; (c) left scapuloacoracoid of *Megaraptor* (MUCPv 341) in ventral view. Abbreviations: fos, fossa. Scale bars equal 200 mm (a, b left) and 100 mm (b right, c).

the ‘boot’ is transversely broad and extends anteriorly beyond the margin of the shaft, unlike in most coelurosaurs in which the pubic boot is transversely narrow and lacks this extension. Furthermore, as in most allosauroids, the pubic peduncle of the ilium is just over twice as long anteroposteriorly as it is broad mediolaterally, proportionally longer than in other basal tetanurans, but shorter than in coelurosaurs, in which the peduncle is about three times as long as broad (Rauhut 2003).

Megaraptor. *Megaraptor* was originally described on the basis of a fragmentary specimen from the Río Neuquén Formation (Turonian–Coniacian) of Neuquén, Argentina (Novas 1998; MCF-PVPH 79). This comprised an ulna, manual phalanx I-1, the ungual phalanx of digit I, and the distal half of metatarsal III. Calvo *et al.* (2004) reported a second specimen (MUCPv 341), comprising a more complete forelimb, one cervical vertebra, two proximal caudal vertebrae, a scapuloacoracoid and a partial pubis from the Portezuelo Formation (Turonian–Santonian). In a very brief report, giving few details, Lamanna *et al.* (2004) reported two new fragmentary skeletons from the Lower Bajo Barreal Formation (middle Cenomanian–Turonian) of Chubut, Argentina.

Megaraptor was tentatively interpreted as a coelurosaure by Novas (1998), due to the slender proportions of metatarsal III and the enlarged, trenchant ungual phalanx (then supposed to belong to pedal digit II and thus resembling the condition in dromaeosaurids). However, Calvo *et al.* (2004) demonstrated that the ungual belonged to manual digit I, nullifying any such similarity. Instead, these authors suggested that *Megaraptor* might represent a new lineage of basal tetanurans more basal than Allosauroidea, as it possessed four metacarpals, a relatively short and broad scapular blade and a broad proximal pubis. However, some basal coelurosaurs

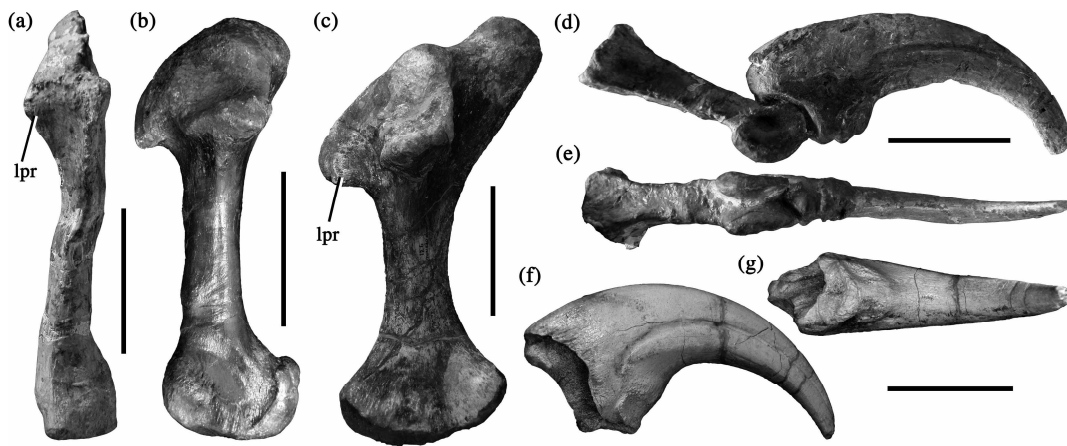


Figure S3. Ulnae and phalanges of *Megaraptor* (a, d–e, MUCPv 341), *Acrocanthosaurus* (b, NCSM 14345) and *Suchomimus* (c, f–g, holotype, MNN GDF 500) in anterior (a–c), lateral (d, f) and ventral (e, g) views. (a, c), right ulnae; (b), left ulna (reversed), (d–e), right phalanx I-2 and ungual I; (f–g), right ungual I. Abbreviations: lpr, lateral process. Scale bars equal 100 mm.

(Osborn, 1917; Xu *et al.*, 2006) and allosauroids (Currie & Zhao, 1994) also possess four metacarpals; *Aerosteon* and *Neovenator* have comparably short, broad scapulae; and it is not clear that a broad proximal pubis is primitive.

Subsequently, in a global phylogenetic analysis of theropods, Smith *et al.* (2007) recovered *Megaraptor* as a carcharodontosaurid allosauroid closely related to derived Gondwanan forms such as *Carcharodontosaurus* and *Giganotosaurus*. This is congruent with the suggestion of Lamanna *et al.* (2004), who proposed that *Megaraptor* was an allosauroid. However, Smith *et al.* (2008) later noted that *Megaraptor* uniquely shared a transversely compressed olecranon process of the ulna, and other features of the forelimb, with spinosaurids (Calvo *et al.* 2004), and recovered *Megaraptor* as a megalosauroid (= spinosauroid). However, some of the proposed synapomorphies are problematic. First, the lateral tuberosity of the ulna of *Megaraptor* is relatively small (Fig. S3a), comparable to, or smaller than, those of many other theropods, including the allosauroids *Allosaurus* (UMNH VP 11463) and *Acrocanthosaurus* (Fig. S3b; Currie & Carpenter 2000). We do not consider this condition homologous with the hypertrophied lateral tuberosity of spinosaurids (Fig. S3c). Second, although *Megaraptor* does possess a longitudinal ventral groove on manual phalanx I-1, this feature is not present in any preserved spinosaurid phalanges (BMNH R9951; MNN GDF 500) and therefore cannot be considered a synapomorphy of *Megaraptor* + Spinosauridae. Third, the first manual ungual of *Megaraptor* is elongate relative to that in many theropods, in common with some megalosauroids, including *Torvosaurus* (Britt 1991) and spinosaurids (Charig and Milner 1997, Sereno *et al.* 1998). However, in *Megaraptor* this bone is very narrow transversely, with a ratio of proximal height to width of 2.75 (Fig. S3d–e). This ratio is substantially higher than those of megalosauroids such as *Suchomimus* (1.75; Fig. S3f–g; MNN GDF 500) and *Torvosaurus* (1.95; BYU 17697). Most other basal tetanurans also have broad, thick manual unguals, including *Allosaurus* (1.6; Madsen 1976) and the carcharodontosaurid *Acrocanthosaurus* (Currie & Carpenter 2000). However, *Chilantaisaurus* (2.7; Hu 1964; Benson & Xu 2008), *Australovenator* (2.4; ungual ?III), and *Fukuiraptor* (2.5; ungual II; Azuma & Currie 2000) have tall, narrow manual unguals, comparable to those of *Megaraptor*.

Despite previous phylogenetic disagreement, several observations support the allosauroid affinities of *Megaraptor*. For instance, the cervical vertebrae strongly

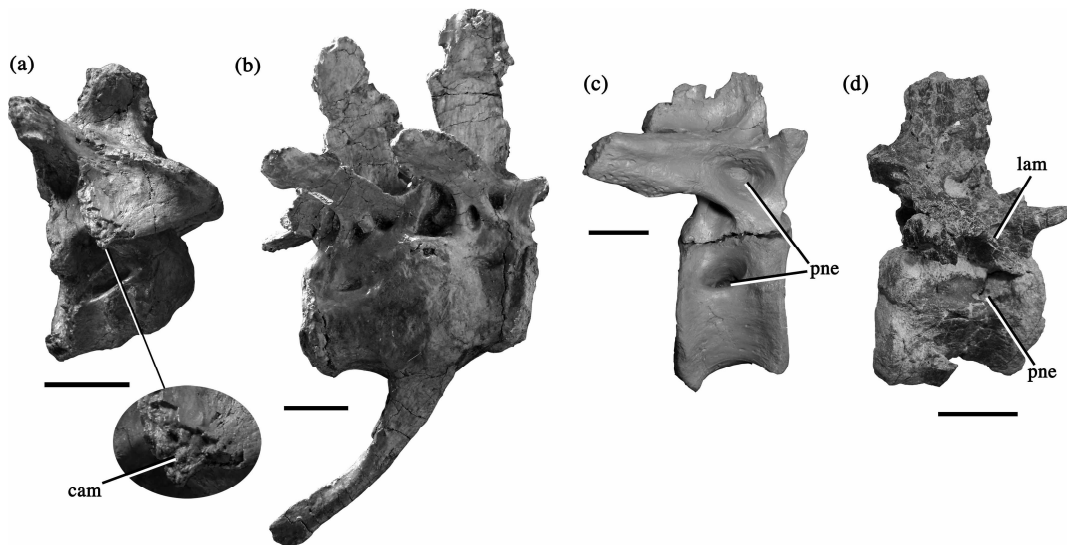


Figure S4: Vertebrae of *Megaraptor* (a–b, MUCPv 341), *Aerosteon* (c, holotype, MCNA-PV-3137) and *Orkoraptor* (d, holotype, MPM-Pv 3457) in right lateral (a–b, d) and left lateral (reversed, c) views. (a), cervical vertebra; (b–d), proximal caudal vertebrae. Abbreviations: cam, camellate internal pneumatic structure; lam, lamina; pne, pneumatic foramen. Scale bars equal 50 mm.

