Zootaxa 2334: 1–46 (2010)
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

The osteology of *Shaochilong maortuensis*, a carcharodontosaurid (Dinosauria: Theropoda) from the Late Cretaceous of Asia

STEPHEN L. BRUSATTE[1,2,6], DANIEL J. CHURE[3], ROGER B. J. BENSON[4] & XING XU[5]

[1]*Department of Paleontology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA. E-mail: sbrusatte@amnh.org*
[2]*Department of Earth and Environmental Sciences, Columbia University, New York, NY, USA*
[3] *Dinosaur National Monument, Box 128, Jensen, UT 84035, USA. E-mail: dan_chure@nps.gov*
[4]*Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge, CB2 3EQ, United Kingdom. E-mail: rbb27@cam.ac.uk*
[5]*Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, P.O. Box 643, Beijing 100044, People's Republic of China. E-mail: xingxu@vip.sina.com*
**Corresponding author. E-mail: sbrusatte@amnh.org*

Table of contents

Abstract

Large-bodied theropod dinosaurs from the Early-mid Cretaceous of the northern continents (Laurasia) are poorly known. One of the most complete and intriguing theropods from this interval is *Shaochilong maortuensis* Hu, 1964 from the Turonian (< 92 Ma) Ulansuhai Formation of Inner Mongolia, China. The phylogenetic placement of *Shaochilong* has long been a subject of debate, as it has been referred to several disparate theropod groups (e.g., Megalosauridae, Allosauridae, Tyrannosauroidea, Maniraptora). In a recent taxonomic reassessment, *Shaochilong* was identified as the first Asian member of Carcharodontosauridae, a clade of allosauroid theropods that was once thought to be restricted to Gondwana and includes some of the largest terrestrial predators to ever live. However, the characters supporting such a placement were only briefly discussed, and a full anatomical description of *Shaochilong* has yet to be presented. We provide a detailed osteological description of the lectotype and paralectotype series, show that *Shaochilong* is a small-bodied and short-snouted carcharodontosaurid, and highlight numerous cranial features shared with other carcharodontosaurids. We argue that the vicariant hypothesis of allosauroid biogeography, in which lineages split in concert with the fragmentation of Pangaea, is poorly supported. Finally, large-scale patterns of theropod evolution and faunal replacement are discussed, and it is argued that allosauroids persisted as large-bodied predators later in the Cretaceous than previously thought.

Key words: Allosauroidea, Carcharodontosauridae, cladistics, China, paleobiogeography, Theropoda

Accepted by R. Butler: 24 Nov. 2009; published: 13 Jan. 2010

Introduction

One of the most frustrating sampling biases in the dinosaur fossil record is the lack of large-bodied theropod fossils from the mid Cretaceous of Laurasia (the northern continents). In a broader sense, the entire Early-mid Cretaceous large theropod fossil record of Laurasia, especially Asia, is woefully incomplete. This frustrates attempts to understand the biogeographic distribution and large-scale evolutionary patterns of Asian theropods, as well as the tempo of theropod faunal turnover in the mid Cretaceous. It is known that basal tetanurans, such as carcharodontosaurids, filled the apex predator niche across North America and Europe during the Early Cretaceous, and that the colossal tyrannosaurids were the dominant carnivores in the Campanian-Maastrichtian (latest Cretaceous) of Asia and North America (Stovall & Langston 1950; Harris 1998; Currie 2000; Currie & Carpenter 2000; Holtz 2004; Brusatte & Sereno 2008). The intervening 40 million years, however, is a dark period in large theropod history.

Only a limited sample of theropod fossils have been discovered from this gap, and most of these are restricted to isolated bones and teeth (Weishampel *et al*. 2004b). Only two substantially complete large theropod specimens are known from the mid Cretaceous of Asia: the colossal basal tetanuran *Chilantaisaurus tashuikouensis* (Hu 1964; Benson & Xu 2008) and a series of cranial and postcranial elements that Hu (1964) referred to a second species of *Chilantaisaurus*, *C. maortuensis*. Both specimens come from the Turonian (ca. 92 Ma) Ulansuhai Formation of Inner Mongolia, China, and both have been the subject of recent taxonomic and anatomical revision. Benson & Xu (2008) redescribed the holotype of *C. tashuikouensis*, argued that it is a neotetanuran (an allosauroid or a basal coelurosaurian), and conclusively demonstrated that, because of lack of overlapping elements, there is no rationale for referring "*C.*" *maortuensis* to *Chilantaisaurus*. Recently, Brusatte *et al.* (2009a) followed suit and erected a new genus, *Shaochilong*, for this specimen. They briefly redescribed some aspects of its cranial and postcranial anatomy, and provided a short discussion of the biogeographic and phylogenetic importance of the specimen.

