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

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Abstract Non-avian theropod dinosaurs attained large body sizes, monopolising terrestrial apex predator niches in the Jurassic–Cretaceous. From the Middle Jurassic onwards, Allosauroidea and Megalosauroidea comprised almost all large-bodied predators for 85 million years. Despite their enormous success, however, they are usually considered absent from terminal Cretaceous ecosystems, replaced by tyrannosaurids and abelisaurids. We demonstrate that the problematic allosauroids *Aerosteon*, *Australovenator*, *Fukuiraptor* and *Neovenator* form a previously unrecognised but ecologically diverse and globally distributed clade (Neovenatoridae, new clade) with the hitherto enigmatic theropods *Chilantaisaurus*, *Megaraptor* and the Maastrichtian *Orkoraptor*. This refutes the notion that allosauroid extinction pre-dated the end of the Mesozoic.

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Neovenatoridae includes a derived group (Megaraptora, new clade) that developed long, raptorial forelimbs, cursorial hind limbs, appendicular pneumaticity and small size, features acquired convergently in bird-line theropods. Neovenatorids thus occupied a 14-fold adult size range from 175 kg (*Fukuiraptor*) to approximately 2,500 kg (*Chilantaisaurus*). Recognition of this major allosauroid radiation has implications for Gondwanan paleobiogeography: The distribution of early Cretaceous allosauroids does not strongly support the vicariant hypothesis of southern dinosaur evolution or any particular continental breakup sequence or dispersal scenario. Instead, clades were nearly cosmopolitan in their early history, and later distributions are explained by sampling failure or local extinction.

Introduction

Theropod dinosaurs have been an ecologically diverse component of terrestrial ecosystems since their Late Triassic origins. Having given rise to birds, they are the most diverse clade of extant amniotes. Non-avian theropods, including the characteristic giant predators of the Mesozoic, became extinct at the end of the Cretaceous, 65 million years ago. Prior to this, for 160 million years, theropods monopolised the role of apex predator in terrestrial ecosystems. They produced numerous distinct lineages of large terrestrial predators among ceratosaurs, megalosauroids, allosauroids and tyrannosaurids.

The basal tetanuran clades Allosauroidea and Megalosauroidea appeared by the Middle Jurassic and were soon

represented by large-bodied taxa such as *Shidaisaurus* and *Megalosaurus* (Wu et al. 2009; Benson 2009). They yielded the first giant taxa (>2 tonnes) in theropod history shortly thereafter (the megalosauroid *Torvosaurus* and the allosauroid *Saurophaganax*; Bakker et al. 1992). These two clades are central to understanding Middle Jurassic–early Late Cretaceous dinosaurian ecosystems, in which they comprised almost all large predators over a span of approximately 85 million years. Currently, the youngest definite allosauroids are from the Turonian of China (Brusatte et al. 2009) and Santonian of Argentina (Sereno et al. 2008). Despite their enormous success, however, basal tetanurans are hitherto unknown from the final 20 million years of the Mesozoic. Instead, the iconic tyrannosauroids, a lineage of previously small-bodied coelurosaurian theropods, achieved masses of several tonnes in Laurasia (e.g. Erickson et al. 2004). In Gondwana, abelisaurid neoceratosaurs diversified to occupy the apex predator niche (e.g. Sampson and Krause 2007; Carrano and Sampson 2008).

Here, we present evidence that six previously enigmatic theropod taxa—*Aerosteon*, *Australovenator*, *Chilantaisaurus*, *Fukuiraptor*, *Megaraptor* and *Orkoraptor*—form a monophyletic clade with the unequivocal allosauroid *Neovenator*. The Maastrichtian age of *Orkoraptor* provides conclusive evidence that allosauroids survived until the end of the Cretaceous and were not extinct, as previously thought. Derived members of this new clade exhibit a unique body plan among otherwise conservative basal tetanurans, highlighted by raptorial forelimbs and cursorial hind limbs that converge on the anatomy of bird-like theropods. In sum, the identification of this new clade, composed primarily of taxa that were only recently discovered and described (since 1996; other than *Chilantaisaurus*), reveals a previously unrecognised major group of basal theropods that were an important component of Mesozoic terrestrial ecosystems.

Comparisons

Basic comparisons and synapomorphies are outlined and summarised below (and see Fig. 1). A comprehensive discussion of the anatomy and taxonomy of the focal taxa and a list of specimens examined are included in the "Electronic supplementary material".