resemble those of carcharodontosaurids and possess a parapophysis located at centrum midlength, a weak but continuous prezygapophyseal-epipophyseal lamina, marked plasticity in the morphology of cervical pneumatic foramina (Calvo *et al.* 2004; Smith *et al.*, 2007) and a camellate internal structure to pneumatic vertebrae (Fig. 4A). As in most allosauroids the acromion process of the scapula is perpendicular to the blade (Molnar *et al.* 1990; Rauhut 2003). Among allosauroids, *Megaraptor* shares several features with *Aerosteon* as well as other taxa considered here: (1) pneumatic foramina (= pleurocoels) in proximal caudal vertebrae (Fig. S4b–d; also present in *Orkoraptor*, oviraptorosaurs; Osmólska *et al.* 2004; and a carcharodontosaurid described by Stromer 1931, pl. 1, fig. 10a; Rauhut 1995); (2) a marked fossa posteroventral to the coracoid glenoid (Fig. S2b–c; also present in dromaeosaurids, e.g. Norell and Makovicky, 1999); (3) a relatively short, broad scapula (Calvo *et al.* 2004; also present in *Neovenator*); and (4) prominent neural arch laminae in proximal caudal vertebrae defining fossa penetrate by foramina, probably pneumatic in origin (Fig. S4b–d). Although low neural arch laminae are present in the proximal caudal vertebrae of some abelisaurids (Bonaparte *et al.* 1990, Coria *et al.* 2002, O'Connor 2007), these are much lower and foramina are absent between them.

Orkoraptor. Novas *et al.* (2008) recently described *Orkoraptor* based on cranial fragments, teeth, the atlantal intercentrum, two proximal caudal vertebrae, a partial tibia and rib fragments (MPM-Pv 3457). The holotype derives from the early Maastrichtian Pari Aike Formation near Los Hornos Hill, in southwestern Santa Cruz Province, Argentina. The fragmentary specimen displays several autapomorphies, distributed across most of the preserved elements and (unusually) including several features of the dentition.

Two characters in particular seemed to indicate coelurosaurian affinities for *Orkoraptor*: (1) the absence of a mesial carina is shared with compsognathids and deinonychosaurs; and (2) the anterodorsally inclined anterior process of the postorbital is observed in some maniraptorans. However, although this feature is

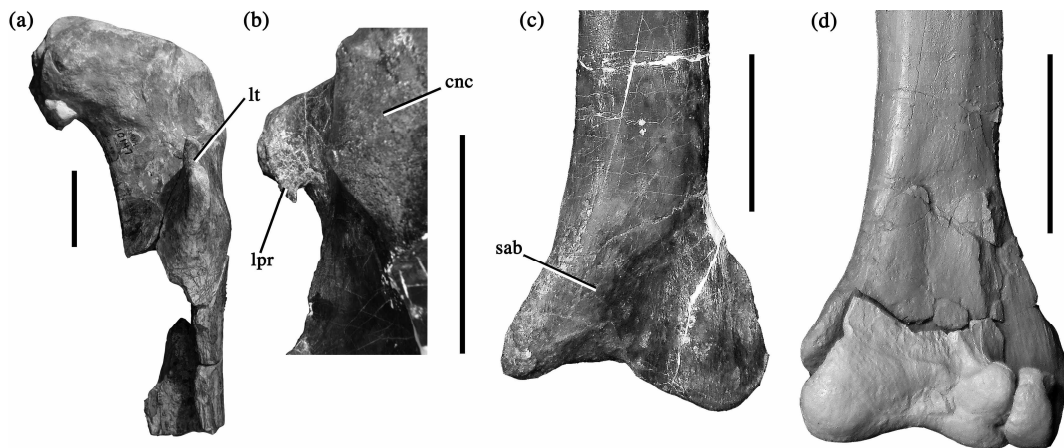


Figure S5: Allosauroid hindlimb bones and in anterior views. (a) left femur of *Acrocanthosaurus* (OMNH 10147); (b), right tibia of *Neovenator* (holotype, MIWG 6348); (c) left tibia of *Neovenator* (MIWG 6348); (d) left tibia and associated tarsals *Aerosteon* (MCNA-PV-3139). Abbreviations: cnc, cnemial crest; lpr, anterior process of lateral condyle; lt, lesser trochanter; sab, supracetabular buttress. Scale bars equal 100 mm.

present in derived coelurosaurs, the preserved portion of the postorbital of *Orkoraptor* is almost identical to that of *Aerosteon* (Fig. 2). Novas *et al.* (2008) added *Orkoraptor*

to the data matrix of Makovicky *et al.* (2005), which includes a selection of coelurosaurs plus *Allosaurus* and *Sinraptor* as outgroups, and recovered it in an unresolved position near the base of Maniraptora. Given the construction of this matrix and the selection of outgroups, it would be difficult to recover *Orkoraptor* in a more primitive position than this, and we do not consider the hypothesis of non-coelurosaur affinities to have been adequately tested. Notably, *Orkoraptor* shares the presence of a pneumatopore on the dorsolateral surface of the atlantal neural arch with *Aerosteon* (Serenó *et al.* 2008, fig. 5A), and the presence of pneumatic foramina and prominent neural arch laminae in proximal caudal centra with both *Aerosteon* and *Megaraptor* (Fig. S4b–d).

***Australovenator*.** *Australovenator* was described by Hocknull *et al.* (2009) based on a partial skeleton (AODF 604) from the Winton Formation (latest Albian) of the ‘Matilda Site’, northwest of Winton, Queensland, Australia. AODF 604 comprises a dentary, ribs, partial forelimbs, ilium and hindlimbs. A detailed description of the astragalus revealed many distinctive features, several of which were also observed in *Fukuiraptor*: an anteroposteriorly and medially expanded medial condyle; a prominent anteroproximal extension of the medial condyle; and a tall, quadrangular ascending process. The astragalus of *Aerosteon* is also similar in possessing a tall ascending process, but lacks the other features of *Australovenator* and *Fukuiraptor* (Fig. S5d); these features are absent in other allosauroids (e.g. Madsen 1976; Currie & Carpenter 2000; Hocknull *et al.* 2009). The phylogenetic analysis of Hocknull *et al.* (2009) recovered *Australovenator* as a basal carcharodontosaurid, more derived than both *Allosaurus* and *Fukuiraptor*.

Australovenator possesses various features that support its membership in the Cretaceous allosauroid radiation, including a femoral lateral condyle that projects further distally than the medial condyle and a proximally inclined femoral head (Hocknull *et al.* 2009). The degree of proximal inclination is less than that in carcharodontosaurids such as *Acrocanthosaurus* (OMNH 10167; Fig. S5a), but comparable to that in *Neovenator* (Hutt *et al.* 1996, fig. 4A). *Australovenator* also

shows additional features uniquely in common with the taxa of interest here: (1) a crest extending distally along the posterior surface of the ulna from the olecranon process; (2) transversely narrow manual ungual phalanges; (3) the femoral lesser trochanter extends to the proximal end of femur (present in *Fukuiraptor*, Azuma & Currie 2000; absent in all other basal tetanurans, including *Neovenator*); (4) the anterolateral process of the tibial lateral condyle curves ventrally (present in *Neovenator* Fig. S5b and indeterminate in other focal taxa but absent in other allosauroids and basal tetanurans; e.g. Madsen 1976); (5) a pneumatic ilium; (6) anterior surface of the distal tibia flat with a narrow medial buttress (shared with *Aerosteon*: Fig. S5d; although a supra-astragalar buttress is primitively present here in *Neovenator*: Fig S5c); (7) slender metatarsal III with ratio of length to minimum transverse width of approximately 13.0 (shared with *Fukuiraptor* and *Megaraptor*; *Chilantaisaurus* [ratio = 7.0] and *Neovenator* [ratio = 7.8] have robust metatarsals).