Here, we supplement the short redescription of Brusatte *et al.* (2009a) with a full osteology of *Shaochilong*. We focus on the braincase, which is one of the most complete and best preserved basal tetanuran braincases currently known. Additionally, we expand on the broader phylogenetic, biogeographic, and evolutionary implications of the specimen, which were only discussed in minor detail by Brusatte *et al.* (2009a). Our description of *Shaochilong* follows on primary descriptive work begun by DJC in the 1990s and continued by SLB and co-authors in 2009. Chure (1998) discussed *Shaochilong* in a published abstract, and Chure (2000) provided a redescription and cursory systematic assessment in his unpublished thesis, which is often cited by dinosaur workers. The current project combines DJC's previous work on the specimen with more recent work on theropod anatomy and phylogeny conducted by SLB, RBJB, and XX. Our aim is to present a comprehensive osteology of a crucial mid Cretaceous large-bodied theropod, which provides primary descriptive data that can be incorporated into wider studies of theropod phylogeny and evolution.

Institutional abbreviations

BYU	Brigham Young University Museum of Earth Sciences, Provo, Utah, USA
FMNH	Field Museum of Natural History, Chicago, USA
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, People's Republic of China
MCF	Museo Carmen Funes, Plaza Huincul, Argentina
MIWG	Museum of Isle of Wight Geology (Dinosaur Isle), Sandown, UK
MNN	Musée National du Niger, Niamey, Niger
MUCP	Museo de la Universidad Nacional del Comahue, El Chocón collection, El Chocón, Argentina
NCSM	North Carolina State Museum, Raleigh, North Carolina, USA
OMNH	Sam Noble Oklahoma Museum of Natural History, Norman, USA
OUMNH	Oxford University Museum of Natural History, Oxford, UK
SGM	Ministère de l'Energie et des Mines, Rabat, Morocco

SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany
UCMP	University of California Museum of Paleontology, Berkeley, USA
UCOBA	University of Chicago Department of Organismal Biology, Chicago, USA
UMNH	Utah Museum of Natural History, Salt Lake City, USA

Systematic Paleontology

Dinosauria Owen, 1842

Saurischia Seeley, 1887

Theropoda Marsh, 1881

Tetanurae Gauthier, 1986

Allosauroidea Marsh, 1878

Carcharodontosauria Benson, Carrano & Brusatte, 2009

Carcharodontosauridae Stromer, 1931

***Shaochilong* Brusatte, Benson, Chure, Xu, Sullivan & Hone, 2009a**

Type and only species: *Shaochilong maortuensis* (Hu 1964)

Diagnosis: As for *Shaochilong maortuensis*, given below.

***Shaochilong maortuensis* (Hu, 1964)**
Figs 1–15

Hu 1964: figs 9–12, pls 1–2
Zhao *et al.* 2008: fig. 325
Brusatte *et al.* 2009a: figs 1–2
1964*Chilantaisaurus maortuensis* Hu (1964: 50 in Chinese, 59 in English)

Lectotype. IVPP V.2885.1, well preserved and nearly complete braincase, including parts of the parietals, supraoccipital, exoccipital-opisthotics, basioccipital, basisphenoids, parasphenoid, prootics, and orbitosphenoids; IVPP V.2885.2, paired frontals, paired parietals, and posterior end of right nasal.

