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The evolution of large-bodied theropod dinosaurs during the Mesozoic in Asia

La evolución de los grandes dinosaurios terópodos durante el
Mesozoico de Asia

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Abstract

The fossil record of large-bodied, apex carnivorous theropod dinosaurs in Eastern Asia is now among the best understood in the world, thanks to new discoveries and reinterpretations of long-neglected fossils. Asia boasts the most complete record of Middle Jurassic theropods globally, as well as one of the best-studied Late Cretaceous theropod faunas, and new research is helping to fill what was previously a 60-million-year gap in the Early-mid Cretaceous fossil record of large Asian predators. In general, the biogeographic affinities of large-bodied Asian theropods over time were intimately related to physical geography, and progressively more derived theropod clades evolved large body size and occupied the apex predator niche throughout the Jurassic and Cretaceous. During the Middle Jurassic, largely endemic clades of basal tetanurans were prevalent in Asia, whereas during the Late Jurassic-mid Cretaceous more derived “intermediate” tetanuran theropods with cosmopolitan affinities occupied the large predator role, including sinraptorids, spinosaurids, and carcharodontosaurians. Finally, during the final 20 million years of the Cretaceous, more derived, bird-like coelurosaurs attained large body size. Foremost among these were the tyrannosaurids, a radiation of northern (Asian and North American) megapredators whose ascent into the apex predator niche was a delayed event restricted to the Campanian-Maastrichtian. As Asia is the focus of intense ongoing dinosaur fieldwork, our understanding of large-bodied theropod evolution will continue to be refined with future discoveries.

Keywords: Asia, Dinosauria, Mesozoic, paleobiogeography, Theropoda, Tyrannosauridae.

Resumen

El registro fósil de los dinosaurios carnívoros terópodos de gran talla en el este de Asia es uno de los mejor conocidos del mundo, gracias a nuevos descubrimientos y reinterpretaciones de fósiles que han permanecido pobremente estudiados durante mucho tiempo. Globalmente, Asia comprende el registro fósil más completo de terópodos del Jurásico Medio, así como una de las faunas finicretácicas mejor estudiadas. Asimismo, las nuevas investigaciones están contribuyendo a completar un hiato de 60 millones de años en el registro fósil de grandes depredadores asiáticos correspondientes al Cretácido inferior-medio. En general, las afinidades biogeográficas de los grandes terópodos asiáticos a través del tiempo se hallan íntimamente ligadas a la geografía física. Progresivamente, varios clados derivados de terópodos evolucionaron grandes tallas corporales, ocupando la cima del nicho de depredador durante todo el Jurásico y el Cretácico. Durante el Jurásico Medio prevalecieron clados de tetanuros basales mayormente endémicos, mientras que durante el Jurásico Superior-Cretácico Medio clados más derivados de terópodos tetanuros “intermedios” de afinidades cosmopolitas ocuparon el papel de gran depredador, incluyendo sinraptóridos, espinosáuridos y carcharodontosáuridos. Finalmente, durante los últimos 20 millones de años del Cretácico, coelurosaurios más derivados con aspecto reminiscente a las aves alcanzaron grandes tallas corporales. Pirmordialmente entre estas formas se hallaban los tiranosáuridos, una radiación septentrional (asiáticos y norteamericanos) de megadepredadores cuyo ascenso a la cumbre del nicho de gran depredador se retrasó hasta el Campaniense y Maastrichtiense. Mientras Asia continúa constituyendo el foco de una intensa actividad paleontológica, nuestros conocimientos sobre la evolución de los grandes terópodos continuará refinándose con el estudio de futuros hallazgos.

Palabras clave: Asia, Dinosauria, Mesozoico, paleobiogeografía, Theropoda, Tyrannosauridae.

1. Introduction

Long overshadowed by discoveries in North America and Europe, the fossil record of Eastern Asian dinosaurs is now among the best documented in the world. Over the past two decades Asia has emerged as an epicenter of vertebrate paleontology research, thanks to the discovery of spectacular fossil sites in China (e.g., Zhou *et al.*, 2003; Xu and Norell, 2006; Varricchio *et al.*, 2008; Xu *et al.*, 2009a,b) and Mongolia (e.g., Dashzeveg *et al.*, 1995; Loope *et al.*, 1998), as well as important new fossils from Japan (e.g., Azuma and Currie, 2000; Kobayashi and Azuma, 2003; Ohashi and Barrett, 2009) and Thailand (e.g., Buffetaut and Suteethorn, 1999). On average, a new Asian dinosaur is described once every two or three weeks, and many of these discoveries have graced the pages of high-impact journals and have been trumpeted in the popular press.

The most familiar and celebrated Asian dinosaurs are the “feathered dinosaurs” of the Jehol Biota, a remarkable assemblage of Early Cretaceous (ca. 125 million year old) carnivorous dinosaurs covered in various types of feathery integument (Ji *et al.*, 1998; Norell and Xu, 2005; Xu and Norell, 2006). Although it was suggested that birds have some relationship with carnivorous theropod dinosaurs as early as the 19th century (e.g., Huxley, 1868), and subsequently proposed that birds were the extant descendants of theropods (e.g., Ostrom, 1969), the discovery of the Jehol fossils in the mid 1990s provided the final, and most visual, piece of evidence: bona fide theropods with feathers. Today, the Jehol fossils, along with specimens from other sites in China such as the Middle-Late Jurassic Daohugou and Yanliao Faunas

(e.g., Xu and Zhang, 2005; Zhang *et al.*, 2008), continue to play key roles in debates over the timing of bird origins (e.g., Chen *et al.*, 1998; Hu *et al.*, 2009), the evolution of avian flight (e.g., Xu *et al.*, 2003), the development of feathers (e.g., Prum and Brush, 2002; Xu *et al.*, 2009c; Zheng *et al.*, 2009), and the evolution of the unique avian hand (Xu *et al.*, 2009a).

The feathered theropods of the Jehol Biota are among the best studied carnivorous dinosaurs in the world, but they all represent small-bodied theropods (most are smaller than an average-sized man). Considerably less is known about the large-bodied theropods of Asia: the apex predators in most Mesozoic terrestrial ecosystems, some of which reached lengths of 10+ meters and masses of more than one tonne (Fig. 1). Comparatively few specimens of large, apex predator theropods are known from Asia, and there are substantial gaps in the fossil record of these carnivores. However, Asia does boast one of the most complete records of Middle Jurassic and Late Cretaceous large theropods from anywhere in the world, and recent discoveries and redescrptions are beginning to reveal long enigmatic details of large theropod evolution during the Late Jurassic-mid Cretaceous of Asia (e.g., Gao, 1999; Azuma and Currie, 2000; Benson and Xu, 2008; Brusatte *et al.*, 2009a; Brusatte *et al.* 2010b; Benson *et al.*, 2010). In this paper, a companion to our presentation at the 10th Mesozoic Terrestrial Ecosystems Symposium in Teruel, we provide an overview of large-bodied theropod evolution during the Mesozoic in Eastern Asia, with a particular emphasis on new specimens and information. We focus on the body fossil record, and particularly on the most complete and best preserved specimens (Fig. 2). We do not cover all Asian theropods

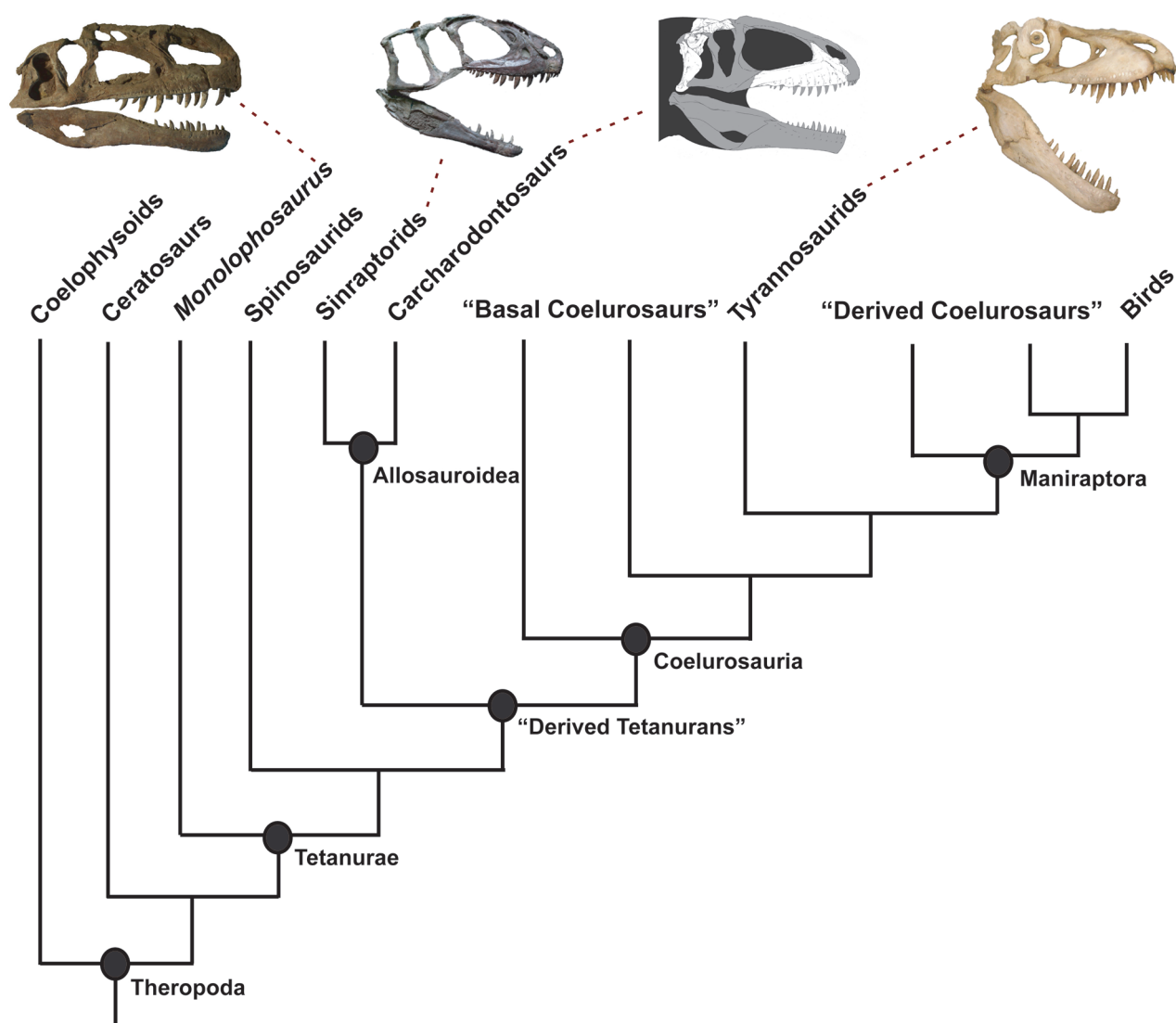


Fig. 1.-A framework phylogeny (genealogical tree) of theropod dinosaurs, with skull images of the most important groups of large carnivores from Asia. Basal theropods such as *Monolophosaurus*, belonging to endemic clades, filled the large carnivore niche in the Middle Jurassic, whereas allosauroid sinraptorids and carcharodontosaurians were the apex predators in the Late Jurassic and Early-mid Cretaceous of Asia, respectively. During the final 20 million years of the Cretaceous, more derived coelurosaurian theropods achieved large body size, most notably tyrannosaurids such as *Tarbosaurus*. Note that some analyses have recovered *Monolophosaurus* as a basal megalosauroid (= spinosauroid, e.g., Benson *et al.*, 2010), so it may group with spinosaurids in this cladogram.