Neovenator is known by three specimens from the Wessex Formation (Barremian, Lower Cretaceous) of the Isle of Wight, UK. These represent most of the skeleton except the forelimbs and posterior two thirds of the skull (Hutt et al. 1996). Numerous skeletal features support a closer relationship to carcharodontosaurids than to *Allosaurus* (Naish et al. 2001; Brusatte et al. 2008). Importantly,

several previously identified autapomorphies of *Neovenator* are identified here as synapomorphies of a more inclusive clade.

Aerosteon, from the Anacleto Formation (Santonian, Late Cretaceous) of Argentina, is represented by the holotype partial skeleton (MCNA-PV-3137; see "Electronic supplementary material" for institutional abbreviations) and a partial hind limb (MCNA-PV-3139; MCNA-PV-3138 is considered Tetanurae indet; "Electronic supplementary material"). Preserved cranial bones do not overlap with material of *Neovenator*, but the scapulocoracoid, pelvis and parts of the axial column and hind limb are represented. A preliminary report proposed carcharodontosaurid affinities (Alcober et al. 1998), but more recent work concluded that it was an allosauroid of uncertain affinities (Sereno et al. 2008).

Aerosteon has never been included in a phylogenetic analysis but shares several features with carcharodontosaurids and *Neovenator*: double cervical anterior pneumatic foramina, pneumatic foramina in all dorsal vertebrae, transversely narrow, sheet-like dorsal hyposphenes (Fig 1b) and a ventral longitudinal ridge on the proximal caudal vertebrae. *Aerosteon* also shares several features with *Neovenator* and other taxa discussed here (see "Electronic supplementary material"). Notably, although a pneumatic ilium was originally proposed as unique among non-maniraptoran theropods (Sereno et al. 2008), the broken ilia of *Neovenator* also contain internal pneumatic spaces (Brusatte et al. 2008).

Megaraptor was originally described on the basis of a fragmentary specimen from the Río Neuquén Formation (Turonian–Coniacian) of Neuquén, Argentina, which was interpreted as a coelurosaur (Novas 1998), due to the slender proportions of metatarsal III and the supposedly dromaeosaurid-like pedal ungual. A second specimen, comprising a more complete forelimb, vertebrae, a scapulocoracoid and a partial pubis from the Portezuelo Formation (Turonian–Santonian), demonstrated that the ungual belonged to manual digit I (Calvo et al. 2004), nullifying the proposed similarity with dromaeosaurids.