Taxonomic note and paralectotype series. Hu (1964) erected *Chilantaisaurus maortuensis* on the basis of cranial bones, an axis and six caudal vertebrae. Although the material was collected from a single locality, Hu (1964) did not explain the degree of association of the bones or provide quarry maps. It is considered likely that the bones represent a single individual, but to provide for the possibility that they will be shown to belong to multiple taxa in future studies we designate the braincase (IVPP V.2885.1) and skull roof fragment (IVPP V.2885.2) as the lectotype (name-bearing type specimen) and consider the remaining material to belong to the paralectotype series: left and right quadrates (IVPP V.2885.3), a right maxilla (IVPP V.2885.4), an axis vertebra (IVPP V.2885.5) and six caudal vertebrae (IVPP V.2885.6–7). The braincase and skull roof piece are both assigned to the lectotype because they clearly fit together as a single specimen (broken along the parietals, which are shared between both pieces). The remaining skull bones and axis probably belong to the same individual as the braincase and skull roof, due to similar size, proximity in the skeleton, non-duplication

of elements, and similar phylogenetic affinities indicated by all elements. The caudal vertebrae are referred with less certainty, as they do not show unambiguous evidence for carcharodontosaurid affinities and are from a more distant part of the skeleton.

In an unpublished thesis, Chure (2000) briefly described the lectotype series of *Shaochilong* and provided a new generic name, "Alshansaurus". Chure's (2000) thesis was circulated to many dinosaur researchers and is often cited. Although the name "Alshansaurus" was never formally published, it has been used by many dinosaur workers as an informal name for the specimen.

Type locality and horizon. Ulansuhai Formation, Maortu, Inner Mongolia Autonomous Region, People's Republic of China (60 km north of Chilantai). The Ulansuhai 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.* 2004b). However, radiometric dating of underlying strata indicates a maximum age of approximately 92 Ma (Turonian, early Late Cretaceous ["mid Cretaceous"]; Kobayashi & Lu 2003, Benson & Xu 2008). We prefer the Turonian date, as it is tied to explicit radiometric data.

Original diagnosis. "Skull small, occipital condyle comparatively large, maxilla with 12 teeth, quadrate relatively small" (Hu 1964: 59).

Emended diagnosis. Allosauroid theropod possessing the following autapomorphies: maxillary antorbital fossa reduced in extent and nearly absent; paradental groove absent on the medial surface of the maxilla; deep, dorsoventrally oriented grooves located dorsally on maxillary interdental plates; pneumatic recess penetrates to posterior end of nasal; dorsoventrally deep sagittal crest on the frontal; large pneumatic foramen (pneumatopore) in the anterodorsal corner of the dorsal tympanic recess of the prootic (Brusatte *et al.* 2009a).

Nomenclatural note. Clade names and phylogenetic definitions follow a recent revision of basal tetanuran taxonomy proposed by Benson *et al*. (2009). Allosauroidea is comprised of four "family"-level clades: Sinraptoridae, Allosauridae, Carcharodontosauridae, and Neovenatoridae. The latter two clades are sister taxa and comprise the rank-free Carcharodontosauria, which is equivalent in definition to Carcharodontosauridae as commonly used by previous authors (e.g., Holtz *et al*. 2004; Sereno *et al*. 2005). These taxonomic changes do not severely affect the terminology used in this monograph. However, *Neovenator* is no longer a "carcharodontosaurid," as commonly considered under previous taxonomies, but rather a "neovenatorid carcharodontosaurian".

Description and comparisons. Skull. A skull reconstruction of *Shaochilong*, drawn by Brett Booth, is presented in Figure 1. The snout of *Shaochilong* is shortened relative to other carcharodontosaurids, which generally possess long snouts despite their large body size (e.g., Sereno *et al.* 1996; Currie & Carpenter 2000; Eddy 2008). In concert with small body size (see below), the short-snouted skull suggests that *Shaochilong* possessed a unique morphotype, and perhaps ecotype, among carcharodontosaurids.

Maxilla. Hu (1964: 59) listed both a right maxilla and a "fragmental left maxilla" among the "material" (taken here as the syntype series) of *Shaochilong maortuensis*. However, we could only locate the right maxilla (IVPP V2885.4; Figs 2–3), which is nearly complete and well preserved. This element was illustrated by Hu (1964: fig. 10), but it is difficult to distinguish original bone and broken margins in this figure. A revised version of this figure was published by Zhao *et al.* (2008: fig. 325) and a photograph was provided by Dong (1992). However, other than a paragraph in the original description (Hu 1964: 60), this bone has not been thoroughly described in the literature.