Fig. 1.- Filogenia ("árbol genealógico") de los dinosaurios terópodos, con imágenes de cráneos de los grupos más importantes de grandes carnívoros de Asia. Terópodos basales como *Monolophosaurus*, pertenecientes a clados endémicos, ocuparon el nicho de gran carnívoro durante el Jurásico medio. Sinraptóridos allosauroides y carcharodontosáuridos fueron los carnívoros ubicados en la cima de la cadena alimenticia durante el Jurásico tardío y el Cretácico temprano-medio de Asia, respectivamente. Durante los últimos 20 millones de años del Cretácico, clados derivados de terópodos coelurosaurios alcanzaron grandes tallas, notablemente tiranosáuridos como *Tarbosaurus*.

here, but only medium-to-large-bodied taxa that were likely apex predators, or otherwise occupied a top predator niche.

2. Overview of Asian Large-Bodied Theropods

Large-bodied theropods first appear in the Asian fossil record during the Middle Jurassic (Fig. 2). They may have been present during earlier time intervals, but are

missing because Late Triassic-Early Jurassic terrestrial sedimentary rocks are rare and often lacking in fossils. Indeed, theropod specimens from the Late Triassic and Early Jurassic are exceptionally uncommon (Weishampel *et al.*, 2004; Zhao *et al.*, 2008). However, the absence of large theropods in the well-sampled Early Jurassic Lufeng Formation may be a genuine signal. Large-bodied theropods, of sizes comparable to those of the Middle Jurassic and later in dinosaur history, are essentially

unknown from the Triassic and Lower Jurassic globally. The earliest truly large taxon is *Shidaisaurus* (Wu et al., 2009) from the early Middle Jurassic of Asia. This is contemporaneous with, or slightly pre-dates, the emergence of large theropods in the Bathonian of Europe (*Megalosaurus*: Benson, 2010).

The Lower Lufeng Formation of Yunnan has yielded what is currently the most informative Early Jurassic theropod from Asia, the holotype of *Dilophosaurus sinensis*, a nearly complete skeleton of a mid-sized theropod (ca. 5-6 meters long) (Hu, 1993). This specimen was

originally referred to the genus *Dilophosaurus*, as its double-crested skull is extremely similar to that of *Dilophosaurus wetherilli* from the Early Jurassic of North America (Welles, 1984). Lamanna et al. (1998) disputed this referral and argued that *D. sinensis* was a more derived theropod not particularly closely related to *D. wetherilli*, but Smith et al. (2007) recovered the two taxa as close relatives in a large phylogenetic analysis. Unfortunately, the holotype of *D. sinensis* has only been briefly described. What is clear is that *D. sinensis* is an extremely basal theropod, in concert with its Early Jurassic age, and

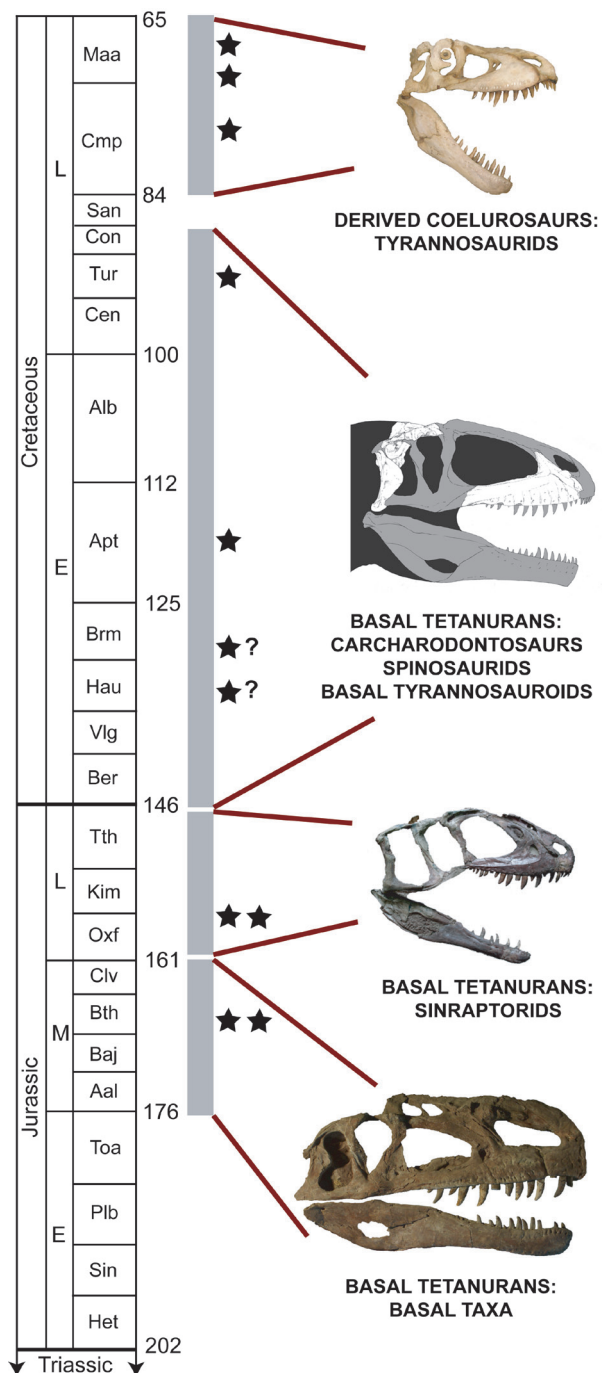


Fig. 2.-Schematic diagram illustrating the major groups of large theropod dinosaurs in Asia throughout the Mesozoic. Different theropod groups filled the large predator niche over time, and in general progressively more derived theropods achieved large body size in Asia throughout the Jurassic and Cretaceous. Thick gray bars represent the general durations of the indicated large theropod faunas, whereas stars represent the age of actual fossil sites that preserve large theropods. Question marks indicate uncertain dating of some fossil sites. The timescale on the left is taken from Walker and Geissman (2009).

Fig. 2.-Diagrama esquemático ilustrando los grupos principales de dinosaurios terópodos de Asia durante el Mesozoico. Diferentes grupos de terópodos ocuparon el nicho de gran depredador durante ese tiempo y, en general, formas progresivamente más derivadas alcanzaron grandes tallas corporales en Asia durante el Jurásico y el Cretácico. Las barras en gris representan, en general, la duración de las faunas de terópodos indicadas, mientras que las estrellas representan la edad de las localidades que han proporcionado grandes terópodos. Los interrogantes indican la datación ambigua de algunas localidades fósiles. La escala temporal de la izquierda se obtuvo de Walker and Geissman (2009).

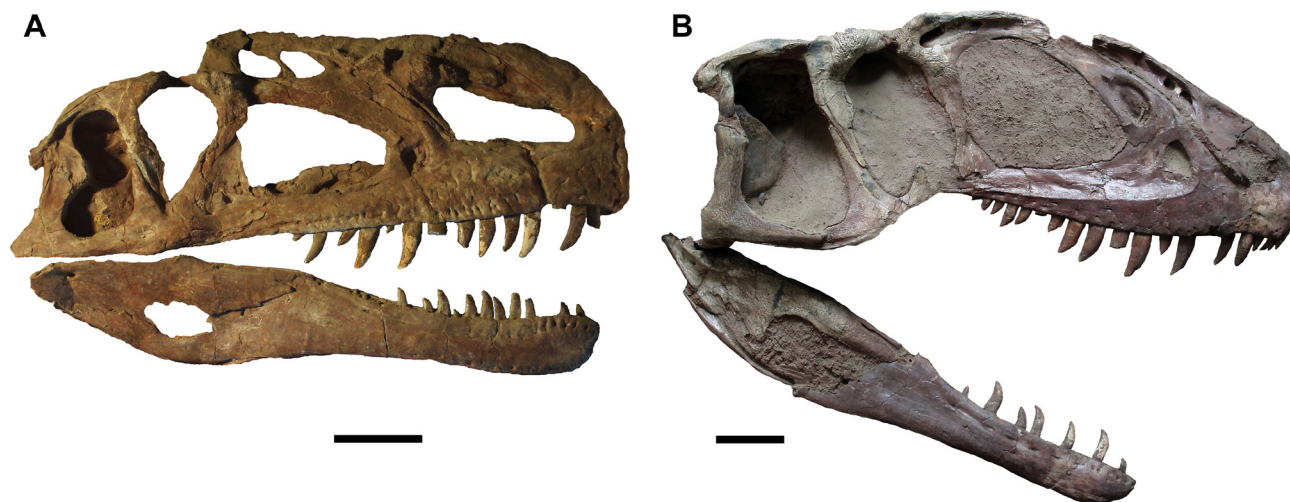


Fig. 3- Skulls of Middle-Late Jurassic Asian theropods in right lateral view. A, *Monolophosaurus jiangi* (IVPP 84019), Middle Jurassic Shishugou Formation of Xinjiang, China; B, *Sinraptor dongi* (IVPP 10600), Late Jurassic (Oxfordian) Shishugou Formation of Xinjiang, China. Scale bars equal 10 centimeters.

