

The first definitive carcharodontosaurid (Dinosauria: Theropoda) from Asia and the delayed ascent of tyrannosaurids

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Abstract Little is known about the evolution of large-bodied theropod dinosaurs during the Early to mid Cretaceous in Asia. Prior to this time, Asia was home to an endemic fauna of basal tetanurans, whereas terminal Cretaceous ecosystems were dominated by tyrannosaurids, but the intervening 60 million years left a sparse fossil record. Here, we redescribe the enigmatic large-bodied

Chilantaisaurus maortuensis from the Turonian of Inner Mongolia, China. We refer this species to a new genus, *Shaochilong*, and analyze its systematic affinities. Although *Shaochilong* has previously been allied with several disparate theropod groups (Megalosauridae, Allosauridae, Tyrannosauoidea, Maniraptora), we find strong support for a derived carcharodontosaurid placement. As such, *Shaochilong* is the first unequivocal Asian member of Carcharodontosauridae, which was once thought to be restricted to Gondwana. The discovery of an Asian carcharodontosaurid indicates that this clade was cosmopolitan in the Early to mid Cretaceous and that Asian large-bodied theropod faunas were no longer endemic at this time. It may also suggest that the ascent of tyrannosaurids into the large-bodied dinosaurian predator niche was a late event that occurred towards the end of the Cretaceous, between the Turonian and the Campanian.

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Introduction

Very little is known about the large-bodied theropod dinosaurs that inhabited Asia during the Early to mid Cretaceous. Carnivores from the Middle to Late Jurassic largely belonged to endemic basal tetanuran clades (Brusatte et al. 2009; Zhao et al. 2009), whereas terminal Cretaceous faunas were dominated by the colossal tyrannosaurids (Currie 2000), but the intervening 60 million years is a dark period in Asian theropod history. Although several

small-bodied coelurosaurs are known from the famous Barremian Jehol Biota of China (Norell and Xu 2005), the record of large theropods from this time consists mostly of isolated teeth and other fragmentary remains (see review in Weishampel et al. 2004). This dearth of information frustrates attempts to understand the Cretaceous biogeographic history of Asia, especially postulated episodes of endemism and faunal interchange based on other clades, and the ascent of tyrannosaurids into the dominant predator role in latest Cretaceous ecosystems.

One of the most complete large theropod specimens from this poorly sampled interval is a series of cranial and postcranial bones from Inner Mongolia, China. These fossils were briefly described by Hu (1964), who assigned them to a new species of the enigmatic theropod *Chilantaisaurus*, *Chilantaisaurus maortuensis*. However, subsequent authors have dismissed this referral, as there is no overlapping material between *C. maortuensis* and the type species of *Chilantaisaurus*, *Chilantaisaurus tashuikouensis* (e.g., Chure 2000; Rauhut 2003; Benson and Xu 2008). Furthermore, researchers have consistently disagreed on the phylogenetic placement of *C. maortuensis*. Hu (1964) classified this species within Megalosauridae, a wastebasket assemblage of large theropods that are now regarded as basal tetanurans, whereas other authors have referred it to a wide variety of theropod groups, including Allosauridae (e.g., Molnar et al. 1990), Tyrannosauroida (Holtz 2004), and Maniraptora (Chure 1998, 2000; Rauhut 2003). Few of these referrals have been based on numerical cladistic analysis, and the fact that this critical specimen remains poorly described has certainly contributed to this confusion.

Here, we redescribe the holotype and only known specimen of *C. maortuensis* and provide a new generic name and revised diagnosis. Cladistic analyses, which incorporate an avalanche of new data from an ongoing renaissance in the discovery and description of basal theropod dinosaurs, allow us to evaluate the affinities of this specimen in unprecedented detail. We reinterpret *C. maortuensis* as the first unequivocal Asian member of Carcharodontosauridae, a clade once thought to be restricted to Gondwana that includes some of the largest terrestrial predators to ever live (Brusatte and Sereno 2008). The discovery of an Asian carcharodontosaurid provides evidence that this clade was cosmopolitan in the Early to mid Cretaceous and that mid Cretaceous Asian large-bodied theropod faunas were no longer endemic. Furthermore, the persistence of large-bodied basal tetanurans (*Shaochilong* and the contemporary *C. tashuikouensis*) in the mid Cretaceous of Asia may indicate that the ascent of tyrannosaurids into the large predator niche was a late event that occurred towards the end of the Cretaceous, after the Turonian.