The right maxilla is nearly complete but is missing the dorsal part of the ascending process as well as the posterior portion of the jugal process bearing the articular facet for the jugal. As preserved the maxilla is 290 mm long anteroposteriorly and 77 mm deep dorsoventrally at the anterior margin of the antorbital fenestra. The tooth row in *Shaochilong* is complete and the jugal process extends 35 mm posterior to it as preserved. However, a substantial portion is missing in this region, as in other allosauroids there is an extensive margin of non-dentigerous bone posterior to the posteriormost alveolus (e.g., Madsen 1976; Currie & Zhao 1993a; Sereno *et al*. 1996; Eddy 2008; Sereno & Brusatte 2008). The main body tapers in depth as it continues posteriorly and becomes confluent with the jugal process, thinning to a depth of 38 mm at the posterior broken

margin. A tapering main body and jugal process is common among theropods but contrasts with the condition in abelisaurids (e.g., Lamanna *et al*. 2002; Sampson & Witmer 2007), some coelurosaurs (e.g., *Dromaeosaurus*: Currie 1995), *Monolophosaurus* (Brusatte *et al.* in press), and *Zupaysaurus* (Ezcurra 2007), which possess maxillae that maintain a relatively constant depth across their length. Posteriorly the jugal process is deflected posteroventrally, beginning at the anterior end of the jugal articulation. Only the base of this deflection is preserved but this region is oriented at an angle of approximately 20 degrees from the anteroposterior trend of the main body. A similar deflection is present in the carcharodontosaurids *Acrocanthosaurus* (Eddy 2008: fig. 14) and *Eocarcharia* (Brusatte & Sereno 2008: figs. 11-13), as well as those megalosaurids in which this region is preserved (*Afrovenator*, UC OBA 1; *Megalosaurus*, OUNHM J.13506), and was employed as a phylogenetic character by Sereno & Brusatte (2008: ch. 8). In contrast, other allosauroids and basal tetanurans only exhibit ventral deflection at the far posterior tip of the jugal process (e.g., Madsen 1976; review in Sereno & Brusatte 2008).