In a global phylogenetic analysis of theropods, Smith et al. (2007) recovered *Megaraptor* as a carcharodontosaurid. However, Smith et al. (2008) later noted that *Megaraptor* shared various features of the forelimb with spinosaurids and recovered *Megaraptor* as a megalosauroid (=spinosauroid). Many of the proposed synapomorphies are problematic and are interpreted differently here (see "Electronic supplementary material"). Notably, although the first manual ungual of *Megaraptor* is large, as in some megalosauroids (e.g. Charig and Milner 1997), its detailed morphology is distinctive. In *Megaraptor*, the ungual is transversely narrow, with a ratio of proximal height to width of 2.75 (Fig. 1g–h). This is substantially higher than
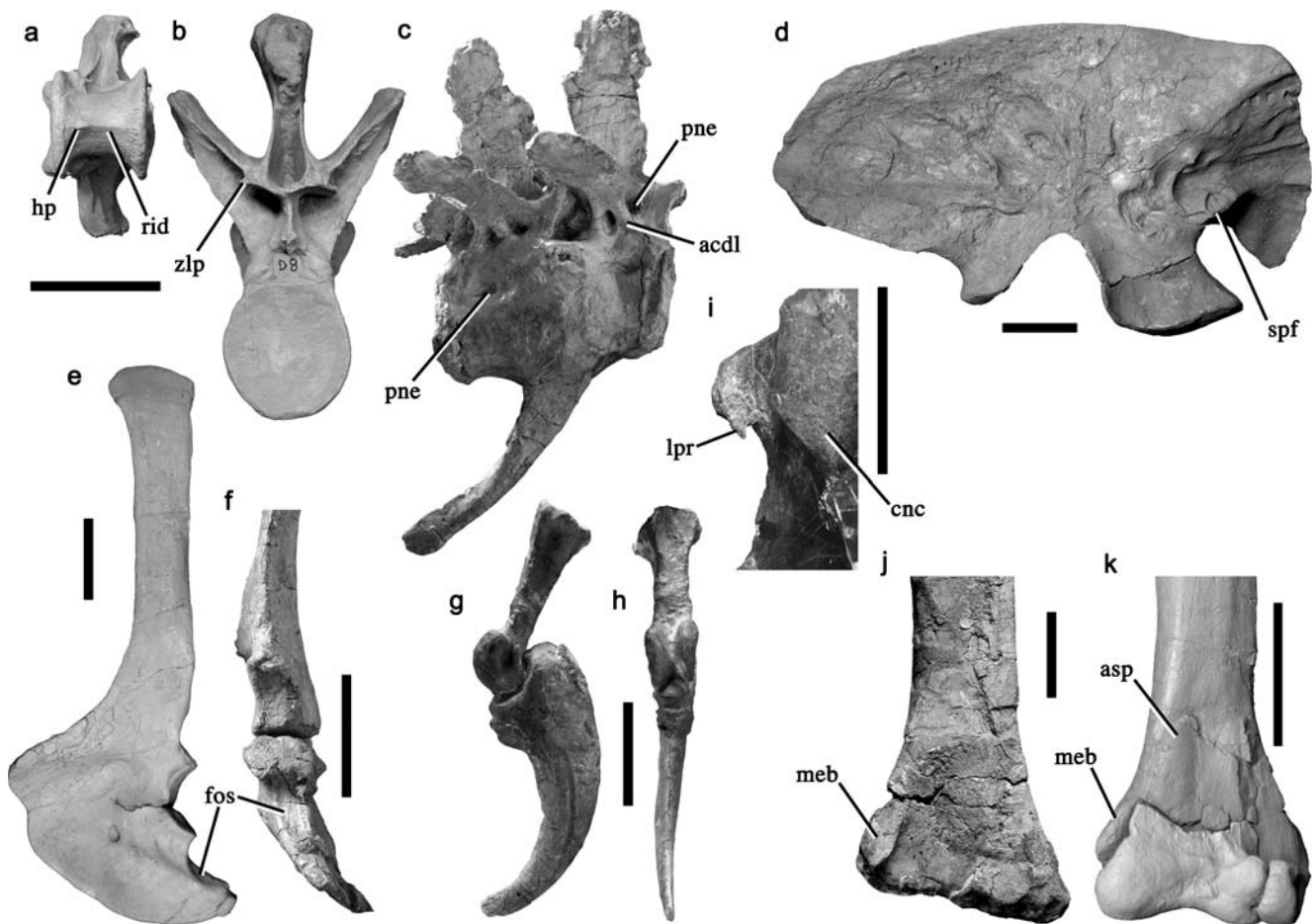
Fig. 1 Neovenatorid anatomy shown by *Aerosteon* (**a–b**, **d–e** MCNA-PV-3137; **k** MCNA-PV-3139), *Megaraptor* (**c**, **f**, **g–h** MUCPv 341), *Neovenator* (**i** MIWG 6348) and *Chilantaisaurus* (**j** IVPP V.2884) in ventral (**a**, **f**, **h**), posterior (**b**), right lateral (**c**), medial (**d**, **g**), lateral (**e**) and anterior (**i–k**) views. **a** Fourth dorsal vertebra; **b** eighth dorsal vertebra; **c** proximal caudal vertebrae; **d** ilium; **e–f** scapulocoracoid; **g–h** right phalanx I; **i** right tibia; **j** right tibia (reversed); and **k** left tibia. *acdl* anterior centrodiapophyseal lamina, *asp* ascending process, *cnc* cnemial crest, *fos* fossa, *hp* hyposphene, *lpr* anterior process of lateral condyle, *meb* medial buttress, *pne* pneumatic foramen, *rid* ridge, *spf* pre-acetabular shelf, *zlp* lateral process of postzyapophysis. *Scale bars* 100 mm

those of other large theropods, including megalosauroids such as *Suchomimus* (1.75; MNN GDF 500) and *Torvosaurus* (1.95; BYU 17697), but similar unguals are known in *Australovenator*, *Chilantaisaurus* and *Fukuiraptor*.