Fig. 3.- Cráneos de terópodos asiáticos del Jurásico medio-tardío en vista lateral derecha. A, *Monolophosaurus jiangi* (IVPP 84019), Jurásico medio de la Formación Shishugou de Xinjiang, China; B, *Sinraptor dongi* (IVPP 10600), Jurásico tardío (Oxfordiense) de la Formación Shishugou de Xinjiang, China. La escala equivale a 10 cm.

is a medium-sized carnivore that is substantially smaller than most of the large-bodied theropods considered in this review.

Subsequently, during the Middle Jurassic, Asia was home to a diverse fauna of medium-to-large-bodied theropods (Figs. 2, 3). Taxa such as *Monolophosaurus*, *Gasosaurus*, and ‘*Szechuanosaurus*’ are known from well-preserved and substantially complete specimens, and additional taxa are known from more fragmentary remains. China, therefore, boasts the highest taxic diversity of Middle Jurassic theropods of all body sizes from anywhere in the world. Unfortunately, most of these taxa have not been described in detail and their affinities remain uncertain. However, new information suggests that some of these taxa constituted endemic clades, or primitive grades, of basal tetanuran theropods (Zhao *et al.*, 2010), likely a result of the paleogeographic separation of Asia from the rest of Pangea during the Middle Jurassic (Smith *et al.*, 1994; Upchurch *et al.*, 2002).

Later, during the Late Jurassic, Asia was home to the sinraptorid allosauroids (Figs. 2, 3). Often thought to be an endemic clade, sinraptorids are now known from Europe (Mateus, 1998; Benson, 2010), suggesting that large theropod faunas were more cosmopolitan during this time. Such cosmopolitanism was even more apparent during the Early-mid Cretaceous, as carcharodontosaurian and spinosaurid theropods, both widespread clades, filled the large predator niche in Asia at this time (Figs. 2, 4-6). Finally, during the terminal 20 million years of the Cretaceous, the apex predator role was occupied by the colossal tyrannosaurids, a clade otherwise only known

from North America (Figs. 2, 7-8). Other derived, bird-like coelurosaurian groups such as the oviraptorosaurs and ornithomimosaurs also developed large body size during this time, although these animals were herbivorous or omnivorous.

In sum, over time different groups of theropods filled the large predator role in Asia, and their distributions reflect the changing paleogeography of the Mesozoic (Fig. 2). During the earliest stage of large-bodied theropod evolution in Asia, the Middle Jurassic, the apex predators belonged to basal theropod clades. Over the next 100 million years, more derived groups of theropods (i.e., those progressively more closely related to birds) developed large body size. The Middle Jurassic large theropod faunas were possibly endemic, whereas Late Jurassic-mid Cretaceous taxa were members of cosmopolitan radiations. By the close of the Cretaceous, however, Asia sported a large theropod fauna of tyrannosaurids and other large coelurosaurs that was similar to faunas in North America, but drastically different from those on the southern continents (Africa, South America, India, Madagascar, Australia). This evolutionary sequence, now understood in unprecedented detail because of the ongoing discovery and description of Asian fossils, is currently the best long-term record of large dinosaur predators on a single landmass.

3. Middle Jurassic

Chinese Middle Jurassic theropods were first reported in 1984. Since then, their fossil record has grown stead-

ily and more Middle Jurassic taxa are known from China than any other geographic region. The occurrence of derived paravian theropods in the Late Jurassic, such as the troodontid *Anchiornis* from the Oxfordian of China (Xu et al., 2009; Hu et al., 2009) and the avian *Archaeopteryx* from the Tithonian of Europe (Meyer, 1861), indicate that critical phases in theropod diversification, body size evolution, and the acquisition of avian biological traits took place in the Middle Jurassic. As a source of continuing discoveries, China has great potential to shed light on this important episode in theropod history, especially concerning large-bodied theropod evolution.

The Xiashaximiao Formation (late Middle Jurassic) of Sichuan Province has yielded *Xuanhanosaurus* (Dong, 1984), '*Szechuanosaurus*' *zigongensis* (Gao, 1993), *Kaijiangosaurus lini* (He, 1984), *Chuangongocoelurus primitivus* (He, 1984) and *Gasosaurus constructus* (Dong & Tang, 1985). *Shidaisaurus jinae* was recently reported from the base of the Upper Lufeng Formation (early Middle Jurassic) (Wu et al., 2009) and *Monolophosaurus* is known from the ?mid-Bathonian–late Callovian (D. Eberth, pers. comm. 2009) part of the Shishougou Formation of Xinjiang Uyghur Autonomous Region (Zhao and Currie, 1994) (Fig. 3A). Most of these taxa pertain to mid-to-large-bodied theropods, and most are known from associated postcranial skeletons.

Most Middle Jurassic theropods from China are generally 'medium-sized' (Table 1; *Gasosaurus*), as are the majority of Middle Jurassic theropods globally. However, *Chuangongocoelurus* is exceptionally small among basal tetanurans (Table 1), with an estimated mass of only 13 kg. The large-bodied *Shidaisaurus* is from the other end of the body size spectrum, as its ilium is 620 mm long (Wu et al., 2009). This is shorter than the largest ilia of *Megalosaurus* (>832 mm; Benson, 2010) from the Bathonian (Middle Jurassic) of the United Kingdom. However, the ilia of *Shidaisaurus* are taller dorsoventrally relative to their length, perhaps indicating that *Shidaisaurus* was only slightly smaller than *Megalosaurus* (estimated body mass approximately 1000 kg; Anderson et al., 1985; Benson, 2009a; Benson, 2010). *Shidaisaurus*, from the lower Middle Jurassic, is the stratigraphically earliest discovery of truly large body size in theropods and may represent the emergence of giant predators for the first time in dinosaur history. Alternatively, their absence in older deposits may simply await further exploration.

The taxonomy and systematics of Middle Jurassic theropods have long been neglected. This is largely due to a paucity of data, as the Middle Jurassic dinosaur record is poorly sampled globally (e.g. Weishampel et al. 2004). However, recent reviews and revisions have focused on the Chinese taxon *Monolophosaurus* (Brusatte

et al., 2010a; Zhao et al., 2010) and the European Middle Jurassic theropod record (Allain, 2001, 2002, 2005; Allain and Chure, 2002; Benson, 2009a, b; and 2010; Benson et al., 2008; Sadleir et al., 2008). As a result, the relationships of many Middle Jurassic taxa are now better understood (Smith et al., 2007; Benson, 2010). The emerging pattern suggests that during the Middle Jurassic, theropods from the three well-sampled regions (Argentina, China, and Europe) formed geographically localized, perhaps 'endemic' clades (Smith et al., 2007; Zhao et al., 2010; Benson, 2010).

Unfortunately, most Chinese Middle Jurassic theropods have not been described in detail since their original publication. As such, their affinities remain uncertain. However, *Monolophosaurus* and *Chuangongocoelurus* show an intriguing combination of derived, tetanuran synapomorphies and primitive features shared with non-tetanurans, which together suggest a basal position within Tetanurae (Zhao et al., 2010). Therefore, understanding the anatomy of Chinese Jurassic taxa may reveal further details of primitive tetanuran anatomy and thus help to resolve the early evolution of this taxonomically diverse and successful theropod clade. Furthermore, the possibility of Middle Jurassic dinosaur provincialism can only be tested by detailed restudy of Chinese Middle Jurassic theropods, coupled with better resolution of the species-level phylogeny of other dinosaur groups. In summary, future exploration of the Chinese Middle Jurassic theropod record promises to yield new insights into the diversification of Tetanurae, the origin of large body size among theropods, and Middle Jurassic paleobiogeography.

4. Late Jurassic

Large-bodied Late Jurassic theropods are well-known globally, especially compared to earlier time intervals, and the Chinese record is no exception. Most taxa were referred to the basal allosauroid clade Sinraptoridae by Currie and Zhao (1994), who provided an excellent description of *Sinraptor dongi* (Fig. 3B). Other taxa have only been preliminarily described, which obstructs our understanding of their systematic placement.

The first reported Late Jurassic Asian theropod taxon, *Szechuanosaurus campi*, was discovered in China over a half century ago (Young, 1942). The holotype of *S. campi* is a series of four teeth from the early Late Jurassic (Oxfordian–early Kimmeridgian: Peng et al., 2005) Shangshaximiao Formation. Unfortunately, these fossils have been considered undiagnostic (Chure, 2000), thus rendering *S. campi* a nomen dubium. A partial skeleton referred to *Szechuanosaurus campi* (Dong et al., 1983) has also been described from the Shangshaximiao For-

		Maxilla length or other measurement	Femur length	Femur circumference	Mass estimate (kg) ¹	Mass estimate (kg) ²	Source
Lower Jurassic	<i>'Dilophosaurus' sinensis</i>	350	590	220	397	436	LDM Z10
	<i>Cryolophosaurus</i> §	-	780	238	492	1072	FMNH PR 1821
	<i>Dilophosaurus wetherilli</i> §	350 (UCMP 77270)	557	160	166	362	UCMP 37302
Middle Jurassic	<i>Chuangongocoelurus</i>	-	205	63	13	14	GCC 20010
	<i>Gasosaurus</i>	-	470	-	-	210	Dong and Tang 1985
Late Jurassic	<i>Sinraptor dongi</i> *	420	876	-	-	1559	Currie and Zhao 1994
	<i>Sinraptor hepingensis</i>	495	980	-	-	2237	Gao 1999
	<i>Yangchuanosaurus shangyuensis</i>	500	850	-	-	1414	Dong et al. 1983
Early Cretaceous	<i>Fukuiraptor</i>	-	507	164	178	268	Currie and Azuma 2006
	<i>Kelmaysaurus</i>	Dentary length = 523	-	-	-	-	IVPP V 4022
	<i>Sinotyrannus</i>	Ilium length = 770	-	-	-	-	Ji et al. 2009
Late Cretaceous	<i>Chilantaisaurus</i>	-	1190	432	2506	4182	Benson and Xu 2008
	<i>Shaochilong</i>	Maxillary tooth row length = 255	-	-	-	-	Brusatte et al. 2009a
	<i>Alioramus</i> *	430	560	170	196	369	Brusatte et al. 2009b
	<i>Beishanlong</i>	-	660	-	-	626	Makovicky et al. 2010
	<i>Deinocheirus</i>	Humerus length = 938	-	-	-	-	Osmólska and Roniewicz, 1970
	<i>Gallimimus</i>	-	673	216	378	667	Christiansen and Farina 2004
	<i>Gigantoraptor</i>	-	1100	352	1433	3246	Xu et al. 2007
	<i>Suzhousaurus</i>	-	840	-	-	1362	Li et al. 2008
	<i>Tarbosaurus</i>	630 (ZPALMgD-1/4)	854	312	1031	1436	Christiansen and Farina 2004

Table 1. Measurements of the femur and other skeletal elements indicating body size in theropods. Most listed taxa are Asian theropods, but a sample of non-Asian taxa, which are close relatives of less complete Asian taxa, are included for comparative purposes (these are denoted by § after the taxon name). Two mass estimates are presented: based on femur circumference, as calculated by equations in Alexander *et al.* (1985) and denoted by 1; based on femur length, as calculated by Christiansen and Fariña (2004) and denoted by 2. The symbol * denotes measurements from immature specimens. All measurements are in millimeters unless otherwise indicated. Abbreviations: FMNH, Field Museum of Natural History, Chicago, USA; GCC, Geological College of Chengdu, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; LDM, Lufeng Dinosaurs Museum, Yunnan, China; UCMP, University of California Museum of Paleontology, Berkeley, USA; ZPAL, Institute of Palaeobiology, Warsaw, Poland.