Taxonomy

Theropoda Marsh 1881
 Tetanurae Gauthier 1986
 Allosauroida Marsh 1878
 Carcharodontosauridae Stromer 1931
Shaochilong, gen nov.
S. maortuensis Hu 1964

Etymology

Shaochi Chinese for “shark tooth,” referring to the “shark-toothed” carcharodontosaurid theropods; long Chinese for dragon.

Materials

IVPP (Institute of Vertebrate Paleontology and Paleoanthropology) V2885.1-7, braincase, frontals, parietals, right nasal, right maxilla, quadrates, axis, and six caudal vertebrae, found associated (Hu 1964). All elements seem to represent a single individual, based on size, matching articulations, and/or shared phylogenetic affinity (Figs. 1 and 2).

Locality and horizon

Ulusuhai Formation, Maortu, People’s Republic of China (60 km north of Chilantai, Inner Mongolian Autonomous Region). The Ulusuhai Formation is often regarded as Aptian-Albian (late Early Cretaceous) based on perceived faunal similarities to other deposits of this age (e.g., Weishampel et al. 2004). However, radiometric dating of underlying strata indicates a maximum age of approximately 92 Ma (Turonian, early Late Cretaceous [“mid Cretaceous”]; Kobayashi and Lu 2003; Benson and Xu 2008).

Diagnosis

Allosauroid theropod possessing the following autapomorphies: maxillary antorbital fossa reduced in extent and nearly absent; paracanthal groove on medial surface of maxilla absent; deep, dorsoventrally oriented grooves located dorsally on maxillary interdental plates; pneumatic recess penetrates to posterior end of nasal; sagittal crest on frontal; large pneumatic foramen at anterodorsal corner of dorsal tympanic recess of prootic.