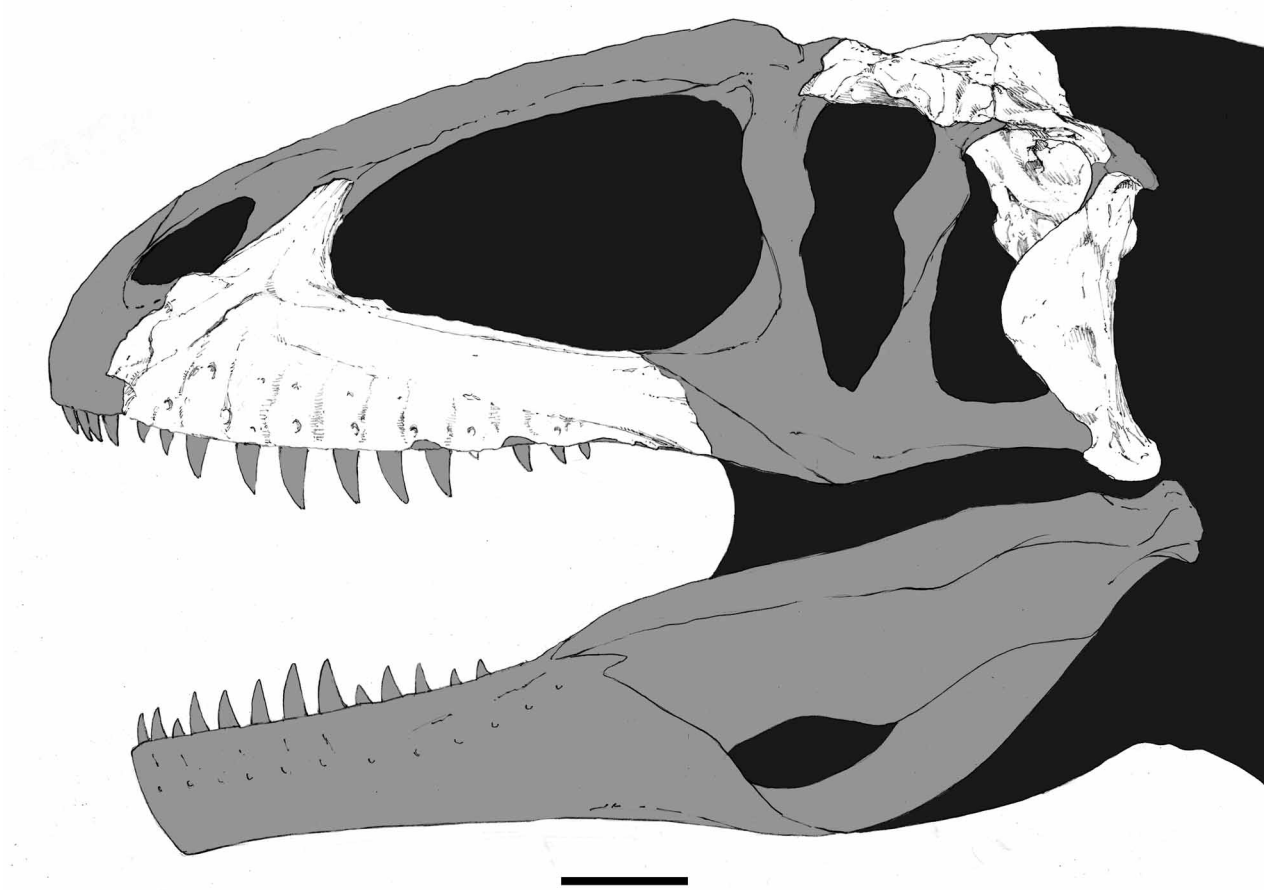

FIGURE 1. Skull reconstruction of *Shaochilong maortuensis*, based upon the paralectotype series described here (IVPP V.2885.1–4). Compared to other carcharodontosaurids, *Shaochilong* has a shortened snout (shorter and deeper skull) and a smaller body size. Reconstruction by Brett Booth. Scale bar equals 5 cm.

As in many other basal tetanurans there is a distinct anterior ramus of the maxilla that projects from the main body anterior to the ascending ramus (e.g., Madsen 1976; Sereno *et al.* 1994; Holtz *et al*. 2004). The separation between the ascending ramus and anterior ramus is slight in *Shaochilong* and the anterior ramus is tall relative to its length (78 mm deep by 35 mm long). It is proportionally taller than in most other theropods that possess an anterior ramus that is taller than long, such as *Ceratosaurus* (Madsen & Welles 2000), and its shape and size are similar to those of some individuals of *Mapusaurus* (MCF-PVPH-108.115; Coria & Currie 2006: fig. 2B). In other *Mapusaurus* specimens the anterior ramus is essentially absent, as it is confluent with the anterior rim of the maxillary body and ascending process (MCF-PVPH-108.169; Coria & Currie 2006: fig

2A). Similarly, the anterior ramus is deep and either confluent with the ascending ramus or weakly demarcated in most other carcharodontosaurids, including *Acrocanthosaurus* (Currie & Carpenter 2000), *Carcharodontosaurus* (Sereno *et al.* 1996; Brusatte & Sereno 2007), and *Eocarcharia* (Sereno & Brusatte 2008). However, *Neovenator* exhibits a prominent anterior ramus (Brusatte *et al.* 2008). The shape of the ramus is variable in non-carcharodontosaurian allosauroids, as it is prominent in *Allosaurus* (Madsen 1976) but confluent with the ascending ramus in *Sinraptor* (Currie & Zhao 1993a).