***Fukuiraptor*.** *Fukuiraptor* was described by Azuma & Currie (2000) based on the holotype specimen (FPDM-V97122), an associated skeleton from the Kitadani Formation (Albian, Lower Cretaceous) of the Kitadani quarry, Katsuyama, Japan. FPDM-V9712201-28 comprises dentary and maxillary fragments, a dorsal centrum and distal caudal vertebra, and a partial appendicular skeleton representing an individual estimated as 4.2 m long with a mass of 175 kg (Azuma & Currie 2000). Fragmentary theropod material (FPDM-V9712229-43) from the Kitadani quarry was tentatively referred to *Fukuiraptor* but most was not figured. This material would benefit from further study, as features suggestive of carcharodontosaurid affinities were mentioned, such as the possible presence of double cervical anterior pneumatic foramina (Azuma & Currie 2000:1739). Additional teeth and appendicular bones from the type locality, housed at the FPDM, were described by Currie & Azuma (2006). Despite its small body size, the holotype is still the largest individual represented, which may indicate either ontogenetic maturity or taphonomic filtering. Therefore, it is not established whether this specimen represents a full-sized individual and histological work is required to confirm its ontogenetic status.

Fukuiraptor was originally identified as a dromaeosaurid based on misidentification of the large, transversely compressed manual unguals as pertaining to the pes (Azuma & Currie 1995). Azuma & Currie (2000), and later Holtz *et al.* (2004), recovered *Fukuiraptor* as a basal allosauroid ('carnosaur') in cladistic analyses. They noted features such as fused interdental plates, *Allosaurus*-like forelimb proportions and the 'wing-like' morphology of the femoral lesser trochanter. They also observed the presence of features that had independently arisen in coelurosaurs, such as the slender humerus, ulna and metatarsus, and extension of the lesser trochanter to the proximal end of the femoral head. *Fukuiraptor* has subsequently been recovered as an allosauroid more basal than Carcharodontosauridae and *Neovenator* (Hocknull *et al.* 2009) and as a basal neotetanuran outside of Allosauroidea and Coelurosauria (Benson in press), and so is currently considered as a basal neotetanuran or allosauroid of uncertain affinities.

We observe that *Fukuiraptor* shares numerous features with other taxa discussed here: (1) as in *Megaraptor* and *Chilantaisaurus* the manual ungual phalanges are transversely compressed relative to those of other basal tetanurans; (2) a crest extends distally from the olecranon process along the posterior surface of the ulna, a morphology proposed as an autapomorphy of *Megaraptor* by Smith *et al.* (2008); (3) the ascending process of the astragalus is 1.7 times the height of its body, comparable to that in *Aerosteon* and *Australovenator* but taller than in other basal

tetanurans, including the allosauroids *Acrocanthosaurus* and *Allosaurus*, in which the height of the process is subequal to the body (Welles & Long 1974; Currie & Carpenter 2000); (4) the metatarsals are long and slender; metatarsal III has a length to minimum transverse width ratio of 13.3, comparable to *Australovenator* and *Megaraptor*, but much more gracile than those of other basal tetanurans (Azuma & Currie 2000), which are generally comparable to *Eustreptospondylus* (8.5; OUMNH J.13558) or *Piatnitzkysaurus* (9.4; MACN-CH 895).

Based on the figures of Azuma & Currie (2000), a referred theropod coracoid (FPDM-V9712243) found five metres from the holotype lacks the marked fossa posteroventral to the coracoid glenoid of *Aerosteon* and *Megaraptor* (Azuma & Currie 2000), this may reflect the primitive retention of absence, as in *Neovenator*. Also, the head of the holotype femur (FPDM-V9712219) is oriented horizontally and not proximomedially as in carcharodontosaurids. However, the femoral shaft is crushed and possibly distorted so it is not clear whether this is the original orientation. Nonetheless, in the phylogenetic analysis detailed below, inclination of the femoral head was scored as horizontal in *Fukuiraptor*.

***Chilantaisaurus*.** *Chilantaisaurus tashuikouensis* was described by Hu (1964), based on a partial appendicular skeleton (IVPP V.2884) from the Ulansuhai Formation (?Turonian, Late Cretaceous) of Inner Mongolia, China. IVPP V.2884 represents a colossal individual, comparable in femoral length to some of the largest theropods, including *Acrocanthosaurus*, *Gigantoraptor* and *Suchomimus* (Benson & Xu 2008). *Chilantaisaurus* has been referred to as a member of Allosauroidea (Harris 1998; based on a chimaera of *Chilantaisaurus* and the Ulansuhai Formation carcharodontosaurid *Shaochilong*), Megalosauroidea (Spinosauroidea; Rauhut 2003) and as a tetanuran of uncertain affinities (Holtz *et al.* 2004). Benson & Xu (2008) redescribed IVPP V.2884 and demonstrated the presence of neotetanuran features, such as an iliac preacetabular fossa and a trapezoidal ('wedge-shaped') cross-section of metatarsal III. Although they were unable to determine whether *Chilantaisaurus* was an allosauroid or a basal coelurosaur, they did note that if it was an allosauroid then the presence of a prominent medial shelf bounding the preacetabular ('cuppedicus') fossa might suggest affinities with *Neovenator* (Fig. S1f). This morphology is also present in *Aerosteon* (Fig. S1e).

Several additional features are shared between *Chilantaisaurus* and other taxa considered here, including *Neovenator*, *Australovenator* and *Aerosteon*. (1) *Chilantaisaurus* has an enlarged manual ungual I with a transversely narrow cross-section. (2) The flat anterior surface of the distal tibia is bounded medially by a vertical ridge. Rauhut (2003) suggested that this indicated a relationship with spinosaurids such as *Suchomimus* (MNN GDF 500), but is also present in *Aerosteon* (Fig. S5d) and *Australovenator* (Hocknull *et al.* 2009). The morphology of the distal tibia is different in most other basal tetanurans, which possess a prominent, proximolaterally oriented supra-astragalar buttress on the anterior surface of the distal tibia (e.g. Madsen 1976; Bonaparte 1986). In *Neovenator* and carcharodontosaurids, including *Acrocanthosaurus* (OMNH 10147), *Mapusaurus* (Coria & Currie 2006) and *Gigantosaurus* (MUCPv-Ch 1) the supra-astragalar buttress is reduced in height and forms a broad, rounded ridge (Fig. S5c). This is also different from the morphology in *Aerosteon*, *Australovenator* and *Chilantaisaurus*. (3) *Chilantaisaurus* also possesses a weakly proximomedially inclined femoral head. The degree of proximomedial inclination is less than in *Acrocanthosaurus* (Fig. S5a), but comparable to that seen in *Australovenator* (Hocknull *et al.* 2009).

Benson & Xu (2008) proposed that the presence of a reduced femoral fourth trochanter and reduced iliac anteroventral process might suggest affinities with basal coelurosaurs. However, if *Chilantaisaurus* represents a hitherto unrecognised coelurosaurian lineage then it must be extremely basal, as it lacks many features present in all other coelurosaurs. For instance, although the iliac pubic peduncle is incompletely preserved, the morphology of its base is only consistent with an anteroposterior length to mediolateral width around 2.0, the ratio seen in allosauroids. Also, the femoral greater trochanter is transversely narrow and not anteroposteriorly expanded into a trochanteric crest, as in all coelurosaurs (Hutchinson 2001). The Turonian age of *Chilantaisaurus* implies a ghost lineage of at least 70 million years if it diverged around the time of the earliest-known coelurosaur, *Proceratosaurus* (Bathonian, Middle Jurassic), and is more consistent with a position within the Cretaceous allosauroid radiation.

(c) Phylogenetic analysis.

In order to demonstrate the systematic affinities of the focal taxa, they were coded for a version of the cladistic data matrix of Benson (in press), modified to reflect our observations in this paper. This matrix was devised specifically to elucidate basal tetanuran relationships and a high proportion of the scores are based on direct examination of specimens (Benson in press). *Aerosteon*, *Australovenator*, *Orkoraptor* and *Shaochilong*, which was recently recognized as a carcharodontosaurid (Brusatte *et al.* 2009), were added to the data matrix, and the scores of *Chilantaisaurus*, *Megaraptor* and *Neovenator* were revised. New characters were added to summarise variation in these taxa and also to reinforce ceratosaurian monophyly based on the results of Carrano & Sampson (2008). This resulted in a matrix of 45 taxa and 233 characters. Details of these modifications, including new characters and taxon scores are given in section (d) of this appendix and a nexus file of the resulting data set is available on request from RBJB.