Tabla 1. Medidas del fémur y otros elementos esqueléticos indicando tamaño corporal en terópodos. Las estimaciones de masa corporal se basan en la circunferencia femoral, calculadas a partir de las ecuaciones de Alexander *et al.* (1985). Aquellos taxones de fuera de Asia están indicados con § después del nombre del taxón, mientras que * denota medidas realizadas en especímenes inmaduros. Abreviaturas: FMNH, Field Museum of Natural History, Chicago, USA; GCC, Geological College of Chengdu, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; LDM, Lufeng Dinosaurs Museum, Yunnan, China; UCMP, University of California Museum of Paleontology, Berkeley, USA; ZPAL, Institute of Palaeobiology, Warsaw, Poland.

mation of Sichuan. This specimen was only briefly described by Dong *et al.* (1983) and its affinities are poorly resolved. It has not been included in many phylogenetic analyses, but Holtz *et al.* (2004) found it as the most basal tetanuran. The ischium of this specimen is 420 mm long, comparable to 'medium' sized theropods such as *Piatnitzkysaurus* (ischium length = 423 mm; mass estimated at 504 kg based on a femoral circumference of 240 mm; Anderson *et al.*, 1985) and most Chinese Middle Jurassic theropods.

Other large-bodied Chinese theropods are larger than this supposed *Szechuanosaurus* specimen, with femoral lengths comparable to some individuals of the tyrannosaurid *Tarbosaurus* (Table 1). These taxa are all sinrap-

torids (Currie and Zhao, 1994): *Sinraptor hepingensis* (Gao, 1992, 1999), *Yangchuanosaurus shangyuensis* (Dong *et al.*, 1978), and *Yangchuanosaurus magnus* (Dong *et al.*, 1983) from the Shangshaximiao Formation of Sichuan, and *Sinraptor dongi* (Currie and Zhao, 1994) from the Shishougou Formation (Oxfordian) of Xinjiang (Fig. 3B). Sinraptorids were also present elsewhere in Asia, as recently a tibia pertaining to this group was described from the Phu Kradung Formation of Thailand, a unit with poor age constraint that may be Late Jurassic or possibly Early Cretaceous in age (Buffetaut and Suteethorn, 2007). Some of these taxa may have grown to enormous sizes: a possible sinraptorid lateral tooth from the Shishougou Formation represents the larg-

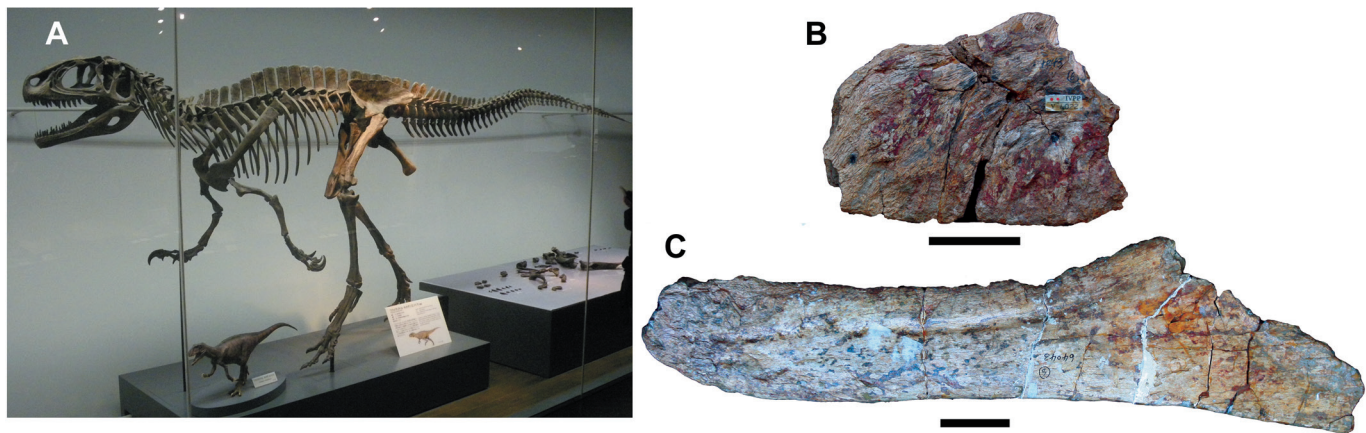


Fig. 4- Early Cretaceous Asian theropods. A, *Fukuiraptor kitadaniensis*, Late Hauterivian-Barremian of Japan; B and C, *Kelmaysaurus petrolicus*, (?Valanginian-Albian of Xinjiang, China. B, left maxilla fragment in lateral view; C, left dentary in lateral view. Scale bars equal 5 centimeters. Photograph in A courtesy of Dave Hone.

Fig. 4.- Terópodos del Cretácico temprano de Asia. A, *Fukuiraptor kitadaniensis*, Hauteriviense tardío-Barremiense de Japón; B y C, *Kelmaysaurus petrolicus*, (?Valanginiense-Albiense de Xinjiang, China. B, fragmento de maxilar izquierdo en vista lateral; C, dentario izquierdo en vista lateral. La escala equivale a 5 cm. Fotografía en A cortesía de Dave Hone.

est reported theropod tooth from the Jurassic and is comparable in size to the lateral teeth of *Tyrannosaurus* (Xu and Clark, 2008). However, other sinraptorids, such as the recently described *Leshansaurus* from the Shangshaximiao Formation, may have been somewhat smaller (femur length of approximately 60 centimeters: Li *et al.*, 2009). Until recently, sinraptorids were often regarded as a uniquely Asian radiation (e.g., Allain, 2002). However, restudy of *Metriacanthosaurus* from the Oxfordian of the United Kingdom suggests that it is nested within the clade, as may be the Late Jurassic Portuguese theropod *Lourinhanosaurus* and the Middle Jurassic French taxon *Poekilopleuron* (Benson, 2010; Benson *et al.*, 2010). If these placements are corroborated they may indicate that Asia was home to cosmopolitan (or at least European-influenced) large theropods during the Late Jurassic, in contrast to the more endemic nature of Middle Jurassic faunas.

5. Early - early Late Cretaceous

Large-bodied theropod fossils from the Early-mid Cretaceous (ca. 145.5-83.5 million years ago) are rare in Asia (Weishampel *et al.*, 2004; Zhao *et al.*, 2008). Only a small sample of specimens is known, most of which were discovered and described several decades ago (e.g., Hu, 1964; Dong, 1973). Most of these were described and figured only briefly, and as a result, their taxonomy and phylogenetic relationships have been contentious (Chure, 2001; Rauhut, 2003a). However, in recent years, important specimens from the Early-mid Cretaceous of China have been restudied, redescribed, and reassessed (Ben-

son and Xu 2008; Brusatte *et al.*, 2009a; Benson *et al.*, 2010; Brusatte *et al.* 2010b), and critical new specimens from Japan (Azuma and Currie, 2000; Currie and Azuma, 2006) and Thailand (Buffetaut *et al.*, 1996, 2008; Milner *et al.*, 2007) have come to light. Together, this new information has helped to illuminate what was previously a 60-million-year dark period in the fossil record of large Asian theropods.

5.1. Early Cretaceous of China, Japan, and Thailand

Early Cretaceous large-bodied theropod fossils are rare in Asia, but substantially complete and informative specimens are known from three countries: China, Japan, and Thailand.

In China, only a single decent specimen of a large Early Cretaceous theropod is known. Described by Dong (1973), this partial skull is comprised of a fragmentary left maxilla and a nearly complete left dentary, and is from the poorly constrained Lianmugin Formation (?Valanginian-Albian) of Xinjiang (Fig. 4B,C). It was named by Dong (1973) as a new genus and species, *Kelmaysaurus petrolicus*, but has been dismissed by many subsequent authors as a nomen dubium because of its fragmentary nature (e.g., Rauhut and Xu, 2005). Similarly, its phylogenetic relationships are poorly resolved, and most authors have regarded it as a basal tetanuran theropod of uncertain affinities (e.g., Molnar *et al.*, 1990; Holtz *et al.*, 2004). Recent reexamination of the material, however, reveals that *Kelmaysaurus* can be diagnosed by a single autapomorphy (a deeply inset and dorsally concave “accessory” groove located anteriorly on the lateral surface

of the dentary) and shares features with the carcharodontosaurian theropods, a cosmopolitan subclade of allosauroids that includes some of the largest terrestrial predators to ever live. Some of these features, however, are also seen in large megalosauroids such as *Megalosaurus* and *Torvosaurus*. The precise affinities of *Kelmayisaurus* remain unclear, but this taxon is the subject of ongoing study (Brusatte, Benson, and Xu, in prep).