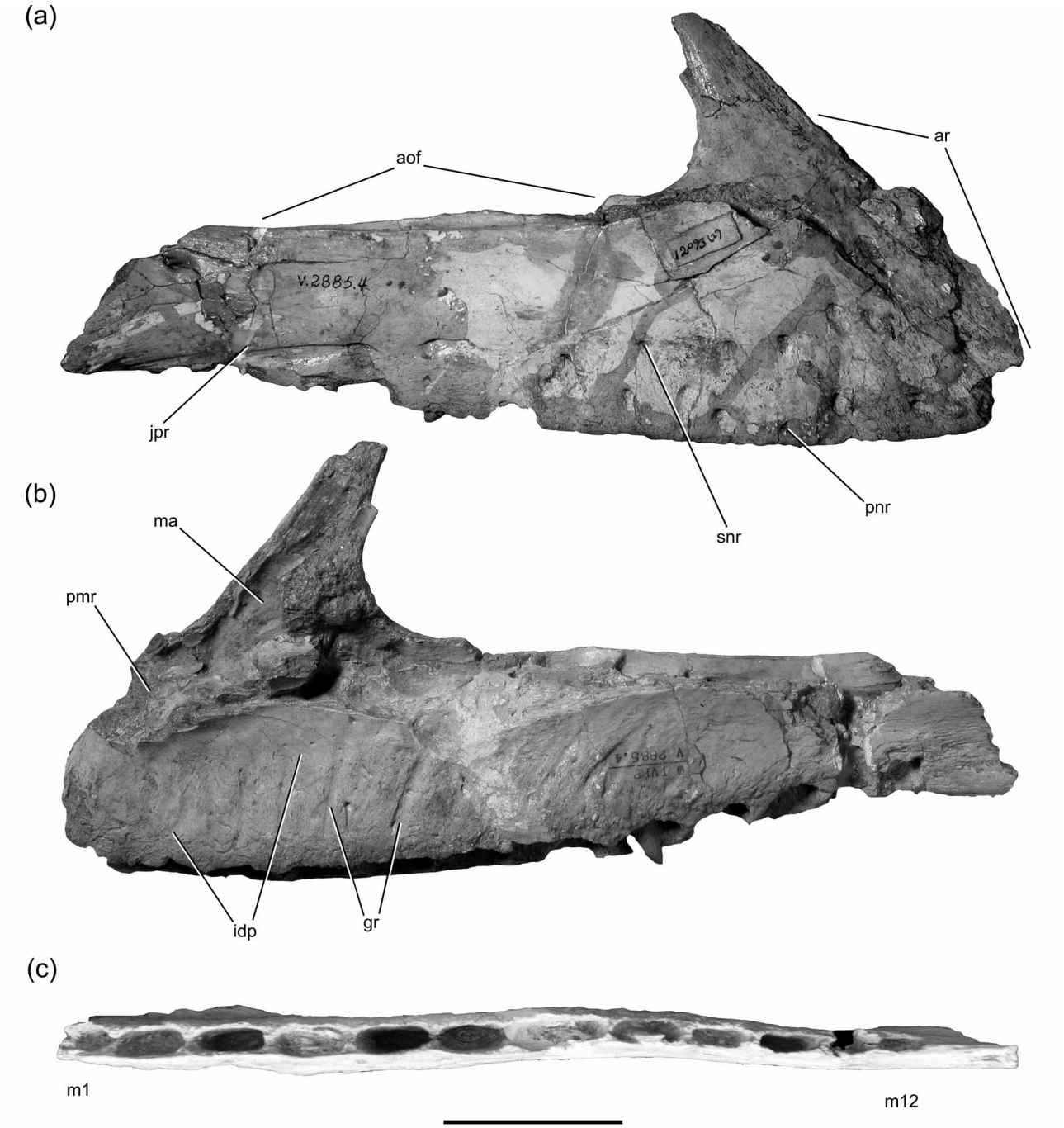

FIGURE 2. Photographs of the right maxilla of *Shaochilong maortuensis* (IVPP V2885.4) in lateral (a), medial (b), and ventral (c) views. Abbreviations: **aof**, antorbital fossa; **ar**, anterior ramus; **gr**, groove; **idp**, interdental plates; **jpr**, jugal process; **ma**, maxillary antrum; **pmr**, promaxillary recess; **pnr**, primary neurovascular foramina row; **snr**, secondary neurovascular foramina row. Designation "**m**" referrs to maxillary tooth position. Scale bar equals 5 cm.

The ascending ramus extends posterodorsally at approximately 45 degrees from the anteroposterior trend of the main body. This is the case in most basal tetanurans, but differs from the nearly vertical orientation of

the ramus in most abelisaurids (e.g., Chatterjee 1978; Bonaparte 1985; Bonaparte *et al.* 1990; Lamanna *et al.* 2002; Canale *et al.* 2009). In *Shaochilong* the ascending ramus is broken dorsally, but by this point it has already strongly tapered (minimum axis "width" measurement in lateral view of 12 mm, compared with 50 mm at its base at the anteroventral corner of the antorbital fenestra). The entire ramus is very thin anteroposteriorly across its length. The overall proportions of the ramus are narrower than those of *Carcharodontosaurus* (Brusatte & Sereno 2007), *Giganotosaurus* (MUCPv-CH-1), and *Mapusaurus* (Coria & Currie 2006), which have relatively narrow ascending rami and narrow antorbital fossae (see below). In contrast, *Acrocanthosaurus* (Currie & Carpenter 2000; Eddy 2008), *Allosaurus* (Madsen 1976), *Eocarcharia* (Sereno & Brusatte 2008), *Neovenator* (Brusatte *et al.* 2008), and *Sinraptor* (Currie & Zhao 1993a) have proportionally wider ascending rami that accommodate a more extensive antorbital fossa.