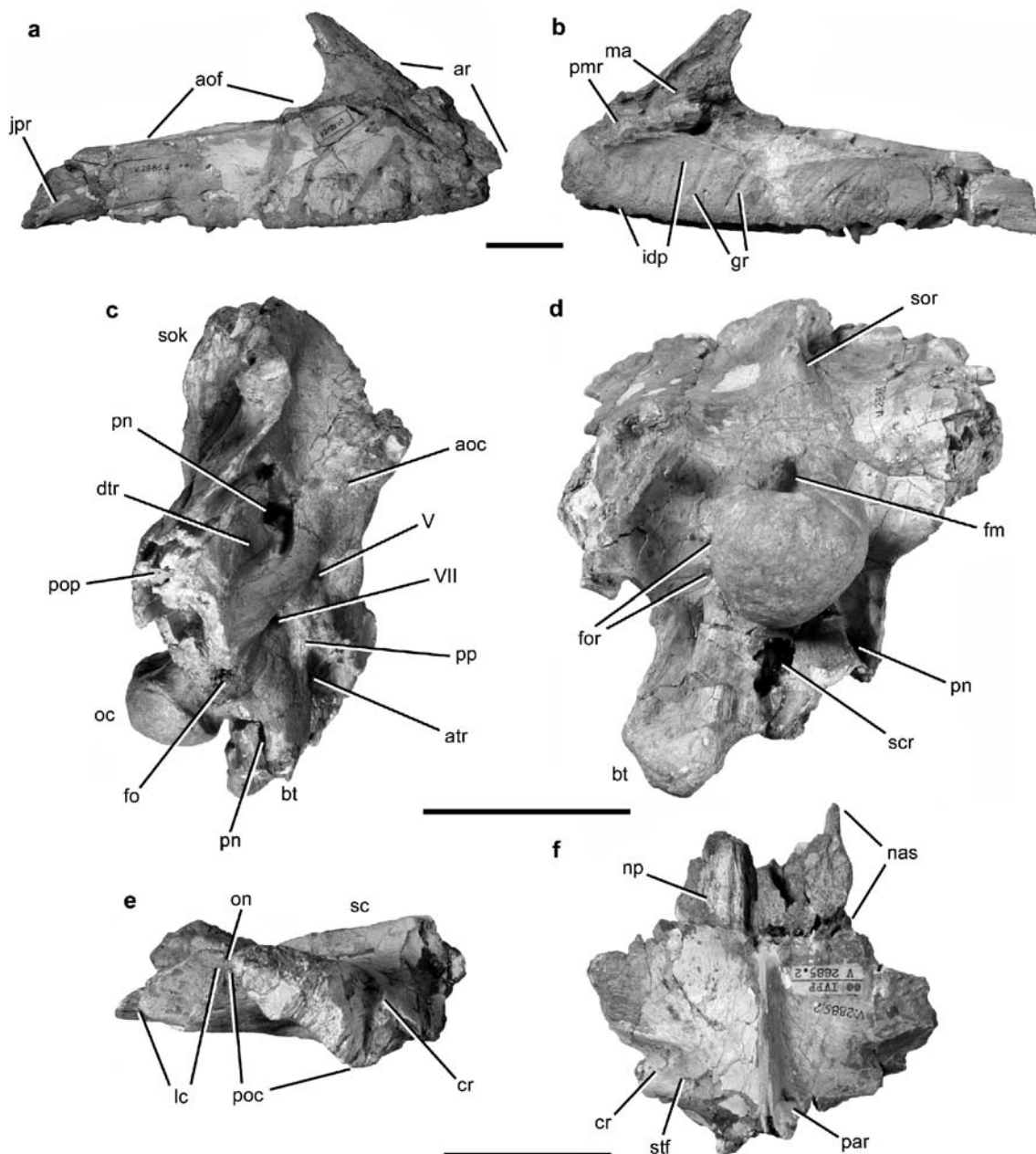


Fig. 1 *Shaochilong maortuensis* IVPP V2885.1-7. Right maxilla in lateral (a) and medial (b) views; braincase in right lateral (c) and occipital (d) views; partial skull roof (nasal, frontal, parietal) in dorsal (e) and left lateral (f) views. *aoc* antotic crest of laterosphenoid, *aof* antorbital fossa, *ar* anterior ramus, *atr* anterior tympanic recess, *bt* basal tuber, *cr* curved crest within supratemporal fossa, *dtr* dorsal tympanic recess, *fm* foramen magnum, *fo* fenestra ovalis, *for* paracondylar openings representing jugular foramen and foramen for nerve XII, *gr* groove, *idp* interdental plates, *jpr* jugal process, *lc*

lacrimal contact, *ma* maxillary antrum, *nas* nasal, *np* nasal prong, *oc* occipital condyle, *on* orbital notch between lacrimal and postorbital contacts, *par* parietal, *pmr* promaxillary recess, *pn* pneumatopore, *poc* postorbital contact, *pop* paroccipital process, *pp* preotic pendant, *sc* sagittal crest, *scr* subcondylar recess, *sok* supraoccipital knob, *sor* supraorbital ridge, *stf* supratemporal fossa, *V* trigeminal nerve foramen, *VII* facial nerve foramina. Scale bars represent 5 cm. Paroccipital processes have been broken, but original published photos (Hu 1964) show that they are strongly downturned

Description and comparisons

The lateral surface of the maxilla is smooth, lacking the characteristic rugose texture of derived carcharodontosaurids. The anterior ramus is deeper than long and the jugal

process is deflected posteroventrally, as in *Acrocanthosaurus* and *Eocarcharia* (Serenó and Brusatte 2008). Lateral exposure of the antorbital fossa is limited ventrally on the main body and on the posterior margin of the ascending ramus, even more so than in derived carcharodontosaurids