In Japan, the Kitadani Formation (Late Hauterivian-Barremian: Kobayashi and Azuma, 2003) of Fukui Prefecture has yielded numerous associated and isolated remains of another carcharodontosaurian, *Fukuiraptor kitadaniensis* (Azuma and Currie, 2000; Currie and Azuma, 2006) (Fig. 4A). *Fukuiraptor* is one of the smallest allosauroid theropods known, with an estimated body mass of 175 kilograms, but is included here since its closest relatives are large-bodied taxa. *Fukuiraptor* was originally described as a basal tetanuran theropod, likely an allosauroid, but its more precise phylogenetic affinities have proven elusive (Brusatte and Sereno, 2008; Hocknull et al., 2009; Benson, 2010). The recent discovery of the Australian allosauroid *Australovenator* (Hocknull et al., 2009) and the South American taxon *Aerosteon* (Sereno et al., 2008), along with the monographic description of the European carcharodontosaurian *Neovenator* (Brusatte et al., 2008), has allowed for a revision of allosauroid phylogeny (Benson et al., 2010). In this recent analysis, *Fukuiraptor* is found to be the sister taxon of *Australovenator*, and both taxa are members of a speciose clade of basal carcharodontosaurians, Neovenatoridae. This clade is cosmopolitan, and in addition to the Asian and Australian forms also includes taxa from Europe (*Neovenator*) and South America (*Aerosteon*, *Megaraptor*, *Orkoraptor*). Additionally, some neovenatorids survived until late into the Cretaceous, and some taxa (such as *Fukuiraptor*) are sleek, mid-sized animals that convergently share many features of the appendicular skeleton and the extent of postcranial pneumaticity with bird-like coelurosaurian theropods. In essence, *Fukuiraptor* and other neovenatorids are more basal theropods mimicking more derived theropods (which are more closely related to birds).

In Thailand, three Early Cretaceous units have yielded remains of two cosmopolitan theropod clades, Allosauroidea and Spinosauridae. The holotype and only known specimen of *Siamotyrannus isanensis*, which comprises much of the pelvis, sacrum, and tail of a ca. 6.5-meter-long theropod, is known from the Aptian or older Sao Khua Formation (Racey et al., 1996; Buffetaut and Suteethorn, 1999). *Siamotyrannus* was originally described as a primitive member of the tyrannosauroid lineage, and one of the oldest members of the group

(Buffetaut et al., 1996). However, more recently it has been reinterpreted as a more basal theropod, likely an allosauroid (Rauhut, 2003a; Holtz et al., 2004; Brusatte and Sereno, 2008). Its more precise affinities, however, remain questionable. Spinosaurid theropods are known from several teeth from the Sao Khua Formation (Buffetaut and Ingavat, 1986), as well as other Early Cretaceous units in southern China (Buffetaut et al., 2008) and Japan (Hasegawa et al., 2003), and the mid Cretaceous Majiacun Formation of Henan Province, China (Hone et al., 2010). Most striking, however, is an as-yet-undescribed partial postcranial skeleton of a spinosaurid from the Aptian Khok Kruat Formation of Thailand (Milner et al., 2007). The discovery of Asian spinosaurids is notable, as previously this group was only known from the Early Cretaceous of Africa, Europe, and South America. It is likely that spinosaurids, like carcharodontosaurians, were a widespread clade during the Early Cretaceous.

Finally, one newly described, fragmentary specimen from the Jehol Biota (Jiufotang Formation, Early Cretaceous) of Liaoning, China deserves comment. Ji et al. (2009) described a fragmentary skull and postcranial remains as a new species of large tyrannosauroid, *Sinotyrannus kazuoensis*, which they estimated may have reached a body length of 9-10 meters. The preserved remains are indeed large, and the ilium (770 mm long anteroposteriorly) is substantially larger than that of other Late Jurassic-Early Cretaceous tyrannosauroids, including "mid-sized" forms such as *Stokesosaurus* (ilium length = 523 mm; see below). Ji et al. (2009) suggested that *Sinotyrannus* may represent an early and primitive member of Tyrannosauridae, the derived subclade of colossal tyrannosauroids otherwise restricted to the Campanian and Maastrichtian (see below). This assessment was based on its large body size, along with one feature of the maxilla (maxillary fenestra overlapped laterally by the lateral lamina) that is seen in only some tyrannosaurids (*Daspletosaurus*, *Tarbosaurus*, *Tyrannosaurus*: Holtz 2001).

However, it is clear that *Sinotyrannus* is a more basal tyrannosauroid. First, the basal Early Cretaceous tyrannosauroid *Eotyrannus* also possesses a maxillary fenestra obscured by the lateral lamina (IWCMS 1997.550), rendering this character homoplastic. Second, *Sinotyrannus* possesses several unique features shared with basal tyrannosauroids such as *Guanlong* and *Proceratosaurus*, including an enlarged external naris, midline nasal crest, an anterior ramus of the maxilla, and a sharp and deep neurovascular groove on the dentary (Xu et al., 2006; Rauhut et al., 2010). It is possible that *Sinotyrannus* forms a clade with these taxa, a hypothesis that remains to be tested by

phylogenetic analysis. In any event, *Sinotyrannus* is likely to be a basal tyrannosauroid that developed large body size independently of derived tyrannosaurids.

5.2. Mid Cretaceous of China

Two substantial, informative specimens of large theropods are known from the Turonian (ca. 92 million years old) Ulansuhai Formation of Inner Mongolia (Figs. 5, 6). Both specimens were originally described by Hu (1964), who referred them to multiple species of the genus *Chilantaisaurus*, *C. tashuikouensis* (the type species of the genus) and *C. maortuensis*. The *C. tashuikouensis* holotype comprises a partial postcranial skeleton of a colossal individual (Fig. 5), which may have reached a body size similar to the giant carcharodontosaurians *Acrocanthosaurus* and *Mapusaurus*, and perhaps even *Tyrannosaurus* (Benson and Xu, 2008). The *C. maortuensis* holotype, on the other hand, includes several cranial bones and vertebrae from a much smaller individual (Fig. 6). Due to the lack of overlapping elements, as well as the considerable size difference, between the two specimens, authors have long argued that *C. maortuensis* cannot reliably be placed in the same genus as *C. tashuikouensis* (Chure, 1998, 2001; Rauhut, 2003a; Benson and Xu, 2008). This suggestion was followed by Brusatte et al. (2009a), who recently erected a new genus for *C. maortuensis*, *Shaochilong*.

Both *Chilantaisaurus* and *Shaochilong* were largely neglected for several decades after Hu's (1964) original descriptions, resulting in uncertainty over their phylogenetic placement (e.g., Harris, 1998; Rauhut, 2003a). Only recently have the two specimens been redescribed and restudied in a phylogenetic context (Benson and Xu, 2008; Brusatte et al., 2009a; Brusatte et al., 2010b). Both are strongly placed within the carcharodontosaurian theropods, *Shaochilong* as a close relative of South American and African taxa (*Carcharodontosaurus*, *Giganotosaurus*, *Mapusaurus*, *Tyrannotitan*) and *Chilantaisaurus* as a neovenatorid, a member of the same clade as *Fukuiraptor* from the Early Cretaceous of Japan (Benson et al., 2010). Therefore, both taxa are members of speciose and cosmopolitan carcharodontosaurian subclades. Combined with the possible carcharodontosaurian affinities of *Kelmayisaurus*, from the Early Cretaceous of China, these specimens suggest that carcharodontosaurians had a long history on the Asian continent. The presence of two carcharodontosaurians in the Turonian of China also indicates that more basal theropods continued to fill the large predator niche in Asia at this time, not tyrannosaurids or their precursors. Interestingly, the substantial size differ-

ence between the contemporary *Shaochilong* and *Chilantaisaurus* suggests that carcharodontosaurians may have filled a variety of body size and ecological niches during the middle Cretaceous (Benson et al., 2010).

5.3. Paleobiogeography, Evolution, and Faunal Change

Very little was known about the evolution of Early-mid Cretaceous large-bodied theropods in Asia until very recently. The redescription of *Shaochilong* and *Chilantaisaurus*, coupled with the discovery of spinosaurids in Thailand and phylogenetic revision of *Fukuiraptor* and other allosauroids, have helped clarify what was previously a 60-million-year dark period in the Asian large theropod record. The most significant result of this new research is that Asia was home to a cosmopolitan large theropod fauna during this time. These theropods, including carcharodontosaurians and spinosaurids, belong to basal tetanuran clades. The more primitive, endemic clades of the Middle Jurassic apparently did not persist into the Early Cretaceous. Similarly, there is only limited evidence that tyrannosaurids and other derived coelurosaurians, the dominant large theropods of the Campanian-Maastrichtian of Laurasia, developed large body size and filled the apex predator niche earlier in time. Instead, the large predators during the Early-mid Cretaceous of Asia belonged to the same groups that dominated the apex niche on other continents during this time. This is not surprising, as Asia was physically reconnected to other landmasses during the Early Cretaceous after the severing of long-standing topographic and oceanic barriers, which had previously isolated Asia for much of the Jurassic (Russell, 1993; Upchurch et al., 2002). Most importantly, regression of the Turgai Sea during the ca. Aptian-Albian resulted in the formation of a European-Asian land connection, which would have allowed terrestrial migration (Smith et al., 1994). Asian sauropods (Upchurch, 1995; Barrett et al., 2002), ornithopods (Norman, 1998), and small-bodied theropods (Xu and Norell, 2006) were also members of cosmopolitan clades during the Early-mid Cretaceous.

A paucity of large theropod taxa from the middle Cretaceous of North America and Europe severely hampers a detailed assessment of biogeography of this age. However, the close relationship between *Shaochilong* and African and South American carcharodontosaurids, as well as the discovery of Asian spinosaurids (a clade that is also known from Europe, Africa and South America), strengthen hypotheses of faunal exchange between the northern and the southern continents as late as the early Late Cretaceous, as suggested by Brusatte et al. (2009a).



Fig. 5.- A montage of select bones from *Chilantaisaurus tashuikouensis* (IVPP V2884) from the mid Cretaceous (Turonian) of Inner Mongolia, China. A, right humerus in anterior view; B, left femur in anterior view; C, left tibia and fibula in anterior view; D, right metatarsus in anterior view. Scale bar equals 10 centimeters.

Fig. 5.- Selección de huesos de *Chilantaisaurus tashuikouensis* (IVPP V2884) del Cretácico medio (Turonense) de Mongolia Interior, China. A, húmero derecho en vista anterior; B, femur izquierdo en vista anterior; C, tibia y fibula izquierdas en vista anterior; D, metatarso derecho en vista anterior. La escala equivale a 10 cm.

Faunal similarities have already been noted between Asia and North America (Russell, 1993). Therefore, Early-mid Cretaceous Asia was home to some dinosaur taxa with North American affinities, and others with southern influence. Together, these various biotic affinities are consistent with suggestions that dinosaur faunas of this age were effectively cosmopolitan (e.g., Barrett *et al.*, 2002; Benson *et al.*, 2010; Brusatte *et al.*, 2010b).