Several observations support the allosauroid affinities of *Megaraptor*: The cervical vertebrae strongly resemble those of carcharodontosaurids and possess a parapophysis located at centrum mid-length, a weak but continuous prezygapophyseal–epiphyseal lamina, marked plasticity in the morphology of cervical pneumatic foramina (Calvo et al. 2004; Smith et al. 2007) and a camellate internal pneumatic structure.

Novas et al. (2008) recently described *Orkoraptor* based on a fragmentary skeleton from the early Maastrichtian Pari Aike Formation near Los Hornos Hill, Santa Cruz Province, Argentina. Two characters suggested coelurosaurian affinities for *Orkoraptor*: (1) the absence of a mesial carina on lateral teeth (shared with compsognathids and deinonycho-

saurians) and (2) the anterodorsally inclined anterior process of the postorbital (present in some maniraptorans). However, *Orkoraptor* lacks other features of derived coelurosaurs, such as a posteromedial process of the quadratojugal that overlaps the posterior surface of the quadrate, which is especially prominent in dromaeosaurs (Rauhut 2003). Furthermore, the postorbital of *Orkoraptor* is almost identical to that of *Aerosteon* (Fig. 2), lacking the robust, ornamented anterior process of other allosauroids. In addition, in both taxa, a pneumatopore is evident on the dorsolateral surface of the atlantal neural arch, and the proximal caudal vertebrae are intensely pneumatised (Sereno et al. 2008; Fig. 1c).

Australovenator was described by Hocknull et al. (2009) based on a partial skeleton from the Winton Formation (latest Albian) of the 'Matilda Site', near Winton, Queensland, Australia. A detailed description of the astragalus revealed many distinctive features, several of which were
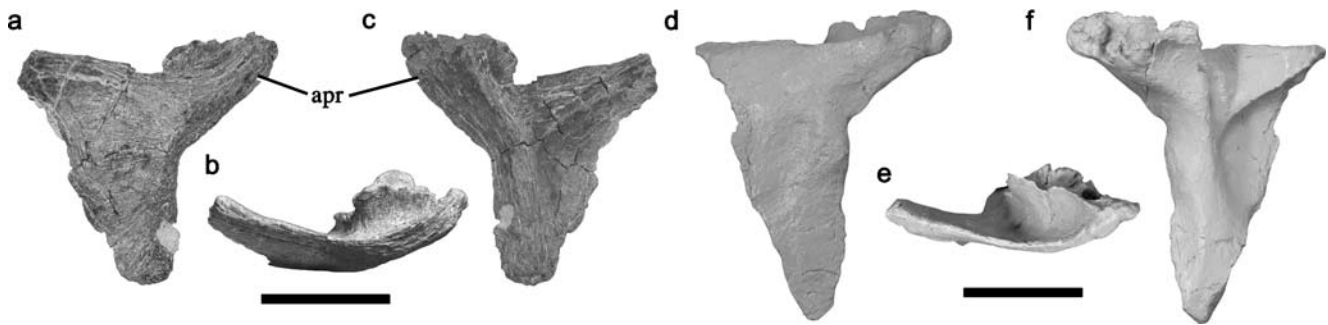
Fig. 2 Right postorbitals of *Orkoraptor* (**a**–**c**) and *Aerosteon* (**d**–**f**) in lateral (**a**, **d**), dorsal (**b**, **e**) and medial (**c**, **f**) views. *apr* anterior process. *Scale bars* 50 mm. Parts **a**–**c** modified from Novas et al. (2008)

uniquely shared with *Fukuiraptor*. However, phylogenetic analysis recovered *Australovenator* as a basal carcharodontosaurid, more derived than both *Allosaurus* and *Fukuiraptor* (Hocknull et al. 2009).

Fukuiraptor is based on the holotype partial skeleton (FPDM-V97122), from the Kitadani Formation (Albian, Lower Cretaceous) of the Kitadani quarry, Katsuyama, Japan (Azuma and Currie 2000), along with fragmentary material (FPDM-V9712229-43) and new specimens (Currie and Azuma 2006). *Fukuiraptor* was originally identified as a dromaeosaurid based on misidentification of the large, transversely compressed manual unguals as pertaining to the pes (Azuma and Currie 1995). It was subsequently recovered as a basal allosauroid ('carnosaur'; Azuma and Currie 2000; Holtz et al. 2004) based on the fused interdental plates, *Allosaurus*-like forelimb proportions and 'wing-like' morphology of the femoral lesser trochanter. *Fukuiraptor* has recently been hypothesised as a basal allosauroid (Hocknull et al. 2009) and as a basal neotetanuran (Benson 2009), and so its affinities have been uncertain.