The matrix was analysed following the search strategy of Benson (in press). The Parsimony Ratchet (Nixon 1999) as implemented by PAUPRat (Sikes & Lewis 2001) combined with PAUP* 4.0b10 for Macintosh (Swofford 1998) was used to search for islands of shortest length trees, which were then explored using Tree Bisection and Reconnection (TBR; Swofford & Olsen 1990) branch swapping implemented by PAUP* 4.0b10. This resulted in 864 most parsimonious trees (MPTs) of length 637 steps, an ensemble consistency index (CI) of 0.4427, a retention index (RI) of 0.6385 and a rescaled consistency index (RC) of 0.2827. The strict consensus of these cladograms included areas of poor resolution (Fig. S6a). For instance, Megalosauridae (*sensu* Benson in press) was completely unresolved within the clade of Megalosauridae + Spinosauridae. This resulted from the unstable phylogenetic position of *Piveteausaurus*. Strict reduced consensus (Wilkinson 2003) was implemented by pruning of *Piveteausaurus* from the set of 864 MPTs. This resulted in a reduction to 54 unique topologies and full resolution of Megalosauridae (Fig. S6b). Poor resolution among more basal megalosauroids and basal tetanurans resulted from the unstable position of *Chuandongocoelurus*, which could either be the most basal tetanuran or form the sister taxon of *Monolophosaurus* (as suggested by Zhao *et al.* 2009) within Megalosauroidea. Pruning of *Chuandongocoelurus* halved the number of unique topologies (consistent with its adoption of two equally parsimonious placement) and resulted in a fully resolved Megalosauroidea (*sensu* Benson in press).

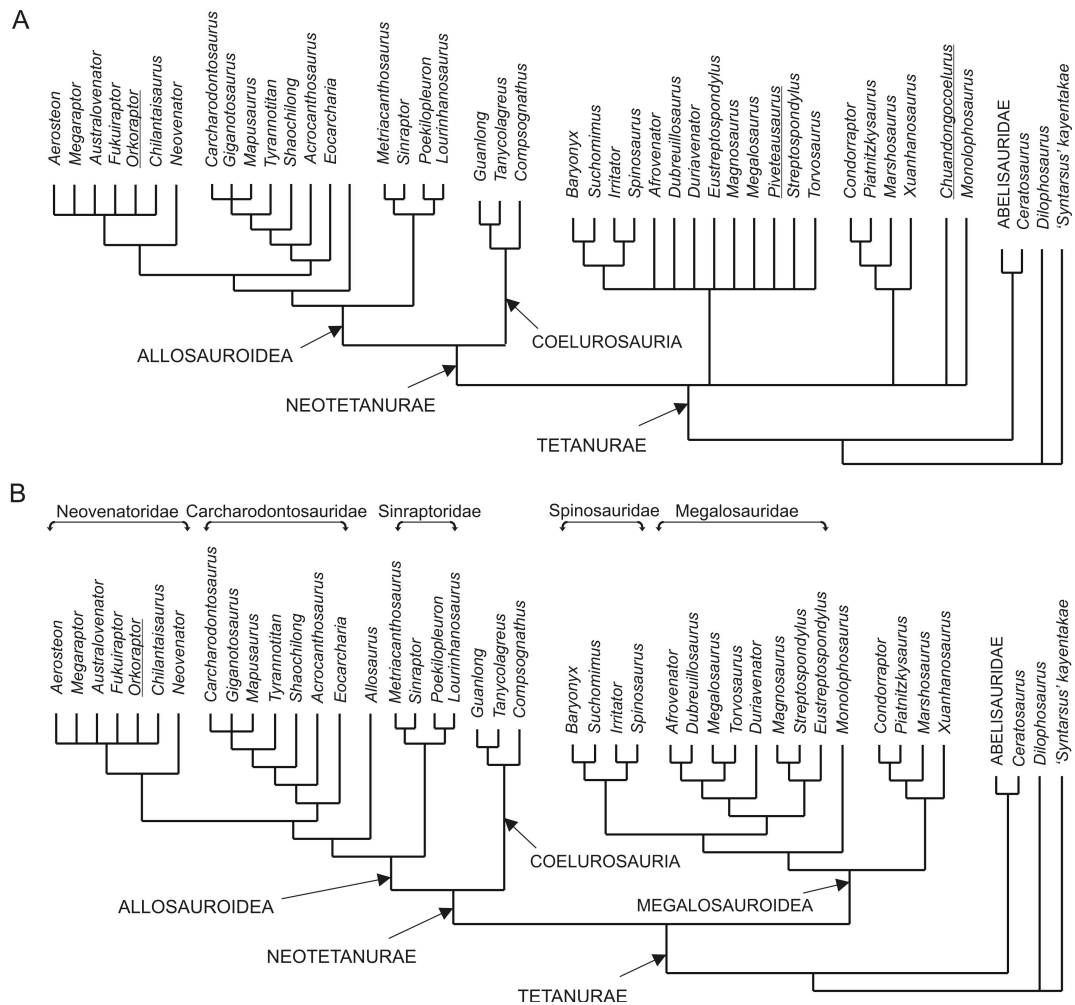


Figure S6. Consensus cladograms from analysis of data set of 45 taxa and 233 characters. ‘Wildcard’ taxa are underlined. A, strict consensus; B, strict reduced consensus after *a posteriori* pruning of *Chuandongocoelurus* and *Piveteausaurus*.

Regardless of lack of resolution among basal tetanurans, a monophyletic Neotetanurae (Allosauroidae + Coelurosauria) was present in the strict consensus, Allosauroidae comprised Sinraptoridae, *Allosaurus*, and a monophyletic grouping of

Cretaceous allosauroids (Figs 3, S6). This grouping contained two major monophyletic clades. The first was well-resolved and included seven taxa that have almost exclusively been regarded as carcharodontosaurids; the second, here termed Neovenatoridae (see below), included *Neovenator*, *Aerosteon*, *Australovenator*, *Chilantaisaurus*, *Fukuiraptor*, *Megaraptor* and *Orkoraptor*. All nodes within Allosauroidae have Bremer support (Bremer 1988) values of 1. This contrasts with support values from analysis of the original data matrix (Benson in press), which were exceptionally high for the clade of Cretaceous allosauroids (5; excluding *Fukuiraptor* which was recovered as a basal neotetanuran) and Carcharodontosauridae excluding *Neovenator* (4). It is likely that the addition of several highly fragmentary forms (Table S2) with limited osteological overlap caused the deflation of support values. Only one node within Neovenatoridae was resolved in the strict consensus: *Neovenator* was the sister taxon of all other neovenatorids. However, the most incomplete taxon, *Orkoraptor* shows little anatomical overlap with many of the better-known taxa and formed the sister taxon of any OTU or node among

Neovenatoridae more derived than *Neovenator* with equal parsimony. When *Orkoraptor* was pruned from the set of MPTs the number of unique topologies was reduced to 96 (from 864; or to 3 when accompanied by deletion of *Chuandongocoelurus* and *Piveteausaurus*). The resulting strict reduced consensus contains a fully-resolved Neovenatoridae. This includes a derived clade comprising sister taxon pairings of *Aerosteon* with *Megaraptor* and *Australovenator* with *Fukuiraptor* (Fig. 3).

OTU	Missing data	OTU	Missing data
<i>Allosaurus fragilis</i>	0.4		
<i>Aerosteon riocoloradensis</i>	65.7	<i>Acrocanthosaurus atokensis</i>	11.6
<i>Australovenator wintonensis</i>	72.9	<i>Eocarcharia dinops</i>	87.6
<i>Chilantaisaurus tashuikouensis</i>	86.3	<i>Carcharodontosaurus saharicus</i>	65.7
<i>Fukuiraptor kitadanensis</i>	74.7	<i>Giganotosaurus carolinii</i>	32.6
<i>Megaraptor namunhuaiquii</i>	85.4	<i>Mapusaurus roseae</i>	46.8
<i>Neovenator salerii</i>	35.6	<i>Shaochilong maortuensis</i>	81.9
<i>Orkoraptor burkei</i>	89.7	<i>Tyrannotitan chubutensis</i>	77.3

Table S2: Proportion of missing data for *Allosaurus* and carcharodontosaurians. Neovenatorids are listed in the left column and carcharodontosaurids in the right column. Taxa not included in the analysis of Benson (in press) are indicated in bold type.