Several explanations are possible for the observed pattern of Early-mid Cretaceous dinosaur cosmopolitanism. First, although Pangea had begun to fragment tens of millions of years before this time, faunal interchange during the Early-mid Cretaceous may have been possible via various dispersal corridors. The trans-Turgai land bridge

is one possible corridor for faunal interchange between northern and southern continents during this time, as Europe was both connected to Asia and located only a short distance from northern Gondwana during the middle Cretaceous (Smith *et al.*, 1994). However, it is also possible that clades such as Spinosauridae, Carcharodontosauridae and Neovenatoridae achieved global distributions prior to the separation of northern and southern landmasses, long before the Early-mid Cretaceous, and persisted in both Laurasia and Gondwana into the early Late Cretaceous. Testing these alternatives will require not only new fossil specimens, but also detailed phylogenetic reassessments and a careful consideration of sampling biases (e.g., Turner *et al.*, 2009).

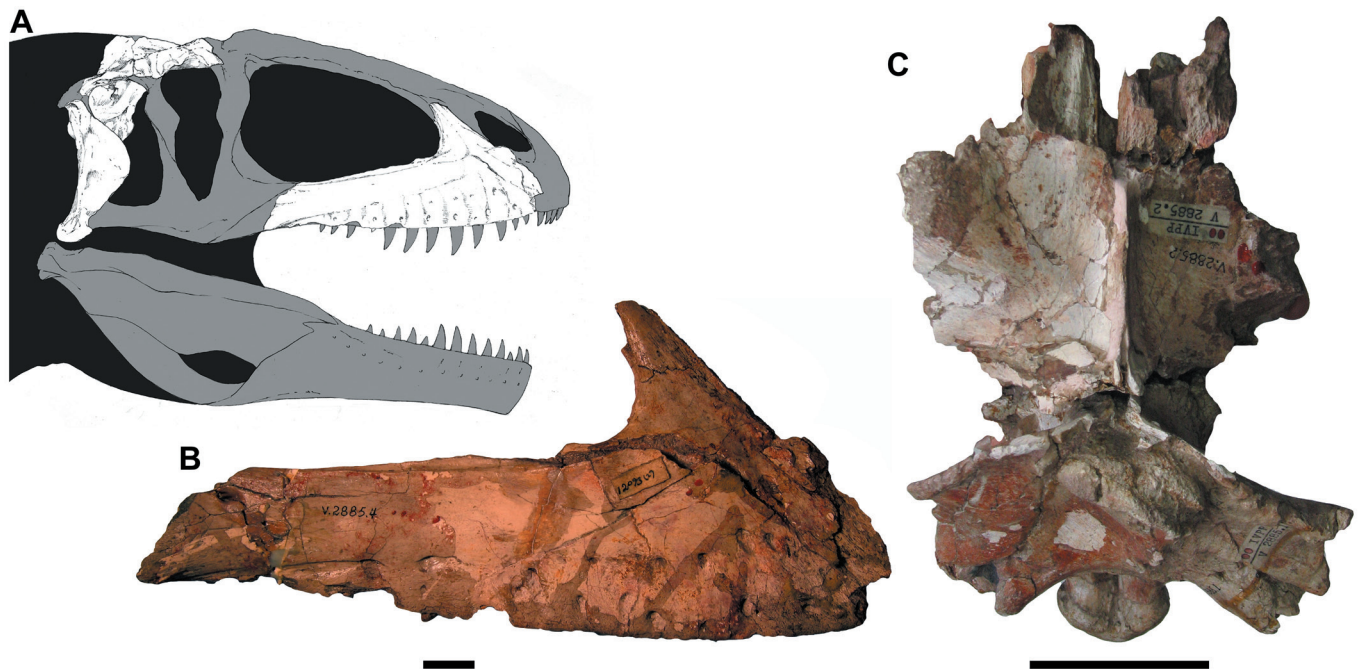


Fig. 6- A skull reconstruction and cranial bones from *Shaochilong maortuensis*, a small-bodied mid Cretaceous (Turonian) carcharodontosaurian theropod from Inner Mongolia, China. A, skull reconstruction (courtesy of Brett Booth); B, right maxilla in lateral view (IVPP V.2885.4); C, braincase and skull roof in dorsal view (IVPP V.2885.1-2). Scale bars equal 5 centimeters.

Fig. 6.- Reconstrucción del cráneo y huesos craneales de *Shaochilong maortuensis*, carcharodontosáurido de pequeño tamaño del Cretácico medio (Turonense) de Mongolia Interior, China. A, reconstrucción del cráneo (cortesía de Brett Booth); B, maxilar derecho en vista lateral (IVPP V.2885.4); C, neurocráneo en vista dorsal (IVPP V.2885.1-2). La escala equivale a 5 cm.

The large theropods from the Early Cretaceous of Thailand are interesting to consider in a biogeographic context, as Southeast Asia is comprised of numerous volcanic arcs and accreted terranes, many of which were originally part of Gondwana (Chen *et al.*, 1993; Metcalfe, 2006). Current geophysical evidence indicates that most of Thailand, including the dinosaur-bearing localities, was accreted to the Asian mainland during the Devonian, Permian, and Triassic (Metcalfe, 2006). Therefore, there is no current evidence that Southeast Asia harbored Gondwanan taxa that dispersed northwards upon drifting terranes. However, some of the Tibetan Plateau and surrounding areas are comprised of terranes that may have accreted later, during the Jurassic and Cretaceous (Murphy *et al.*, 1997; Zhang, 1999). Dinosaur fossils are rare in Tibet (Zhao, 1983; Weishampel *et al.*, 2004), but future discoveries may reveal whether the Cretaceous dinosaur faunas of southern Asia had a Gondwanan influence due to terrane accretion.

6. Terminal Cretaceous (Campanian-Maastrichtian)

In contrast to the Early-middle Cretaceous, the final 20 million years of the Cretaceous is well represented by a

bounty of large-bodied theropod fossils from China and Mongolia (e.g., Currie, 2000; Weishampel *et al.*, 2004). Without exception, all of these large theropods are coelurosaurs, and several are particularly closely related to birds. The most common of these animals, and the undisputed apex predators in the Maastrichtian (and perhaps Campanian) ecosystems of Asia, are the tyrannosaurids (Figs. 7,8). Among the largest terrestrial predators to ever live, tyrannosaurids are some of the most common fossils in the Nemegt Formation and other Maastrichtian units across Asia (Currie, 2000). However, other coelurosaur groups, including the ornithomimosaur, oviraptorosaurs, and therizinosauroids, also developed large body size during this time, although none of these animals were predators in the traditional sense (Xu *et al.*, 2007). In all, Asia has one of the best records of terminal Cretaceous theropods from anywhere in the world.

6.1. Campanian-Maastrichtian of China and Mongolia: Tyrannosaurids

Tyrannosaurids, the subclade of coelurosaurian theropods that includes *Tyrannosaurus rex* and several close relatives, are only known from the Campanian-Maas-

trichtian of Asia and North America. In general, tyrannosaurids are characterized by their enormous body size (up to 13 meters long and perhaps five tonnes in mass), large skulls, powerful jaw muscles, horns over the eyes, and atrophied forelimbs (Holtz, 2004). Tyrannosaurids belong to the much more inclusive clade Tyrannosauroidae, an ancient and speciose lineage of theropods that originated by the Middle Jurassic (Rauhut et al., 2010). Some of the oldest and most primitive tyrannosauroids, *Guanlong* and *Dilong*, are known from the Late Jurassic and Early Cretaceous of China, respectively (Xu et al., 2004, 2006). However, these taxa, as well as most other basal tyrannosauroids, were mostly small-bodied animals, with few reaching sizes larger than a man (Madsen, 1974; Rauhut, 2003b; Benson, 2008; Rauhut et al., 2010). Some basal tyrannosauroids attained “medium sizes” (i.e., up to four meters long and 300 kilograms in body mass), including *Stokesosaurus langhami* from the Tithonian (Late Jurassic) of Europe (Benson, 2008) and *Xiongguanlong* from the Aptian-Albian (Early Cretaceous) of Asia (Li et al., 2010). Regardless, the recent discovery of the basal tyrannosauroid *Raptorex* from the Barremian-Aptian

(Early Cretaceous) Yixian Formation (He et al., 2006) of Inner Mongolia shows that many of the characteristic tyrannosaurid features, such as the large head, strong jaw muscles, and small forelimbs, originated in a small animal that was only a few meters long and less than 100 kilograms in mass (Serenó et al., 2009).

The major “break” in tyrannosauroid evolution is between the mostly small, primitive Middle Jurassic-Early Cretaceous taxa and the colossal, derived Campanian-Maastrichtian tyrannosaurids of North America and Asia. Unfortunately, fossils bridging this break are rare, but Early-mid Cretaceous rocks of Asia hold out great potential for future discoveries. Currently, two unequivocal tyrannosaurids are known from the Maastrichtian of Asia: *Tarbosaurus* (Fig. 8) and *Alioramus* (Fig. 7). Furthermore, the puzzling genus *Alectrosaurus* also inhabited Asia during the Late Cretaceous. Often regarded as a Cenomanian taxon, *Alectrosaurus* has recently been re-dated as Campanian (Van Itterbeeck et al., 2005). Although *Alectrosaurus* is clearly a member of the tyrannosauroid lineage, it is unclear whether it is part of the derived tyrannosaurid radiation or whether it represents a



Fig. 7.-A montage of select bones from *Alioramus altai* (IGM 100/1844), a long-snouted and gracile tyrannosaurid theropod from the Late Cretaceous (Maastrichtian) of Mongolia. A, left maxilla in lateral view; B, left lacrimal in lateral view; C, left jugal in lateral view; D, left dentary in lateral view; E, anterior cervical vertebra in anterior view; F, right ilium in lateral view; G, right ischium in lateral view; H, right crus (tibia, fibula, calcaneum, astragalus) in anterior view. Scale bars equal 5 centimeters. Photographs by Mick Ellison, American Museum of Natural History.

Fig. 7.-Selección de huesos de *Alioramus altai* (IGM 100/1844), un terópodo tiranosáurido grácil y de rostro alargado correspondiente al Cretácico tardío (Maastrichtiense) de Mongolia. A, maxilar izquierdo en vista lateral; B, lacrimal izquierdo en vista lateral; C, yugal izquierdo en vista lateral; D, dentario izquierdo en vista lateral; E, vértebra cervical anterior en vista anterior; F, íleon derecho en vista lateral; G, isquiún derecho en vista lateral; H, parte distal de un miembro inferior (tibia, fibula, calcáneo, astrágalo) en vista anterior. La escala equivale a 5 cm. Fotografías realizadas por Mick Ellison, American Museum of Natural History.