Chilantaisaurus tashuikouensis is based on a partial appendicular skeleton from the Ulansuhai Formation (?Turonian, Late Cretaceous) of Inner Mongolia, China (Hu 1964). It has been referred to Allosauroidea (Harris 1998; based on a chimaera of *Chilantaisaurus* and the co-faunal carcharodontosaurid *Shaochilong*), Megalosauroidea (=Spinosauroidea; Rauhut 2003) and Tetanurae *incertae sedis* (Holtz et al. 2004). Benson and Xu (2008) recently demonstrated the presence of neotetanuran features, such as an iliac pre-acetabular fossa and a trapezoidal cross section of metatarsal III.

We can now demonstrate that the many distinctive or purportedly autapomorphic features of these taxa occur more widely and in fact represent synapomorphies of a previously unrecognised theropod clade ("Systematic palaeontology"; see "Electronic supplementary material"). These features reflect morphological adaptations of the vertebrae, forelimb and hind limb. A number of these

occur in parallel within coelurosaurs and have contributed to previous misclassifications (e.g. Azuma and Currie 1995; Novas 1998).

Phylogenetic analysis

The taxa discussed above were scored for a version of the cladistic data matrix of Benson (2009). This matrix was devised specifically to elucidate basal tetanuran relationships based primarily on direct examination of specimens. *Aerosteon*, *Australovenator*, *Orkoraptor* and *Shaochilong* were added, and the scores of *Chilantaisaurus*, *Megaraptor* and *Neovenator* were revised. New characters were added to document variation in these taxa. This resulted in a matrix of 45 taxa and 233 characters. Details of these modifications, including new characters and taxon scores, and methods used to analyse the data are given in the "Electronic supplementary material", and a nexus file of the resulting data set is available on request from RBJB.

Analysis of the matrix resulted in 864 most parsimonious trees (MPTs) of 637 steps. The strict consensus showed a monophyletic Neotetanurae comprising Allosauroidea + Coelurosauria. Allosauroidea included Sinraptoridae, *Allosaurus* and a monophyletic group of Cretaceous allosauroids (Fig. 3). This contained two major clades. The first included seven taxa that are regarded as carcharodontosaurids; the second (Neovenatoridae fam. nov.) included *Neovenator*, *Aerosteon*, *Australovenator*, *Chilantaisaurus*, *Fukuiraptor*, *Megaraptor* and *Orkoraptor*. *Neovenator* was the sister taxon of all other neovenatorids, which formed a derived polytomy. However, the most incomplete taxon, *Orkoraptor*, shows little anatomical overlap with other taxa and acted as a 'wildcard'. When *Orkoraptor* was pruned from the set of MPTs, the number of unique topologies was reduced to 96. The resulting reduced strict consensus contains a fully resolved Neovenatoridae with a derived clade containing sister taxon pairings of *Aerosteon* + *Megaraptor* and *Australovenator* + *Fukuiraptor* (Fig. 3).

Fig. 3 Relationships of Cretaceous allosauroids based on the phylogenetic analysis herein (ensemble consistency index= 0.4427, retention index=0.6385, rescaled consistency index= 0.2827). *Filled circles* indicate Gondwanan taxa; *empty circles* indicate Laurasian taxa. *Grey rectangles* highlight closely related taxa of similar age, indicating that temporal occurrence influences cladogram structure. Bremer support for all nodes equals one
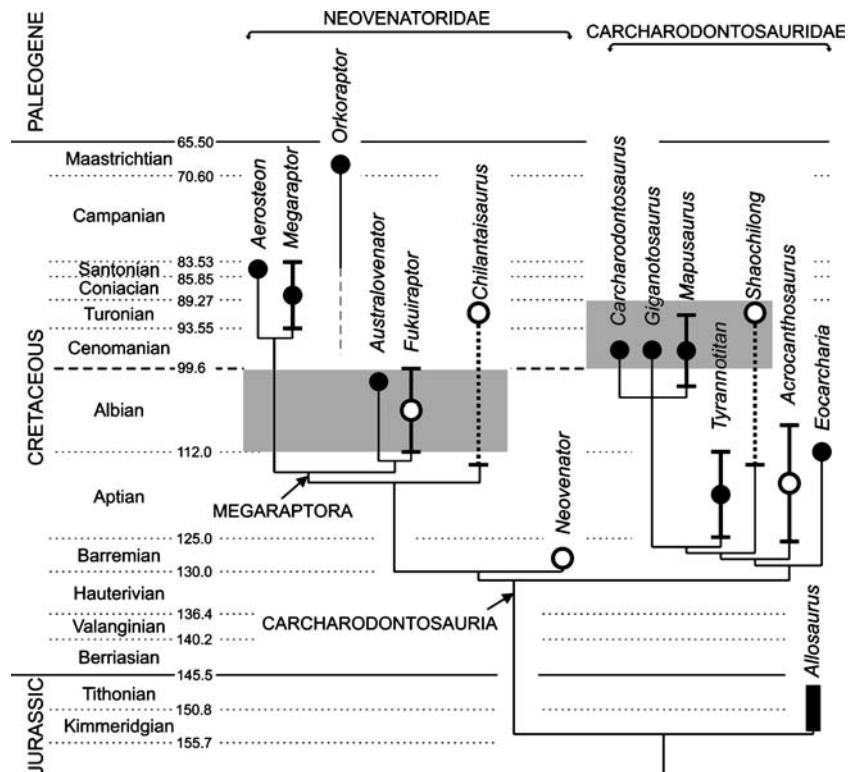
Systematic palaeontology