Because the referred specimens of *Aerosteon* (MCNA-PV-3138, 3139) do not overlap with the holotype (MCNA-PV-3137) and cannot be demonstrated to represent the same taxon, scores based on the referred specimens were removed from the matrix. MCNA-PV-3139 was then added as a separate OTU and the data were reanalysed. This resulted in 20064 MPTs of 637 steps. The topology of the strict consensus cladogram was identical to that recovered by the original analysis (Fig. S6a). Both *Aerosteon* specimen OTUs (MCNA-PV-3137, 3139) were recovered in a polytomy comprising Neovenatoridae more derived than *Neovenator*. Even after pruning of *Orkoraptor* this node lacked internal resolution, presumably due to the reduced degree of anatomical overlap between neovenatorid OTUs. This result supports the provisional referral of MCNA-PV-3139 to *Aerosteon*, but there is no grounds to refer the isolated metatarsal II (MCNA-PV 3138), which does not show any neovenatorid synapomorphies or features of clades or taxa within Neovenatoridae.

(d) Systematic Palaeontology

Dinosauria Owen, 1842

Theropoda Marsh, 1881

Tetanurae Gauthier, 1986

Allosauroidea Marsh, 1878

Carcharodontosauria new clade

Included taxa: Carcharodontosauridae and Neovenatoridae.

Phylogenetic definition: The most inclusive clade comprising *Carcharodontosaurus saharicus* and *Neovenator salerii* but not *Allosaurus fragilis* or *Sinraptor dongi* (rank-free, stem-based).

Diagnosis: Allosauroid theropods diagnosed by numerous unambiguous synapomorphies: nasals of subequal width throughout their length; pneumatic quadrate (reversed in *Shaochilong*); a single Meckelian foramen in the dentary; ventral surface of axial intercentrum inclined anterodorsally; camellate (*sensu* Britt 1993) vertebral pneumaticity; double anterior pneumatic foramina (pleurocoels) variably developed in the cervical series; pneumatic foramina present in all presacral vertebrae; dorsal hyposphenes forming transversely-narrow sheets; anteroposterior length of pubic distal expansion more than 60% of pubic shaft length; iliac articular surface of ischium deeply concave ('socket'-like); femoral head inclined proximomedially (possibly reversed in *Fukuiraptor*); medial malleolus of distal tibia projects almost medially; supra-astragalar ridge of tibia reduced to a low convexity (transformed in *Chilantaisaurus* and more derived neovenatorids) proximomedial fossa of fibula more than two-thirds the proximal anteroposterior width of the fibula; ratio of fibular distal anteroposterior width to minimum shaft width less than 1.7.

Various potential synapomorphies of Carcharodontosauria recovered under ACCTRAN optimisation are only known among carcharodontosaurids: pneumatic jugal; supraoccipital extends ventrolaterally, forming a large contribution to dorsal margin of foramen magnum; neck of occipital condyle invaded by a pair of ventrolateral pneumatic cavities that join medially within the bone. Some of these features represent reversals from the primitive condition for Allosauroidea: width between basal tubera greater than occipital condyle width; exoccipital-opisthotic not separated from basal tubera by a notch; two posterior surangular foramina present. *Remarks:* The content of this clade effectively matches that of Carcharodontosauridae as previously defined (Holtz *et al.* 2004, 102: *Carcharodontosaurus saharicus* and all taxa sharing a more recent common ancestor with it that with *Allosaurus fragilis* or *Sinraptor dongi*; Sereno *et al.* 2005; Brusatte & Sereno 2008). However, under this definition 'Carcharodontosauridae' (*sensu* Holtz *et al.* 2004) contains many more taxa than when it was originally defined, encompassing all Cretaceous allosauroids. We believe that the distinctive features of *Neovenator* and close relatives justify familial distinction and, as such, it is more practical to erect a rank-free name, Carcharodontosauria, for the entire well-supported clade of allosauroids more closely related to *Carcharodontosaurus* than to *Allosaurus* and *Sinraptor*. Note that the occurrence of *Allosaurus* in the Late Jurassic (e.g. Gilmore 1920, Madsen 1976) implies the presence of basal carcharodontosaurians during this epoch.

Family Neovenatoridae new family

Included taxa: *Neovenator salerii*, *Aerosteon riocoloradensis*, *Australovenator wintonensis*, *Fukuiraptor kitadanensis*, *Megaraptor namunhuaiquii*, *Orkoraptor burkei* and *Chilantaisaurus tashuikouensis*.

Additional included material: NMV P186076, an ulna from the Eumeralla Formation at Dinosaur Cove (late Aptian–early Albian), Victoria, Australia. This is not diagnostic to the genus or species level as potential autapomorphies are widely distributed among neovenatorids. Smith *et al.* (2008) suggested that the transversely narrow olecranon process of NMV P186076 indicated a relationship with *Megaraptor* but the specimen has been crushed transversely, accentuating its transverse narrowness. Otherwise, it does not show autapomorphies of any particular neovenatorid taxon.

Phylogenetic definition: The most inclusive clade comprising *N. salerii* but not *Ca. saharicus*, *A. fragilis* or *S. dongi* (stem-based).

Diagnosis: Carcharodontosaurian theropods diagnosed by several unambiguous synapomorphies: middle–posterior dorsal vertebrae with small, flange-like lateral extensions of the postzygapophyseal facets; proximal caudal vertebrae bearing ventral longitudinal ridge (independently derived in some carcharodontosaurids); scapula length to minimum anteroposterior width ratio of 7.5–9; iliac preacetabular fossa bounded dorsomedially by a prominent shelf; femoral lateral condyle projects further distally than medial condyle (independently derived in *Carcharodontosaurus*; Stromer 1931); ilium with external foramina and internal pneumatic spaces; anterolateral process of the tibial lateral condyle curves ventrally as a pointed process.

Additional features may be synapomorphies of Neovenatoridae but their condition is unknown in basal members: anterior process of postorbital transversely unexpanded and lacking surface rugosity of other allosauroids (only known in *Aerosteon* and *Orkoraptor*); pneumatic foramen in dorsolateral surface of atlantal neural arch (*Aerosteon* and *Orkoraptor*); ratio of humerus length to femur length at least 0.4 (*Australovenator*, *Chilantaisaurus* and *Fukuiraptor*); humerus deltopectoral crest length 0.43–0.49 times humeral length (increased from the condition in other allosauroids); anterior surface of distal humerus lacks well-defined fossa (*Chilantaisaurus* only); metacarpal IV present (*Megaraptor* only); gracile metacarpals at least 2.4 times as long as their minimum width; manual ungual phalanges dorsoventrally tall and transversely narrow with ratio of proximal height to width > 2.3; crest extends distally along posterior surface of ulna from olecranon process; vertical ridge on lateral surface of ilium absent (*Aerosteon* only).

Remarks: A derived grouping of neovenatorids excluding *Neovenator* is supported a single unambiguous synapomorphy: the presence of a vertical ridge located medially on the anterior surface of the distal tibia. The presence of an astragalar ascending process more than 1.6 times the height of the astragalar body may be correlated with the morphology of the distal tibia so we consider it as a synapomorphy of this derived clade although its condition is not known in *Neovenator*. The condition of other potential synapomorphies that diagnose this derived clade under the ACCTRAN optimization criterion is not known in *Chilantaisaurus*: posterodorsally inclined, step-like ridge located lateral to the hyposphene within the infrapostzygapophyseal fossa; pneumatic foramina (pleurocoels) in proximal caudal centra (only known in *Aerosteon* and *Megaraptor*); proximal caudal neural arches with prominent centrodiapophyseal laminae defining by deep fossae containing foramina (*Aerosteon*, *Megaraptor*, *Orkoraptor*); lesser trochanter extends to proximal end of femur (*Australovenator* and *Fukuiraptor*).

Megaraptora new clade

Included taxa: *Aerosteon*, *Australovenator*, *Fukuiraptor*, *Megaraptor*, *Orkoraptor*.

Additional included material: Hocknull *et al.* (2009) referred the isolated astragalus (NMVP 150070) described by Molnar *et al.* (1981) from the Wonthaggi Formation (Valanginian–Aptian, Lower Cretaceous) of Victoria, Australia to *Australovenator* based on its detailed resemblance with the holotype specimen. However, given its

older provenance and the numerous similarities with the astragalus of *Fukuiraptor*, we cannot exclude the possibility that it pertains to a distinct, but currently indeterminate, member of the same clade.