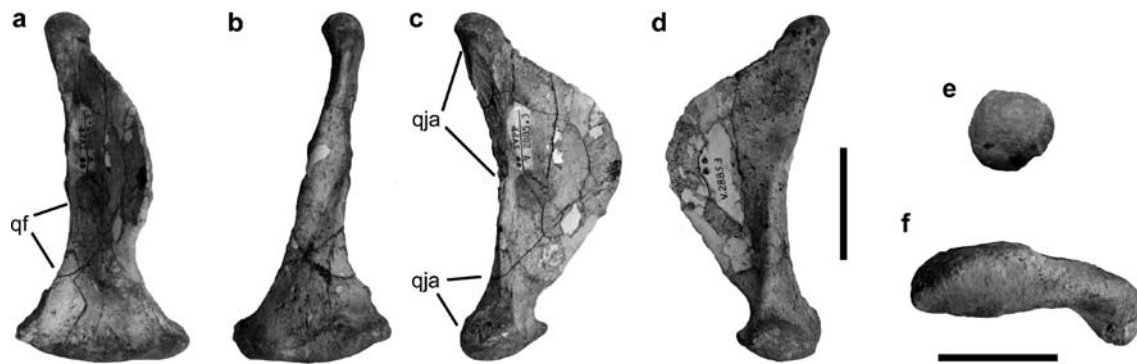


Fig. 2 *Shaochilong maortuensis* IVPP V2885.3. Right quadrate in anterior (a), posterior (b), lateral (c), medial (d), proximal (e), and distal (f) views. *qf* quadrate foramen, *qja* quadratojugal articular surface. Scale bars represent 5 cm

(Coria and Currie 2006; Brusatte and Sereno 2007). Promaxillary and maxillary fenestrae are not evident, possibly due to breakage, but there is only a small region of fossa that could have housed them in life. However, a promaxillary recess and maxillary antrum are visible through broken surfaces in medial view. The interdental plates are fused into a long sheet with a rugose, finely pitted surface texture and an autapomorphic series of deep grooves dorsally. Individual plates are more than twice as deep as long, a derived feature of carcharodontosaurids (contra Chure 1998). Above the plates, the paradental groove is autapomorphically absent.

The posterior end of the right nasal houses a deep pneumatic recess, subdivided into multiple pockets. Pneumatic nasals are characteristic of allosauroids, but *Shaochilong* uniquely possesses an internal recess that remains deep at the posterior end of the nasals.

The most spectacular feature of the frontal is a tall and sharp sagittal crest that rises 10 mm above the smooth dorsal surface of the bone. Sagittal crests are known in some coelurosaurids but are absent in non-coelurosaurian tetanurans; furthermore, the crest of *Shaochilong* is unique among theropods, as it rises from the broad dorsal surface of the frontals, unlike in coelurosaurids and abelisaurids in which transverse narrowing of the frontals produces a thin midline crest. The frontals are fused to each other and to the parietals, as is characteristic of carcharodontosaurids. Additional carcharodontosaurid features include anteriorly limited supratemporal fossae and a curved crest for muscle attachment within each fossa (Coria and Currie 2002; Brusatte and Sereno 2008). Enlarged articulations for the postorbital and lacrimal/prefrontal, combined with the absence of a frontal orbital rim, indicate that the postorbital and lacrimal made contact above the orbit as in carcharodontosaurids (Brusatte and Sereno 2008).

The quadrate is apneumatic as in *Allosaurus* (Madsen 1976), *Sinraptor* (Currie and Zhao 1993), and other non-coelurosaurian theropods, whereas it is extensively pneuma-

tized in other carcharodontosaurids (Currie and Carpenter 2000; Coria and Currie 2006). The quadrate foramen is small and was located between the quadrate and quadratojugal.

The braincase is among the best preserved basal tetanuran braincases currently known. It is short, deep, and extensively pneumatized, as in carcharodontosaurids. The dorsal tympanic recess on the prootic is deeply embayed and penetrated anteriorly by a large, autapomorphic pneumatic foramen. Paracondylar pneumatopores lead into a medial recess below the endocranial cavity as in carcharodontosaurids (Coria and Currie 2002). The basisphenoid recess is large, and although eroded ventrally, its widely divergent and thick walls suggest that it was expansive, likely intermediate between the shallow pockets of most theropods and the deep funnels of some carcharodontosaurids (Sereno et al. 1996; Brusatte and Sereno 2007).