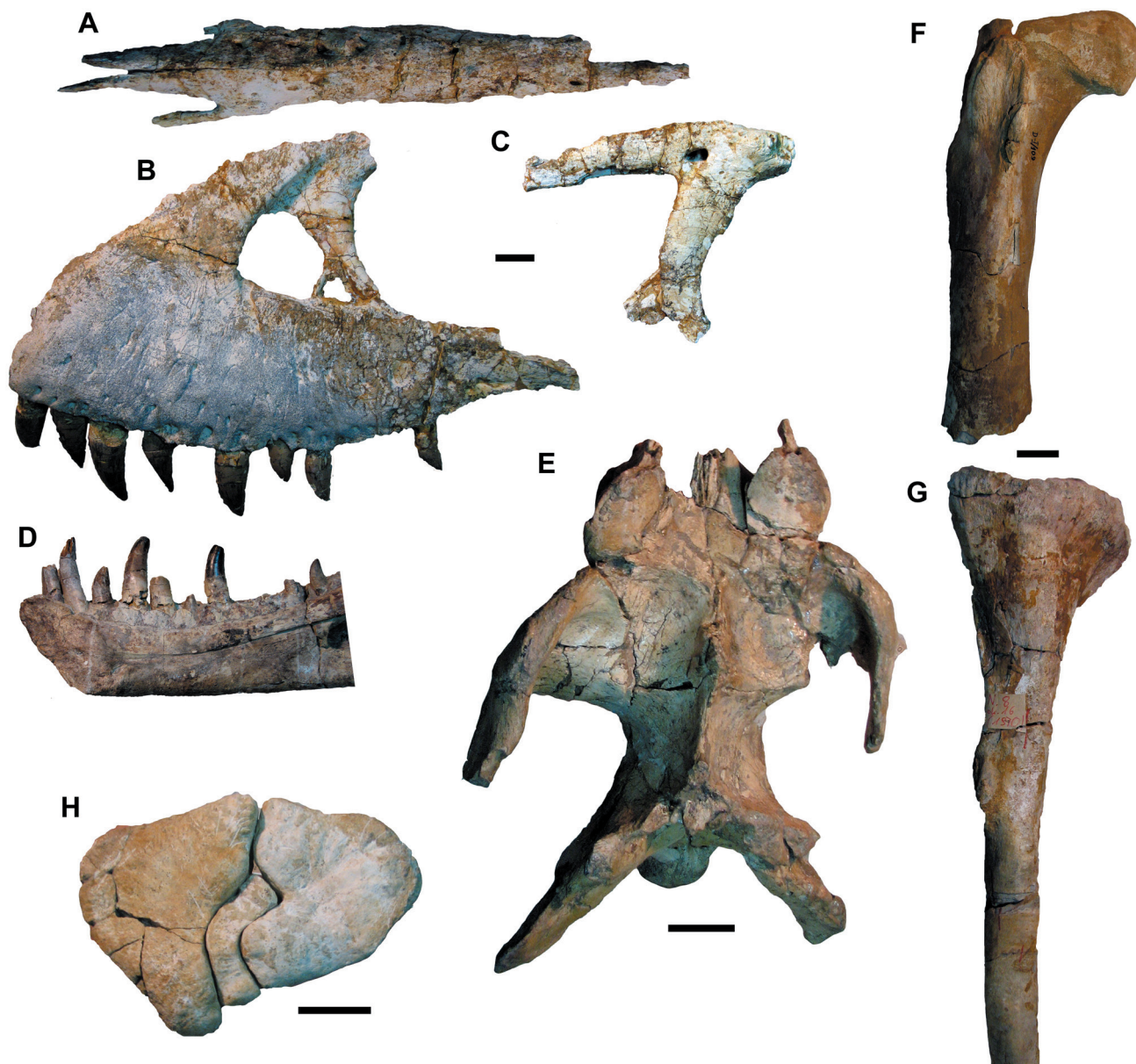


Fig. 8.-A montage of select bones from *Tarbosaurus bataar* (ZPAL collection), a deep-snouted and robust tyrannosaurid theropod from the Late Cretaceous (Maastrichtian) of Mongolia. A, fused nasal in dorsal view (ZPAL MgD-I/4); B, left maxilla in lateral view (ZPAL MgD-I/4); C, left lacrimal in lateral view (ZPAL MgD-I/4); D, right dentary in medial view (ZPAL MgD-I/5); E, skull roof and braincase in dorsal view (ZPAL MgD-I/3); F, right femur in anterior view (ZPAL MgD-I/109); G, left fibula in lateral view (ZPAL MgD-I/188); H, metatarsals II-IV in proximal view (ZPAL MgD-I/76). Scale bars equal 5 centimeters. One scale bar for A-D and one scale bar for F-G.

Fig. 8.- Selección de huesos de *Tarbosaurus bataar* (colección ZPAL), un terópodo tiranosáurido robusto y de profundo rostro del Cretácido tardío (Masstrichtiense) de Mongolia. A, nasales fusionados en vista dorsal (ZPAL MgD-I/4); B, maxilar izquierdo en vista lateral (ZPAL MgD-I/4); C, lacrimal izquierdo en vista lateral (ZPAL MgD-I/4); D, dentario derecho en vista medial (ZPAL MgD-I/5); E, basicráneo y parte superior del cráneo en vista dorsal (ZPAL MgD-I/3); F, fémur derecho en vista anterior (ZPAL MgD-I/109); G, fibula izquierda en vista lateral (ZPAL MgD-I/188); H, metatarsos II-IV en vista proximal (ZPAL MgD-I/76). La escala equivale a 5 cm. Una escala corresponde a A-D y otra a F-G.

more basal tyrannosaurid taxon. The type material, from the Iren Dabasu Formation of Mongolia, has only been briefly described (Gilmore, 1933; Mader and Bradley, 1989), contributing to this uncertainty. It is currently under study by Thomas Carr. Additional material from the Late Cretaceous of Mongolia has been referred to *Alec-*

trousaurus, but these fossils have been poorly described and figured and have been largely inaccessible to many workers (e.g., Perle, 1977).

The unequivocal tyrannosaurid *Tarbosaurus* is one of the most familiar Asian dinosaurs (Fig. 8). The closest relative (sister taxon) of the iconic *Tyrannosaurus rex*,

Tarbosaurus is known from numerous Maastrichtian fossil sites in Mongolia and China (Maleev, 1955, 1974; Currie, 2000; Hurum and Sabath, 2003; Weishampel et al., 2004; Zhao et al., 2008). *Tarbosaurus* strongly resembles its cousin *Tyrannosaurus* in most aspects of its anatomy: it was an enormous predator, with a large skull, robust cranial bones, a strongly interlocking lower jaw, rugose brows above the eyes, robust and mediolaterally thickened teeth, and proportionally reduced forelimbs. Like *Tyrannosaurus*, the skeleton of *Tarbosaurus* became more stocky and robust, and the skull shorter and deeper, as an individual grew into adulthood (Carr, 1999; Carr and Williamson, 2004). The adult skull of *Tarbosaurus* was ideally suited for strong bite forces (Erickson et al., 1996; Hurum and Currie, 2000) and an unusual “puncture-pull” feeding style in which the teeth could literally crunch through bone (Erickson and Olson, 1996; Rayfield, 2004).

The second Asian tyrannosaurid, *Alioramus*, deviates from *Tarbosaurus* and its other close relatives. Although deeply nested within the tyrannosaurid clade, *Alioramus* is the only known departure from the “classic” tyrannosaurid body plan (Fig. 7). It does not possess the deep and robust skulls, thick teeth, and stocky skeletons of other tyrannosaurids, but rather has an elongate and weak skull with numerous horn-like projections (Brusatte et al., 2009b). Furthermore, it was approximately half the body size of *Tarbosaurus* and *Tyrannosaurus*, with a more gracile, lighter, and pneumatic postcranial skeleton.

Until recently, *Alioramus* was among the most intriguing, yet poorly-understood large theropod dinosaur genera. It was named by Kurzanov (1976) on the basis of a fragmentary skeleton, including a partial skull that seemed to be long-snouted and gracile. However, because the holotype was incomplete, only briefly described and figured, and largely inaccessible to researchers, many mysteries about *Alioramus* remained. It was unclear whether *Alioramus* was a tyrannosaurid proper or a more basal member of the tyrannosauroid stem (Holtz, 2001, 2004; Currie et al., 2003), and some workers even suggested that it may be an aberrant juvenile of *Tarbosaurus* (Currie, 2003). This debate was put to rest by the recent description of a spectacularly preserved and substantially complete specimen from the Nemegt Formation of Mongolia (Brusatte et al., 2009b).

The new fossil unquestionably shows that *Alioramus* was smaller and more gracile than its close relatives, and possessed a longirostrine skull. Despite its peculiar body form, *Alioramus* was recovered as a tyrannosaurid, and indeed a particularly close relative of *Tyrannosaurus* and *Tarbosaurus*, in a cladistic analysis (a relationship previ-

ously suggested by Currie et al., 2003). *Alioramus* and *Tarbosaurus* lived side-by-side during the Maastrichtian, and their divergent body forms may have allowed them to co-exist via ecological niche partitioning. Indeed, the long and weak skull of *Alioramus* lacks all of the integral components of “puncture-pull” feeding seen in *Tarbosaurus*, suggesting that *Alioramus* fed on smaller prey (Brusatte et al., 2009b).

6.2. Early-Late Cretaceous of China and Mongolia: Other Coelurosaurian Taxa

Members of other coelurosaurian theropod clades developed large body size during the Early-Late Cretaceous in Asia. However, most of these taxa were not carnivores (Kobayashi et al., 1999; Kobayashi and Lu, 2003; Barrett, 2005; Zanno et al., 2009), and thus did not fill the apex predator role in Asian ecosystems. Examples of giant, non-carnivorous theropods are known from three separate coelurosaurian clades: Oviraptorosauria, Therizinosauroida, and Ornithomimosauria. Although these taxa span the Early and Late Cretaceous, they are all discussed here for simplicity.

The enormous oviraptorosaur *Gigantoraptor*, from the Iren Dabasu Formation of Inner Mongolia, may have reached masses of 1400 kilograms (Xu et al., 2007). Like most other oviraptorosaurs, *Gigantoraptor* had a short, deep, and toothless skull fronted by a beak, which was likely used to crop vegetation or crush small invertebrates and/or eggs. It lived alongside the tyrannosauroid *Alectrosaurus*, which was approximately the same size but likely a more traditional predator.