Theropoda Marsh (1881)
Tetanurae Gauthier (1986)
Allosauroidea Marsh (1878)

Carcharodontosauria new clade

Included taxa Neovenatoridae and Carcharodontosauridae (Carcharodontosauridae is redefined in the "Electronic supplementary material")

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

Remarks The content of this clade matches that of Carcharodontosauridae as previously defined (Holtz et al. 2004: 102). Accordingly, many features previously ascribed to carcharodontosaurids are now synapomorphies of Carcharodontosauria (see "Electronic supplementary material"). 'Carcharodontosauridae' (sensu Holtz et al. 2004) now contains many more taxa than when it was originally defined, encompassing all Cretaceous allosauroids. As we believe that the distinctive features of *Neovenator* and close relatives justify familial distinction, it is practical to erect a rank-free name, Carcharodonto

sauria, for the well-supported clade of Carcharodontosauridae + Neovenatoridae.

Neovenatoridae new family

Included taxa N. salerii (type species), *Aerosteon riocoloradensis, Australovenator wintonensis, Chilantaisaurus tashuikouensis, Fukuiraptor kitadanensis, Megaraptor namunhuaiquii* and *Orkoraptor burkei*

Additional included material NMV P186076, an ulna from the Eumeralla Formation at Dinosaur Cove (late Aptian– early Albian), Victoria, Australia, referred to cf. *Megaraptor* (Smith et al. 2008). The cited autapomorphies are widely distributed among neovenatorids, and the specimen is herein identified as Neovenatoridae indet.

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

Diagnosis Carcharodontosaurian theropods with the following: (1) middle–posterior dorsal vertebrae with small, flange-like lateral extensions of postzygapophyseal facets (Fig. 1b); (2) ventral longitudinal ridge in proximal caudal vertebrae (independently derived in Carcharodontosauridae); (3) scapula short and broad

(length: minimum width ratio=8.0–9.0; Fig. 1e) relative to other derived allosauroids; (4) iliac pre-acetabular fossa bounded dorsomedially by a prominent shelf (Fig. 1d; also present in tyrannosauroids); (5) femoral lateral condyle which projects further distally than medial condyle; (6) pneumatic ilium; and (7) anterolateral process of tibial lateral condyle curves ventrally as a pointed process (Fig. 1i). Additional potential synapomorphies of Neo-venatoridae and included clades, mainly pertaining to elongate, raptorial forearms (missing data in *Neovenator*; e.g. Fig. 1e–h), are summarised in the "Electronic supplementary material".

Megaraptora new clade

Included taxa Ae. ricocoloradensis, Au. wintonensis, F. kitadanensis, M. namunhuaiquii, O. burkei

Additional included material An isolated astragalus (NMV P150070) from the Wonthaggi Formation (Valanginian–Aptian, Lower Cretaceous) of Victoria, Australia (Molnar et al. 1981), referred to *Australovenator* by Hocknull et al. (2009). Given its older age and numerous similarities with the astragalus of *Fukuiraptor*, we consider it an indeterminate megaraptoran related to these two taxa.