Phylogenetic definition. The most inclusive clade comprising *M. namunhuaiquii* but not *Ch. tashuikouensis*, *N. salerii*, *Ca. saharicus* or *A. fragilis* (rank-free, stem-based).

Diagnosis: Neovenatorid theropods with the following unambiguous synapomorphy: long, gracile metatarsals with a ratio of length to minimum width of at least 12.5. Incomplete knowledge of *Chilantaisaurus* and *Neovenator* means that other potential synapomorphies of Megaraptora are only recovered under DELTRAN optimization. These include: crest extends distally along posterior surface of ulna from olecranon process. Humeral distal condyles inclined anterodistally, giving the bone an S-shaped curve is recovered as a megaraptoran synapomorphy under ACCTRAN as it is only known in *Fukuiraptor*.

Remarks: Within Megaraptora, *Australovenator* and *Fukuiraptor* are united by a single unambiguous synapomorphy, a prominent posterolateral extension of the astragalus (Hocknull *et al.* 2009). A prominent fossa on the coracoid posteroventral to the glenoid is a unambiguous synapomorphy uniting *Aerosteon* and *Megaraptor*. The affinities of *Orkoraptor* within Megaraptora are currently uncertain.

Family Carcharodontosauridae Stromer, 1931

Included taxa: *Carcharodontosaurus saharicus*, *Acrocanthosaurus atokensis*, *Eocarcharia dinops*, *Giganotosaurus carolinii*, *Mapusaurus roseae*, *Shaochilong maortuensis*, *Tyrannotitan chubutensis*.

Revised phylogenetic definition: The most inclusive (stem-based) clade comprising *Carcharodontosaurus saharicus* but not *Neovenator salerii*, *Allosaurus fragilis* or *Sinraptor dongi*.

Diagnosis: Carcharodontosaurian theropods diagnosed by several unambiguous synapomorphies: promaxillary foramen of maxilla enlarged to form a fenestra (independently derived in sinraptorids); pneumatic fenestra in maxillary ascending process (= excavatio pneumatica; Witmer 1997), unlike in sinraptorids and *Ceratosaurus* this forms a distinct, open fenestra; postorbital contacts lacrimal; postorbital process developed as a small spur (transformed to a large, curving flange in *Acrocanthosaurus* and more derived carcharodontosaurids); anteroventral end of maxillary paracanthal groove (defining the dorsal margin of the interdental plates) slants anteroventrally.

The condition of other potential carcharodontosaurid synapomorphies recovered under ACCTRAN optimization is unknown in *Eocarcharia*: anterior end of dentary expanded dorsoventrally and squared off by anteroventral ‘chin’-like process; longitudinal groove on lateral surface of dentary around midheight well-defined; dorsal neural spines transversely broad anteriorly and posteriorly with central regions of the lateral surfaces embayed by deep troughs forming an ‘I-beam’-like structure; tall dorsal neural spines more than 1.9 times centrum height.

(e) New characters and revised scores.

Modified characters.

Ch. **115**. Lumped original states 0 (pleurocoels absent in dorsal vertebrae) and 1 (present in anterior dorsal vertebrae) to make a single state 0.
Dorsal vertebrae, pleurocoels (pneumatic foramina): absent or present in anterior dorsal vertebrae (0); present in all dorsal vertebrae (1) (Harris 1998, ch. 66; modified from Russell & Dong 1993, ch. 27).

Ch. **166**. Modified to reduce the number of states.
Ilium, pubic peduncle length to width ratio: approximately 1 or lower [non-tetanurans; *Eustreptospondylus*, *Fukuiraptor*] (0); 1.3–1.75 [megalosauroids, sinraptorids] (1); 2–2.5 [derived allosauroids] (2); 3 or greater [coelurosaurs] (3).

Ch. **174**. Included a new state: more than 60% shaft length (2).
Pubis, ratio of distal expansion length to shaft length: less than 0.3 (0); more than 0.5 (1); more than 0.6 [carcharodontosaurids] (2) (modified from Gauthier 1986, ch. 48)

Ch. **190**. Included a new state: lesser trochanter rises to level of proximal surface of femoral head (2) (*Australovenator*, *Fukuiraptor*, coelurosaurs).
Femur, placement of lesser trochanter: distal (0); around midheight of femoral head (1); rises to level of proximal surface of femoral head (2) (modified from Pérez-Moreno *et al.* 1999, ch. 39).

Ch. **206**. Included a new state: suprastragalar buttress present but reduced to a low, rounded, proximolaterally inclined ridge (3) (Fig. S5c: *Neovenator*, *Acrocanthosaurus*, *Giganotosaurus*, *Mapusaurus*).
Bracing for ascending process of astragalus on anterior side of distal tibia: distinct ‘step’ running obliquely from mediiodistal to lateroproximal (0); bluntly rounded vertical ridge on medial side (1); anterior side of tibia more or less flat (2); suprastragalar buttress present as a low, rounded, proximolaterally inclined ridge (3) (modified from Rauhut 2003, ch. 207).

Additional characters.

214. Middle posterior dorsal vertebrae, lateral small, flange-like lateral extensions of postzygapophyseal facets: absent (0); present (1) (Fig. S1c–d; New character; *Aerosteon*, *Neovenator*).

215. Proximal caudal vertebrae, neural arches: centrodiaepophyseal laminae weak (0); centrodiaepophyseal laminae present, comparable in prominence to those of the dorsal vertebrae (1) (Fig. S4b–d; new character; *Aerosteon*, *Megaraptor*, *Orkoraptor*).

216. Coracoid, prominent fossa posteroventral to glenoid: absent (0); present (1) (Fig. S2b–c; new character. *Aerosteon*, *Megaraptor*, dromaeosaurids).

217. Ilium, large external pneumatic foramina and internal spaces: absent (0); present (1) (New character. Sereno *et al.* 2008: *Aerosteon*, *Australovenator*, *Neovenator*).

- 218.** Maxilla, anterior end of dorsal margin of interdental plates on medial surface: horizontal (0); inclined anteroventrally (1) (New character; carcharodontosaurids, megalosaurids).
- 219.** Ulna, olecranon process: transversely broad and bulbous (0); transversely narrow and ‘blade-like’ (1) (Calvo *et al.*, 2004; Smith *et al.* 2008, ch. 348; *Megaraptor*, spinosaurids).
- 220.** Lateral teeth, mesial carina: present (0); absent (1) (*Orkoraptor*, compsognathids, deinonychosaurians).
- 221.** Metatarsal III, relative proportions: short and thick ratio of length:shaft transverse width <12.0 (0); long and gracile, ratio >12.5 (1) (*Australovenator*, *Fukuiraptor*, *Megaraptor*, various coelurosaurs).
- 222.** Maxilla, interdental plates: low, less than 1.5 times as high as wide (0); tall, more than 1.7 times as high as wide (1) (modified from Brusatte & Sereno 2008, ch. 15; *Megalosaurus*, *Torvosaurus*, derived carcharodontosaurids).
- 223.** Manual ungual phalanges, relative width: transversely broad proximal height:width <2.0 (0); transversely narrow, proximal height:width >2.4 (1) (Fig. S2d–e; new character. *Australovenator*, *Chilantaisaurus*, *Fukuiraptor*, *Megaraptor*, some coelurosaurs e.g. *Tanycolagreus*)
- 224.** Tibia, anterolateral process of the lateral condyle: absent or a horizontal projection (0); prominent and curves ventrally (1) (Fig. S5b; new character; *Australovenator*, *Neovenator*).
- 225.** Ulna, crest extends distally along posterior surface from olecranon process: absent (0); present (1) (Smith *et al.* 2008, ch. 350: *Australovenator*, *Fukuiraptor*, *Megaraptor*).
- 226.** Atlantal neural arch, pneumatic foramen in dorsolateral surface: absent (0); present (1) (New character; Sereno *et al.* 2008; *Aerosteon*, *Orkoraptor*).
- 227.** Astragalus, ascending process height: low, subequal to height of astragalar body or lower (0); high, at least 1.6 times the height of the astragalar body (1) (Welles & Long 1974; Hocknull *et al.* 2009; *Aerosteon*, *Australovenator*, *Fukuiraptor*, coelurosaurs).
- 228.** Femur, greater trochanter width: narrower than caput, outline in proximal view tapers laterally (0); as wide as caput forming trochanteric crest (1) (Hutchinson 2001; coelurosaurs).
- 229.** Dorsal neural arches, pneumaticity: moderate (0); extreme (1) (Ceratosauria; cf. Carrano & Sampson 2008).
- 230.** Sacral neural arches, pneumaticity: weak or absent (0); well-developed (1) (Ceratosauria; cf. Carrano & Sampson 2008).