The supraoccipital has a rugose, knob-like dorsal process. As in derived carcharodontosaurids and *Sinraptor*, the occipital surface slopes posteroventrally (Coria and Currie 2002). The paroccipital processes are strongly downturned, terminating ventral to the occipital condyle as is characteristic of allosauroids. These processes are apneumatic and do not twist distally, unlike those of many coelurosaurids (e.g., Makovicky and Norell 1998; Norell et al. 2004). The single trigeminal (V) nerve opening lies posterior to the nuchal wedge as in carcharodontosaurids (Coria and Currie 2002) and two separate facial (VII) nerve openings are present, a condition otherwise known only in *Acrocanthosaurus* (Franzosa and Rowe 2005). The antotic crest, a ridge on the laterosphenoid that divides the orbital and temporal spaces, is thickened as in carcharodontosaurids, but unlike *Allosaurus*, *Sinraptor*, and most theropods (Sampson and Witmer 2007). Both the interorbital septum and the sphenethmoid are unossified; the former is missing and the latter is inferred to be absent due to the lack of attachment scars on the ventral surface of the frontal.

The braincase of *Shaochilong* helps clarify a confusing feature in other carcharodontosaurids. Coria and Currie (2002) described the fenestra ovalis of *Carcharodontosaurus* and *Giganotosaurus* as facing posteriorly and opening onto the occiput. This interpretation, based on clearly broken bone surfaces in both taxa, was challenged by Brusatte and Sereno (2007). In *Shaochilong*, this region is well preserved on both sides, and the fenestra ovalis is clearly present on the lateral wall of the braincase, but located on the anterior surface of the crista tuberalis (=metotic strut of many authors). Thus, it faces mostly anteriorly and is placed far lateral (22 mm) to the endocranial cavity. Coria and Currie (2002) were correct in that the fenestra ovalis is reoriented in an antero-posterior direction, but the crista tuberalis (“metotic strut”) walls it off posteriorly and prevents it from opening onto the occiput.

Phylogenetic analysis

To assess the relationships of *Shaochilong*, we performed two separate phylogenetic analyses. First, since previous studies have allied *Shaochilong* with various disparate theropod groups (Megalosauridae, Allosauridae, Tyrannosauroidae, Maniraptora), we tested its position in global theropod phylogeny using the recent analysis of Smith et al. (2007), which includes representatives of every group with which *Shaochilong* has previously been united. When included in this analysis, *Shaochilong* falls out deeply nested within the carcharodontosaurids (see [Electronic supplementary material](#)).

Second, we tested the affinities of *Shaochilong* within Allosauroidae using the less inclusive analysis of Brusatte and Sereno (2008). This includes a larger sample of allosauroid taxa and characteristics relevant to allosauroid ingroup phylogeny, as well as updated scorings based on redescriptions of several taxa (Brusatte and Sereno 2007; Brusatte et al. 2008; Sereno and Brusatte 2008) that were not incorporated into the data matrix of Smith et al. (2007). This analysis returned two most parsimonious trees (length=188, CI=0.60, RI=0.70), which differ only in placing either *Shaochilong* or the South American *Tyrannotitan* as the sister taxon to Carcharodontosaurinae (*Carcharodontosaurus*, *Giganotosaurus*, *Mapusaurus*; see [Electronic supplementary material](#)). *Shaochilong* is nested deeply within Carcharodontosauridae and is more derived than the well-known North American *Acrocanthosaurus*. Interestingly, *Tyrannotitan* is found to be more derived than in the original analysis, and depending on the resolution of the polytomy, it may fall within an endemic clade of African and South American carcharodontosaurids, as has been suggested (Fig. 3; Novas et al. 2005; Coria and Currie 2006).