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 (III) with a ratio of length to minimum width ≥12.5. Incomplete knowledge of *Chilantaisaurus* and *Neovenator* means that other potential synapomorphies of Megaraptora, pertaining to cursorial hind limbs (Fig. 1j–k) and pneumatic caudal vertebrae (Fig. 1c), are only recovered under DELTRAN optimisation (see "Electronic supplementary material").

Discussion

Neovenatorid palaeobiology

Although *Neovenator* is comparable in size and skeletal proportions to *Allosaurus* and therefore likely similar in general ecology and predatory biology to other basal tetanurans, megaraptorans show substantial modifications. The forearm is elongate, and the manual unguals are enlarged and transversely narrow, suggesting increased

raptorial ability of the forelimb. The hind limb shows adaptations for increased cursoriality (Carrano 1999): elongation of the metatarsals relative to more proximal elements and a tall femoral lesser trochanter. Megaraptorans also exhibit modification of the ankle joint (elongate ascending process of the astragalus, distinct astragalar buttress on the tibia) and relatively smaller body sizes. Indeed, the largest known individual of *Fukuiraptor* is estimated at 175 kg in mass (Azuma and Currie 2000; cf. Anderson et al. 1985). If this represents adult size (currently unclear), *Fukuiraptor* was uncommonly small among basal tetanurans.

Other theropod clades independently derived similar limb proportions. Some ceratosaurs (*Elaphrosaurus* and related forms, noasaurids) and coelurosaurs (alvarezsaurids, caenagnathids, ornithomimids, troodontids and tyranno-saurids) possess elongate distal hind limb elements, which are often interpreted as reflecting improved cursorial ability (e.g. Russell 1972; Holtz 1995; Carrano 1999). Likewise, avian-line theropods show a trend towards increasing forelimb length (e.g. Gauthier 1986; Padian and Chiappe 1998). However, although present in highly derived coelurosaurs, these features are unknown in basal tetanurans. In fact, basal tetanuran hind limb proportions and postcranial anatomy are widely conservative, and Neovenatoridae is significant as the first example of a marked departure from this basic body plan.

Derived neovenatorids show additional features that arose convergently among coelurosaurs, including pectoral and pelvic pneumaticity otherwise known only in birds (Sereno et al. 2008). Megaraptorans may have been 'coelurosaur parallels' in Cretaceous ecosystems, allowing them to co-exist with more distinctive large-bodied abeli-saurids and carcharodontosaurids. It is noteworthy that neovenatorids are currently unknown from the terminal Cretaceous ecosystems of North America and Asia, the only well-sampled faunas in which true coelurosaurs (tyrannosaurids) were apex predators.

However, not all derived neovenatorids were small, sleek coelurosaur mimics. *Chilantaisaurus* (Turonian) retained a short metatarsus and weighed approximately 2.5 tonnes (minimum femoral circumference of 432 mm; cf. Anderson et al. 1985). It thus attained, or perhaps retained, body size comparable to the largest allosaurid (*Saurophaganax*) and some carcharodontosaurids (*Mapusaurus*) and tyrannosaur-ids. Contrastingly, *Shaochilong*, a co-faunal carcharodonto-saurid, is substantially smaller than even large subadult *Allosaurus* specimens (Brusatte et al. 2009). Therefore, the roles of carcharodontosaurids (large-bodied apex predators) and neovenatorids (smaller, cursorial forms) were not fixed. Such variability is not surprising given the approximately 14-fold difference between the smallest and largest neo-venatorids (Fig. 4).
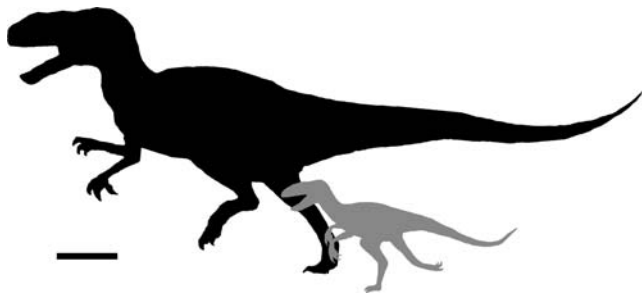
Fig. 4 Silhouettes of *Chilantaisaurus* (*black*; femoral length 1,190 mm) and *Fukuiraptor* (*grey*, femoral length 507 mm) showing size disparity among neovenatorids. *Scale bar* 1 m

Cretaceous terrestrial palaeobiogeography

Cretaceous allosauroids have been implicated in various biogeographic scenarios. Foremost among these is that the group evolved vicariantly in concert with the breakup of Pangaea (Harris 1998; Sereno 1999; Brusatte and Sereno 2008). In this hypothesis, the branching pattern of allosauroid evolution reflects the breakup pattern of Pangaea into Gondwana and Laurasia and subsequently into smaller landmasses.