231. Sacrum, transverse dimensions of mid-sacral centra relative to other sacrals: equivalent (0); constricted (1) (Ceratosauria; cf. Carrano & Sampson 2008).

232. Astragalus, prominent proximolateral extension: absent (0); present (1) (New character. Hocknull *et al.* 2009; *Australovenator*, *Fukuiraptor*).

233. Distal end of femur morphology: central depression connected to crista tibiofibularis by a narrow groove (0); anteroposteriorly oriented shallow trough separating medial and lateral convexities (1) (New character; see Benson 2009:figs 8–9; neotetanurans).

Revised scores.

Aerosteon ricoloradensis

????????????????????????????????????????????????????????????00000000????10?00????????????????????
 ??????????????01?0?0?10????????????102120101011000001????21????????10012?????????
 ?????????????10121201010122101????????????????????????????010101210?120??1111??0??
 ???11?0?0?

Australovenator wintonensis

????????????????????100????0????????????????????????????????????????????????????????????????
 00000??{12}?01?0?0?00????????????????????????????????????????????????????????????????10
 000?011??0?0????????????????????????????????????2012101111000101012102120?1??1?001?
 111?10??11

Chilantaisaurus tashuikouensis

????????????????????????????????????????????????????????????????????????????????????????
 ?????????????????????????????????????????????????????????????????????????????????????011001??????
 ???10??1212??1????????????????????2??{12}?11??1000??101?1??1??11??????0?1??
 ??0??1

Fukuiraptor kitadanensis

????????????????????1000????0????????????????????????????????????????????????????????????
 ???????0?0010?00?0????????????0{12}?{12}?1????????????????????????????????120010?
 ?100??????0?????1????1????????????????????101210111100010101??????011?0?0??
 101?1?10??1?

Megaraptor namunhuaiquii

????????????????????????????????????????????????????????????????????????????????????
 ?????????????????????????????????0212?1?1?1??????????1??1??11?12??????0000
 10111000?????????012????????????????????????????????????????????????????????11??1?1?1??
 ??????

Neovenator salerii

10??0000100110210100100110011101????????????????????????????????????0????????????
 ??10010002?0100100?0010?????111001102120111010000001?0?2010110101??12??
 ??????????????????0??121201010122101011?11120?110111100010101230111?111
 0010?000?1??0000?1

Orkoraptor burkei

????????????????????????????????????????????????0000000????????????????????
 ?????????????01?0?00?0????????????????????1????????????1????????????????
 ?????????????????????????????????????????????01010????????????1????1????1??
 ????

Shaochilong maortuensis

?????000000210101001000?????0?1????????????????????00?00????10100110110
 ?????????????????????????????100?110????????????????????????????????
 ?????????????????????????????????????????????????????????????????????
 ??????

Allosaurus fragilis

{01}011100010011021{01}10010000001010110{01}0131100101000001100010{01
 }0000010100011100010100012101001102001011110100011011101000000000100
 0001011?1021012100011100001001110011111201010121101001110100101110111
 0000101010001110110000000000000000001

Eocarcharia dinops

?????00001111212??01000????????????????????11000?1????????????????????
 ??????????1?01????10????????????????????????????????????????????????
 ?????????????????????????????????????????????????????????????????????
 ????

Acrocanthosaurus atokensis

10101?000001112121001000100000?02111121?0011112002111100010000000011
 01100012011001001001?020?1001101100?10021201?1?10120001?1?0010?1?10210
 121100110011111010100?11?????????221010101?011020111011100001010113021
 2011000?10001000?000?01

Carcharodontosaurus

?????0?0000021010100100010001111?11?21?0?11120?????????0011101??1??11
 011?????0????0?0010?0021?????????0?0?1?1?1?0?????????1????????????
 ?????????????????????????????????????????2??1201111?0?????????3?????????1?0?1?
 ???0?????

Giganotosaurus carolinii

00????00?000?10101?0100010002111?1?12110011112002???10?00?011101??10?1
 1011?2101001?0000010?0021?1??11000000212010101012000?0??20?0?10?0???1??
 ??????????????????0?1112010101221010101?01102011?01??0?010101230212???
 ???????1????0000?1

Mapusaurus roseae

?????0000021010100100010002111?1????1100111120?2???10?0000????????
 ???2101?0???000010?002101?????????02?2?1?1?1012000??1?20?0?1??21??11?
 011?????1?????0?????????1??????01?1101?02??1101?1?0001010123021?0110??
 ???10??000?01

Tyrannotitan chubutensis

????????????????????1?0????{12}????1????????????????????????????????

??2?01?0?????0??0?0020??????????0212?1?1?1012000??0??????????1?1????????
 ??????????0??????????0?2????????11????20?11011100??????1???2?????00????0???
 ???00??1

'Syntarsus' kayentakae

20?101100111100?0??0????000200?01021200?10?0000?1011100??0010002000000
 000??010?1??1?010??000?00?100?0?11001000001???0?00??00?10??????0??010
 110?0??????0?00001?0?00001?01010?011?0??000000100001{01}01101000000132?
 00??000??00?0?0000000

ABELISAURIDAE

001{01}000000002000{01}1001010{01}{01}0010?{01}2011000??0110020020110
 100010001{01}0000?00101?0010000110{12}0001010000010001?00010210000{01
 }01000100010000{01}2110011010011101000000?0100000{01}0100001000020?01
 00001001101100001101011100120??3200000000000000000011100

Afrovenator abakensis

???????0101110?1?1000000?????????01112100000001110?0101?1?000??????????
 ??????????????0?011020000????00011100?11?1?010?0?000?????????011100??????1?
 ???????1001??00?110111?0?0?20??1101?10110110100100000?00?1101001?1?00?
 010000000?000???

Baryonyx walkeri

21010?1121??????1110100?11?0????0011310010????????????00?0?????000100?11
 1?0?1010113?12100?1?1100011??11101101110100101020110??00??01?01??10?1
 110001100??????1?????11?1010?????0?00100??111??100001?????????01?????0?
 ?010?0000??0???

Ceratosaurus nasicornis

001110000001201010001000111000?01011131000000000100110110100000100000
 001010000000100010001010000000001?0000020000100000210001??10020100110
 101011000?????001000?1??100001?01010?010?00100110110000110101110011003
 3000000?00?0?0?0000011100

Compsognathus longipes

10???100000?002?0??000?000000?00010100?0??000?200?????0?0?10?0?????????
 ??????00??1?01001?02000010?0?1?????1?110100??000?000??00001?01111?01?
 ???1000??00?0100?00?13????01?101?1??100?1?????1?1?????0????1??????1?????
 0?100??01?0????

Condorraptor currumili

????????????????????????????????????????????????????????????????????????
 ??????????0100?0010?????????0011110?01010?000100?10?2?11??????????????
 ??????????0?1?0110?100?????0??100??????010100001000??????????00??00??0
 ???000??

Dilophosaurus wetherilli

201?0010011110000000{01}10{01}???20100201?100?101000?0101110000010??02
 000010001?001010011?101000010000?1?000?11000?0000000000100000?000201
 00000101001000100100010000110000001100000?00?0001??110110000000000000
 00000?2000000000000000000000000000

Dubreuillosaurus valesdunensis

1????001011201001000000????????011????00?0?111000??????00?000101101
0?0?101111100000110200001????????01?1??0?????0?0??00?0?1??1?0??????
????????????????????????????????????????????????????????????1??0?0?0?????1??000????????1?0?
00???????????

Eustreptospondylus oxoniensis

2????001100??11?1000000?????????11011000000011?000101?0?00?00010100
10?0?1011111?0000?00?0000?????1?111011101?000101000000?00?0?????1????0
12000?????????????????0?010110?0?20?0?101?001??111100100000000?0100000?010
00?00?000?0?0000000

Guanlong wucaii

0?00?001001102?0???????10000?02110102?00?000?00100??2??010?0?????????
?????0?01??110000?0?20?0?01?????????1?00?????00??0?0??0?1?????2????000??
?1000?1011010?21213?0?00?10?0?10?0?1????21????0?0????????0???1?1?0?0?0
00000001100001

Irritator challengeri

?????????0?02?0?11????11?000?01001130?010?0?0?0?0?0?2?000?00000100011
100?????????????1?0121101?110?????????????????????????????????????????????
?????????????????????????????????????????????????????????????????????????
?????????