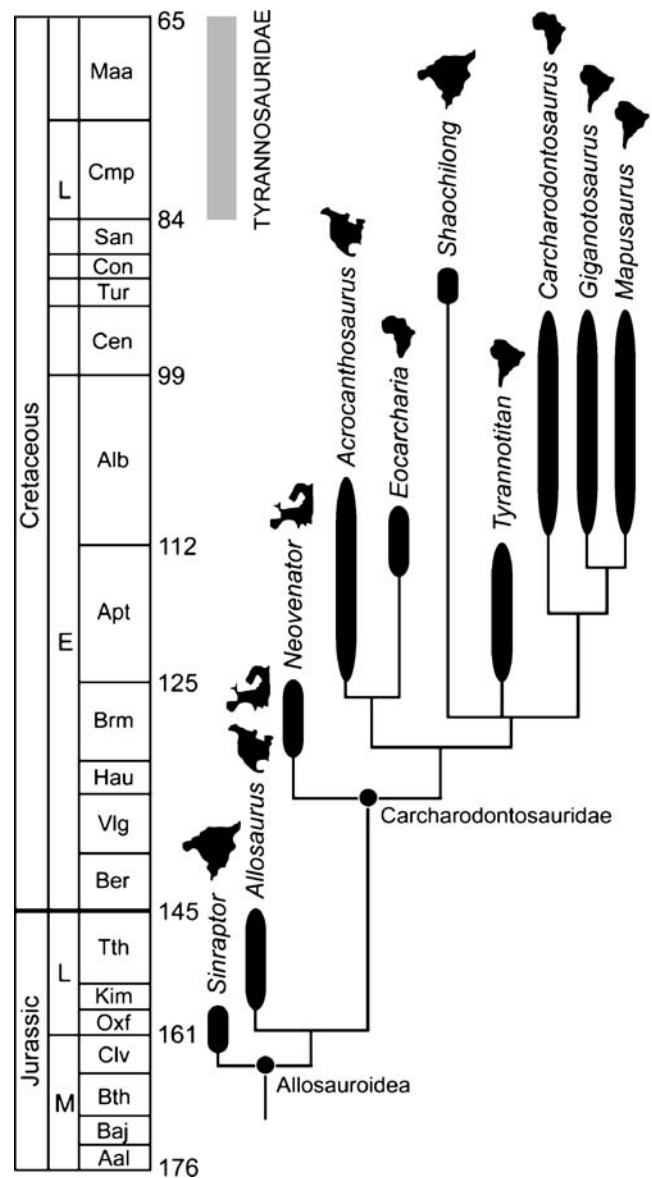


Fig. 3 Phylogenetic relationships of *Shaochilong maortuensis* and other allosauroid theropods superimposed on the Mesozoic time scale. *Thick black bars* represent the finest possible stratigraphic resolution for each taxon (they are not observed ranges). *Silhouettes* above each taxon denote geographic occurrences. *Thick gray bar* represents the temporal range of large-bodied tyrannosaurids in North America and Asia

Discussion

Although previously assigned to many disparate theropod groups, *Shaochilong* is here identified as a carcharodontosaurid for the first time. This placement is strongly supported and corroborated by numerous synapomorphies, enumerated above. Accordingly, *Shaochilong* is the first definitive carcharodontosaurid known from Asia. Chure et al. (1999) described an isolated tooth from Japan as a possible carcharodontosaurid, but the characteristics con-

sidered to support this affinity are in fact widespread among theropods (Brusatte et al. 2007). Identification of *Shaochilong* as a carcharodontosaurid indicates that this clade, which is often regarded as an endemic Gondwanan group (Currie and Carpenter 2000; Allain 2002; Novas et al. 2005), was cosmopolitan during the Early to mid Cretaceous. Carcharodontosaurids are also known from North America (*Acrocanthosaurus*), Europe (*Neovenator*), South America, and Africa during this time, and are only missing from the fossil records of Australia and Antarctica, two poorly sampled landmasses.