The therizinosauroid *Suzhousaurus*, from the Aptian-Albian (Early Cretaceous) Xinminpu Group of Gansu, is one of the largest members of this bizarre group of derived theropods (Li et al., 2007, 2008). The femur of one specimen is 84 centimeters long, about 20% shorter than average-sized *Allosaurus* femora (Madsen, 1976; Christiansen, 1999). Only parts of the postcranial skeleton are known, and skull bones have yet to be discovered. However, other therizinosauroids have unusual skulls with leaf-shaped teeth, similar in many ways to those of “prosauropod” herbivores. Other features of the skull, including its general shape, are also similar to “prosauropods,” and give further evidence that these aberrant theropods were primarily herbivorous (Clark et al., 2004). Other Asian therizinosauroids, such as *Therizinosaurus cheiloniformis* from the Late Cretaceous of Mongolia, also achieved large body size. Most remarkably, the manual claws of this species may have approached 50-100 centimeters in length (Maleev, 1954; Barsbold, 1976). Un-

fortunately, many of these taxa are also fragmentary, and there is no evidence that any of them were primarily carnivorous.

Several Asian ornithomimosaurids attained large size, including the Early Cretaceous *Beishanlong* and the Late Cretaceous *Gallimimus* and *Deinocheirus*. *Beishanlong* is known from several postcranial bones from the Aptian-Albian Xinminpu Group of Gansu (Makovicky et al., 2010). Its femur is 66 centimeters long, resulting in a body mass estimate of approximately 626 kilograms. A similar size was reached by *Gallimimus*, one of the best known ornithomimosaurids, which is commonly found in the Maastrichtian Nemegt Formation (Osmólska et al., 1972; Makovicky et al., 2004). Perhaps the largest ornithomimosaur of all was the enigmatic *Deinocheirus*, another Maastrichtian Nemegt taxon that is only known from a single fragmentary specimen, including a pair of enormous forelimbs that measure approximately 2.4 meters in length and are capped by 25-cm-long claws (Osmólska and Roniewicz, 1970). Some authors estimate that *Deinocheirus* may have been up to 9000 kilograms in mass (Valkenburgh and Molnar, 2002), although further specimens are clearly needed to better understand this puzzling animal. Cranial material remains unknown for *Deinocheirus* and *Beishanlong*, but the skull of *Gallimimus* is similar to that of most other ornithomimosaurids in lacking teeth and possessing a beak at the front of the jaws. This skull shape, along with the possession of gastric mills in the gut, suggests that ornithomimosaurids were herbivores or possibly suspension feeders that lived near the water's edge (Norell et al., 2001; Barrett, 2005).

Finally, among more traditional predatory coelurosaurs, there are few obvious examples of non-tyrannosaurid taxa obtaining large body size during the Late Cretaceous of Asia. The dromaeosaurid *Achillobator* from the Late Cretaceous of Mongolia (Hicks et al., 1999) may have reached a body mass of approximately 350 kilograms (Perle et al., 1999; Turner et al., 2007), but other dromaeosaurs, as well as troodontids, alvarezsaurids, and bona fide avians, were small-bodied animals that rarely reached sizes larger than an average man.

6.3. Paleobiogeography, Evolution, and Faunal Change

The large-bodied theropod fossil record from the Campanian and Maastrichtian of Asia has long been among the best studied and most complete from anywhere in the world. Along with faunas from western North America, and a lesser extent those from South America and Europe, the Asian fossils have helped researchers understand the evolution of dinosaurs during the waning years

of the Mesozoic (Weishampel et al., 2004). In short, they represent some of the best, and only, evidence of dinosaur communities that lived within a few million years of the catastrophic end-Cretaceous mass extinction. These fossils reveal two important patterns of large-bodied theropod evolution.

First, only tyrannosaurids are known to have occupied the large predator niche during the terminal Cretaceous of Asia. This is in contrast to earlier time periods, when multiple groups of large predators, such as the spinosaurids and carcharodontosaurians of the Early Cretaceous, obtained large body size. Such depauperate faunas, in which only a single clade filled the large predator role, are also seen in the Campanian and Maastrichtian of North America, which was also dominated by tyrannosaurids (Holtz, 2004; Weishampel et al., 2004). Although comparatively little is known about the terminal Cretaceous faunas in Africa, Europe, and South America, the few Campanian and Maastrichtian dinosaur fossil sites on these landmasses offer no evidence for multiple groups of large predators (Weishampel et al., 2004). One exception may be South America, as new evidence suggests that mid-to-large-sized allosauroids persisted alongside abelisaurid ceratosaurs in the large predator niche until late into the Cretaceous (Benson et al., 2010). However, only one allosauroid fossil from the Maastrichtian of South America has been described (*Orkoraptor*) and its age is suspect (Novas et al., 2008). Therefore, it seems likely that depauperate keystone predator faunas, exemplified by only a single large predator or multiple large predators of a single restricted clade, may have characterized terminal Cretaceous dinosaur communities globally.

Second, the large tyrannosaurid predators of Late Cretaceous Asia are closely related to North American taxa. Indeed, tyrannosaurids are only known from North America and Asia, and large-bodied forms are only known from the final 20 million years of the Cretaceous (Currie, 2000; Holtz, 2004; Brusatte et al., 2009a). The more inclusive tyrannosaurid clade, which originated approximately 100 million years before *Tarbosaurus* was dominating Maastrichtian ecosystems in Asia, is also known from Europe, but has yet to be recorded in Africa, Antarctica, Australia, India, Madagascar, or South America. Therefore, all current evidence suggests that the tyrannosaurid clade was solely a Laurasian group, restricted to the northern continents. Tyrannosaurids are one of many dinosaur groups that exhibited trans-Laurasian (or at least Asian and North American) distributions during the Late Cretaceous; others include ceratopsians, hadrosaurs, and pachycephalosaurs (e.g., Sereno, 2000; Upchurch et al., 2002). This repeated biogeographic pattern is not surprising, as by the

Late Cretaceous the configuration of the major continents was beginning to resemble the modern situation, in which northern and southern landmasses are largely separated by oceanic barriers. In sum, Asian large theropods are some of the primary evidence used to support hypotheses of Late Cretaceous dinosaur provincialism.

Large derived tyrannosaurids are still unknown from Europe but this is potentially due to sampling bias, since Campanian-Maastrichtian fossil sites are rare on this landmass, and large theropods are particularly uncommon discoveries (Weishampel *et al.*, 2004). However, great uncertainty remains. Asia was separated from Europe (which was largely a series of islands) by the Turgai Sea during the Late Cretaceous, from the Cenomanian or Turonian onwards, and it is possible that this seaway formed a barrier to faunal interchange (Cox, 1974; Smith *et al.*, 1994). Small theropods with European and Asian distributions, such as compsognathids and ornithomimosaurs, suggest that such interchange did occur during the Late Jurassic-Early Cretaceous (e.g., Ji *et al.*, 2003). Unfortunately, the poor Campanian-Maastrichtian European record makes it difficult to assess if and when this interchange ceased, and whether Asian faunas were more similar to those from North America or Europe during the waning years of the Cretaceous. Evidence from other dinosaur clades suggests that European and North American faunas may have been most similar to each other during the Late Cretaceous (Upchurch *et al.*, 2002), and mammal fossils have been used to argue for North American-European high latitude dispersal during this time (Martin *et al.*, 2005). However, it must be kept in mind that western and eastern North America were separated by the Western Interior Seaway during the Late Cretaceous, and thus it is plausible that western North America shared taxa with Asia and eastern North America with Europe.

7. Discussion and conclusions

Large-bodied theropods had a long history in Asia and were present from at least the early Middle Jurassic until the very end of the Cretaceous, a time span of at least 100 million years. During this time, the evolution of these dinosaur apex predators was far from static. The oldest large theropods of Asia, from the Middle Jurassic, belonged to largely endemic clades of basal tetanuran theropods. Endemic clades are known from other areas at this time, and most likely reflect provincialism that developed soon after the initial fragmentation of Pangea. However, as Asia was reconnected to other landmasses during the Late Jurassic-Early Cretaceous, large theropod faunas

of this time developed a more cosmopolitan flavor. The major apex predators of this time, the Late Jurassic sinraptorids and the Early-mid Cretaceous carcharodontosaurians and spinosaurids, had close relatives on other landmasses. In particular, it seems that Early-mid Cretaceous dinosaur faunas as a whole were essentially cosmopolitan, despite the continued separation of Pangea into various landmasses. By the terminal Cretaceous, however, more derived bird-like theropods had assumed the large predator role in Asia. These animals, most prominently the colossal tyrannosaurids, were closely related to North American taxa, and along with other dinosaur clades indicate that terrestrial vertebrate faunas were provincial at this time. Most importantly, Asia and North America shared taxa, including tyrannosaurids, to the exclusion of the southern continents, a pattern that surely reflected the now great separation between the former components of Laurasia and Gondwana.

Our understanding of Asian large theropod evolution can be summarized in two general statements. First, the biogeographic affinities of large Asian theropods over time was intimately related to physical geography, especially the slow fragmentation of Pangea and the establishment and severing of various connections with other landmasses. Second, over time progressively more derived theropod clades evolved large body size and occupied the apex predator niche, beginning with basal tetanurans in the Middle Jurassic, continuing with “intermediate” spinosaurids, sinraptorids, and carcharodontosaurians in the Late Jurassic-mid Cretaceous, and ending with coelurosaurs in the Campanian-Maastrichtian. However, it is possible, and even probable, that these patterns will be challenged by future fossil discoveries. Indeed, much of this picture has been pieced together over the past two decades, especially with the discovery of new taxa in China, Mongolia, Japan, and Southeast Asia and the redescription of long-neglected specimens. Dinosaur fieldwork is active across the Asian continent, and the potential for future discoveries is tantalizing.

Note Added in Proof:

After this paper was accepted, Benson *et al.* (2010) described a theropod pubis from the Early Cretaceous of Australia as pertaining to a tyrannosauroid. Therefore, it is likely that tyrannosauroids were present in the southern continents early in their evolution, but there still is no indication that they inhabited anywhere but the northern continents during the Late Cretaceous. (Benson, R.B.J., Barrett, P.M., Rich, T.H., Vickers-Rich, P. (2010): A southern tyrant reptile. *Science*, 327: 1613).

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