However, seven of the allosauroid taxa in our cladistic analysis were unknown to Harris (1998) and Sereno (1999), and even now, only 14 taxa are known globally from the 80 million years of Cretaceous time. In fact, only one to two allosauroid taxa are known from most continents during the Early and Late Cretaceous, while the remaining landmasses lack allosauroid fossils entirely. Sampling is especially problematic because occurrences are clustered in time and space, and simulation studies indicate that uneven geographic sampling impairs the ability of biogeographic analyses to recover true signals and can lead to an increase in the recovery of erroneous signals (Turner et al. 2009).

In the few time intervals where wider geographic samples of allosauroids are known, major clades appear to have essentially global distributions. The early Late Cretaceous record is dominated by Gondwanan taxa such as *Carcharodontosaurus* in Africa and *Giganotosaurus* and *Mapusaurus* in South America, but the closely related carcharodontosaurid *Shaochilong* is now known from the Turonian of China (Fig. 3; Brusatte et al. 2009). Similarly, late Early Cretaceous neovenatorids are known only from Australia (*Australovenator*) and Japan (*Fukuiraptor*) and are sister taxa (Fig. 3). This suggests that time influences allosauroid cladogram structure as strongly as geography. In other words, taxa of similar ages from different continents are as often closely related as are taxa of different ages from the same continent. Based on this observation, most major clades of Cretaceous allosauroids likely had near-cosmopolitan distributions prior to the

Campanian–Maastrichtian, and our view of their 'biogeography' arises from patchy spatiotemporal sampling. It is likely that the fossil record is currently too poor to confirm or refute the role of vicariance in allosauroid evolution.

Smith et al. (2008) suggested that the occurrence of a '*Megaraptor*'-like ulna (NMV P186076; herein considered Neovenatoridae indet.) from the Aptian–Albian of Australia indicated dispersal between east and west Gondwana as late as the mid-Cretaceous. However, our data show that neovenatorids were even more widely distributed during the mid-Cretaceous (*Fukuiraptor* is from Japan), plausibly due to an earlier origin rather than a mid-Cretaceous dispersal event. Thus, it cannot be used to support any particular biogeographic hypothesis.

Late survival of allosauroids and Cretaceous faunal compositions

Basal tetanurans (allosauroids and megalosauroids) were previously thought to have gone extinct well before the end of the Cretaceous, either in the Cenomanian (Holtz et al. 2004) or slightly later (Sereno et al. 2008; Brusatte et al. 2009). Regardless of the exact timing, Late Cretaceous allosauroids have been viewed as anomalous—rare, relictual, large-bodied taxa in ecosystems otherwise dominated by tyrannosaurids and abelisaurids (Calvo et al. 2004; Holtz et al. 2004; Sereno et al. 2008). The recognition of Neovenatoridae challenges both points. First, the presence of *Orkoraptor* in the latest Cretaceous of South America demonstrates the persistence of neovenatorid allosauroids until the very end of the Mesozoic. Second, Neovenatoridae is a speciose clade that played a variety of roles in Cretaceous terrestrial ecosystems, from long-limbed, cursorial predators (*Australovenator*, *Megaraptor*) to gigantic carnivores (*Chilantaisaurus*). The longevity and geographic dispersion of neovenatorids are inconsistent with a 'relictual' role and instead show the clade to have been an important and hitherto unrecognised component of global dinosaur faunas throughout the Cretaceous.

Latest Cretaceous neovenatorids are currently known only from South America, where they are found alongside large-bodied abelisaurids. Neovenatorids have not been recovered from the terminal Cretaceous deposits of western North America and eastern Asia, both of which preserve tyrannosaurid-dominated faunas. These are among the best-sampled dinosaur faunas of any interval, and the absence of neovenatorids there may be genuine. However, large-bodied predators are not well enough known from the Campanian–Maastrichtian of Europe, Australia, Africa, southern North America or southern China to exclude the possible survival of neovenatorids in these regions.

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