Given that carcharodontosaurids represent a global radiation, the referral of *Shaochilong* to this clade provides evidence that the mid Cretaceous large-bodied theropod faunas of Asia had a cosmopolitan flavor. A similar pattern has long been noted for sauropods (Upchurch 1995; Barrett et al. 2002) and ornithomimids (Norman 1998) and is thought to reflect a burst of faunal interchange after the severing of long-standing oceanic and topographic barriers (Russell 1993; Upchurch et al. 2002). However, the small theropod faunas of Early Cretaceous Asia have been described as relict biotas, in which remnants of widespread Jurassic clades persisted in isolation (Luo 1999; but see Xu and Norell 2006). It has been unclear whether large dinosaurian predators conformed to either of these hypothesized patterns, due to the immense gap in the record between the largely endemic Middle to Late Jurassic faunas (Brusatte et al. 2009; Zhao et al. 2009) and the tyrannosaurid-dominated Late Cretaceous assemblages. *Shaochilong* helps fill this gap, as do several recent discoveries that also provide support for Early Cretaceous interchange. The enigmatic *Fukuiraptor* (Azuma and Currie 2000) and *Siamotyrannus* (Rauhut 2003)—the two other relatively complete large Asian Early Cretaceous theropods—appear to belong to Allosauroidea, a large and widespread clade that includes carcharodontosaurids. Even more striking, spinosaurid theropods, previously known from Africa, Europe, and South America, have recently been described from Asia (Milner et al. 2007; Buffetaut et al. 2008).

If the details of our phylogenetic hypothesis are correct, the closest relatives of *Shaochilong* among carcharodontosaurids are all Gondwanan taxa. This finding is surprising and may cast doubt on one of the most prominent Mesozoic biogeographic scenarios: the hypothesis that allosauroids evolved vicariantly in concert with the breakup of Pangea (e.g., Harris 1998; Sereno 1999; Brusatte and Sereno 2008). This scenario predicts that Asian allosauroids should be positioned basally on the cladogram, as Asia was the first landmass to break away from Pangea, but the affinities of *Shaochilong* suggest the origination of allosauroid clades prior to major continental breakup events. Alternatively, the placement of *Shaochilong* as a derived carcharodontosaurid closely related to southern taxa may be evidence for

northern–southern interchange in the Early Cretaceous. Such interchange has been envisioned as “island-hopping” across the Tethys (Gheerbrant and Rage 2006). However, most discussions of Early Cretaceous Asian interchange have only noted similarities to contemporary faunas in Europe and North America at this time, as opposed to Gondwana (e.g., Russell 1993).

Carcharodontosaurids are part of the larger allosauroid radiation of the Middle Jurassic to mid Cretaceous. *Shaochilong* is the youngest known Laurasian allosauroid and extends the temporal range of this lineage on the northern continents until younger than 92 million years ago (based on the radiometric date of Kobayashi and Lu 2003). This helps considerably to bridge the gap between the youngest Laurasian allosauroids (previously *Acrocanthosaurus* from the ?Aptian–Albian, ca. ?125–100 million years ago, of North America) and the oldest large-bodied tyrannosaurids, which first appear suddenly in the Campanian in both North America and Asia (ca. 83.5 million years ago; Holtz 2004). As the mid Cretaceous record of North America is poor (e.g., Cifelli et al. 1997), *Shaochilong* may help constrain the timing of tyrannosaurid ascent in Laurasia as a whole. Although *Shaochilong* is only a single data point, its identification as a carcharodontosaurid suggests that basal tetanurans, not tyrannosaurids, were still the dominant large-bodied predators in Laurasia throughout the mid Cretaceous. This suggestion is reinforced by the contemporary *C. tashuikouensis*, an even larger theropod that also belongs to a non-tyrannosauroid basal tetanuran lineage (see [Electronic supplementary material](#); Benson and Xu 2008). Thus, we suggest that the rise of tyrannosaurids as large-bodied predators may have been a relatively sudden event restricted to the last 15–20 million years of the Cretaceous, despite the origination of the tyrannosauroid clade in the Late Jurassic (Xu et al. 2006; Benson 2008) and the presence of smaller tyrannosauroids in Asia throughout the Early Cretaceous (Xu et al. 2004; Li et al. 2009). This prediction can only be tested by the discovery of additional large theropods from the Early–middle Cretaceous of Asia and North America. The reinterpretation of *Shaochilong* as a carcharodontosaurid, along with the recent discovery of the Santonian (ca. 84 Ma) *Aerosteon* from Gondwana (Sereno et al. 2008), indicates that allosauroids persisted as large predators across the globe for longer than previously thought.

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