Lourinhanosaurus antunesi

?????????????????????????????????????????????????????????????????????????
????????????????????????????????????01?1??000?0?000?0?10010?1??1?????????????
?????????0?1111?001?0?0?????01100??10111010?0?000?0110011????00?0???????
?00000?1

Magnosaurus nethercombensis

??????????????????00??????????????????????????????????????????????????1
011?1?????0?00?0000??????????0?????0?????0?????????????????????????????
?????????????????????????????????????????????????????????????????????????
?????

Marshosaurus bicentissimus

00??0000001001100000000??00??0?0?????????0??1100010000?0?00000000?11
100?????????1000?0?0?0?0?0??10011110111110000101000?????????????1?????0?
0??????????????0?????1?????????????????????????????????????????????????
?0????0?0?????

Megalosaurus bucklandii

??????00001?11?1000011?????????1?????????????????????????????????????
000011??000110?0010?0?0??????01?1?1?01010200000010010?????00?00?121??
000?????????001101110010?0?00101?1111011010010000001001100?????1000001
0001?00?00000?0

- Britt, B. B. 1991. Theropods of Dry Mesa Quarry (Morrison Formation, Late Jurassic), Colorado, with emphasis on the osteology of *Torvosaurus tanneri*. Brigham Young University Geology Studies 37, 1–72.
- Britt, B. B. 1993. Pneumatic postcranial bones in dinosaurs and other archosaurs. Unpublished PhD thesis, University of Calgary. 383 pp.
- 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.
- Carrano, M. T. & Sampson, S. D. 2004. A review of coelophysoids (Dinosauria: Theropoda) from the Early Jurassic of Europe, with comments on the late history of the Coelophysoidea. Neues Jahrbuch für Geologie und Paläontologie Monatshefte 2004, 537–558.
- Coria, R. A. & Currie, P. J. 2006. A new carcharodontosaurid (Dinosauria, Theropoda) from the Upper Cretaceous of Argentina. Geodiversitas 28, 71–118.
- Coria, R. A. & Salgado, L. 1995. A new giant carnivorous dinosaur from the Cretaceous of Patagonia. Nature 377, 224–226.
- Coria, R. A., Chiappe, L. M. & Dingus, L. 2002. A new close relative of *Carnotaurus sastrei* Bonaparte 1985 (Theropoda: Abelisauridae) from the Late Cretaceous of Patagonia. Journal of Vertebrate Paleontology 22, 460–465.
- Currie, P. J. & Carpenter, K. 2000. A new specimen of *Acrocanthosaurus atokensis* (Dinosauria: Theropoda) from the Lower Cretaceous Antlers Formation (Lower Cretaceous, Aptian) of Oklahoma, USA. Geodiversitas 22, 207–246.
- Currie, P. J. and Zhao, X. -J. 1994. A new carnosaur (Dinosauria: Theropoda) from the Jurassic of Xinjiang, People's Republic of China. Canadian Journal of Earth Sciences 30[for 1993], 2037–2081.
- Holtz, T. R. Jr. 2001 The phylogeny and taxonomy of the Tyrannosauridae. In *Mesozoic Vertebrate Life* (eds D.H. Tanke & K. Carpenter), pp. 64–83. Bloomington: Indiana University Press.
- Hutchinson, J. R. 2001. The evolution of femoral osteology and soft tissues on the line to extant birds (Neornithes). Zoological Journal of the Linnean Society 131, 169–197.
- 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 24, 81A.
- Madsen, J. H., Jr. 1976. *Allosaurus fragilis*: a revised osteology. Utah Geological and Mineralogical Survey, Bulletin 109, 3–163.
- Makovicky, P. J., Apesteguía, S., Agnolin, F. L., 2005. The earliest dromaeosaurid theropod from South America. Nature 437, 1007–1011.

- Molnar, R. E., Seriozha, M. K. and Dong, Z. –M. 1990. Carnosauria; pp. 169–209 in D. B. Weishampel, P. Dodson and H. Osmólska (eds.), *The Dinosauria*. University of California Press, Berkeley.
- Nixon, K. C. 1999. The Parsimony Ratchet, a new method for rapid parsimony analysis. *Cladistics* 15, 407–414.
- Norell, M. & Makovicky, P. J. 1997. Important features of the dromaeosaur skeleton: information from a new specimen. *American Museum Novitates* 3215, 1–28.
- O'Connor, P. M. 2007. The postcranial axial skeleton of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. *Society of Vertebrate Paleontology Memoir* 8, 127–162.
- Osborn, H. F. 1917. Skeletal adaptations of *Ornitholestes*, *Struthiomimus*, *Tyrannosaurus* *Bulletin of the American Museum of Natural History* 35, 733–771.
- Osmólska, H., Currie, P. J. & Barsbold, R. 2004. Oviraptorosauria; pp. 165–183 in D. B. Weishampel, P. Dodson and H. Osmólska (eds.), *The Dinosauria*, 2nd Edition. University of California Press, Berkeley.
- Pérez-Moreno, B. P., Chure, D. J., Pires, C., Marques da Silva, C., Dos Santos, V., Dantas, P., Póvoas, L., Cachão, M., Sanz, J. L. and Galopim de Carvalho, A. M. 1999. On the presence of *Allosaurus fragilis* (Theropoda: Carnosauria) in the Upper Jurassic of Portugal: first evidence of an intercontinental dinosaur species. *Journal of the Geological Society* 156, 449–452.
- Rauhut, O. W. M. 1995. Zur systematischen Stellung der afrikanischen Theropoden *Carcharodontosaurus* Stromer 1931 und *Bahariasaurus* Stromer 1934. *Berliner Geowissenschaftliche Abhandlungen (E)* 16, 357–375.
- Russell, D. A. and Dong, Z. –M. 1993. The affinities of a new theropod from the Alxa Desert, Inner Mongolia, People's Republic of China. *Canadian Journal of Earth Sciences* 30, 2107–2127.
- Sereno, P. C., Dutheil, D. B., Iarochene, M., Larsson, H. C. E., Lyon, G. H., Magwene, P. M., Sidor, C. A., Varrichio, D. J. & Wilson, J. A. 1996. Predatory dinosaurs from the Sahara and Late Cretaceous faunal differentiation. *Science* 272, 986–991.
- Sereno, P. C., Beck, A. I., Dutheil, D. B., Gado, B., Larsson, H. C. E., Lyon, G. H., Marcot, J. D., Rauhut, O. W. M., Sadleir, R. W., Sidor, C. A., Varrichio, D. D., Wilson, G. P. and Wilson, J. A. 1998. A long-snouted predatory dinosaur from Africa and the evolution of spinosauroids. *Science* 282, 1298–1302.
- Sikes, D. S. and Lewis, P. O.. 2001. Beta software, version 1. PAUPRat: PAUP implementation of the parsimony ratchet. Distributed by the authors. Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs.

- Stromer, E. 1931. Wirbeltier-Reste der Baharije-Stufe (unterstes Cenoman). 10. Ein Skelett-Rest von *Carcharodontosaurus* nov. gen. Abhandlungen der Bayerischen Akademie des Wissenschaften. Mathematisch-naturwissenschaftliche Abteilung 9, 1–23.
- Swofford, D. L. 1998. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.
- Swofford, D. L. and Olsen, G. J. 1990. Phylogeny reconstruction; pp. 411–501 in D. M. Hillis and C. Moritz (eds.), *Molecular Systematics*. Sinauer Associates, Sunderland, Massachusetts.
- Welles, S. P. & Long, R. A. 1974. The tarsus of theropod dinosaurs. *Annals of the South African Museum* 64, 191–218.
- Wilkinson, M. 2003. Missing data and multiple trees: stability and support. *Journal of Vertebrate Paleontology* 23, 311–323.
- Xu, X., Clark, J. M., Forster, C. A., Norell, M. A., Erickson, G. M., Eberth, D. A., Jia, C. and Zhao, Q. 2006. A basal tyrannosauroid dinosaur from the Late Jurassic of China. *Nature* 439, 715–718.
- Zhao, X. -J., Benson, R. B. J., Brusatte, S. L. & Currie, P. J. 2009. The postcranial skeleton of *Monolophosaurus jiangi* (Dinosauria: Theropoda) from the Middle Jurassic of Xinjiang, China, and a review of Middle Jurassic Chinese theropods. *Geological Magazine*.