Only some regions of the surfaces for contact with the premaxilla, nasal, and jugal are observable. The premaxilla is contacted via the anterior surface of the anterior ramus of the maxilla, which is broadly convex in lateral view. Furthermore, when seen in lateral view, the premaxilla-maxilla suture trends strongly posterodorsally. This is also the case in most other allosauroids (e.g., Currie & Zhao 1993a; Brusatte & Sereno 2007), but differs from the more vertical contact in *Allosaurus* (Madsen 1976) and *Neovenator* (Brusatte *et al.* 2008).

The nasal articulates with the anterior surface of the ascending ramus and may have continued onto the dorsal surface of the ramus more posteriorly, although this region is broken in the paralectotype maxilla (IVPP V.2885.4). Few details of the nasal suture are evident and it is unclear whether the maxilla contributed to the floor of the external naris. However, it is evident that the nasal articulation is located solely on the anterior surface of the anterior ramus and does not face laterally, unlike in abelisaurids (Wilson *et al.* 2003; Sereno *et al.* 2004; Sereno & Brusatte 2008). Furthermore, the nasal articulation does not terminate ventrally in the blunt pit that is characteristic of abelisaurids (Wilson *et al.* 2003; Sereno *et al.* 2004).

Although most of the jugal articulation is broken, the jugal clearly sat within a deep trough on the posterior part of the jugal process of the maxilla. Whether this trough was partially exposed laterally as in some allosauroids (e.g., *Acrocanthosaurus*: Eddy 2008; *Eocarcharia*: Sereno & Brusatte 2008), due to a lower lateral wall, is unclear. However, it is evident that the most anterior region of the trough is a deep embayment hidden in lateral view, and thus the complete articular surface on the maxilla is not entirely laterally facing as is often considered a synapomorphy of abelisaurids (e.g., Wilson *et al.* 2003; Sereno *et al.* 2004).

The lateral surface of the maxilla is generally smooth, although it is slightly rugose anteriorly and above the tooth row. This form of sculpturing is similar to that of most theropods, and is not as extensive as in the derived carcharodontosaurids *Carcharodontosaurus*, *Giganotosaurus*, and *Mapusaurus* (Brusatte & Sereno 2008) and abelisaurids (Lamanna *et al.* 2002; Sampson & Witmer 2007; Sereno & Brusatte 2008). In *Carcharodontosaurus*, elongate grooves and ridges ornament most of the lateral surface, a texturing that has been described as autapomorphic for the genus (Brusatte & Sereno 2007). The surface texture is mottled, with random rugosities that do not form distinct ridges or grooves, in *Giganotosaurus* (Coria & Salgado 1995), *Mapusaurus* (Coria & Currie 2006), and the neovenatorid carcharodontosaurian *Neovenator* (Brusatte *et al.* 2008). In contrast, the lateral surface of the maxilla in *Acrocanthosaurus* (Currie & Carpenter 2000), *Allosaurus* (Madsen 1976), *Eocarcharia* (Sereno & Brusatte 2008), and *Sinraptor* (Currie & Zhao 1993a) is smooth and little different in texture from that in *Shaochilong*.

The lateral surface of the maxilla of *Shaochilong* is pierced by numerous foramina, which are especially abundant immediately dorsal to the tooth row. These foramina form two distinct series: a primary series that is approximately 10 mm dorsal to the tooth row and a secondary series that is positioned 35 mm above the tooth row. Foramina in both rows are large, measuring up to 5 mm in diameter, and form a linear series that approximately parallels the tooth row. The two rows merge posterior to the eighth alveolus, and the final foramen in the conjoined rows (located above the ninth alveolus) opens posteriorly into a deep and elongate groove. A discrete secondary row is also present in *Acrocanthosaurus* (Eddy 2008), *Carcharodontosaurus saharicus* (Brusatte & Sereno 2007), *Eocarcharia* (Sereno & Brusatte 2008), and possibly *Mapusaurus* (Coria & Currie 2006: fig. 2). Foramina are located in this region in other taxa (e.g., *Allosaurus*: Madsen 1976), but

are not always set into a discrete row. However, whether this represents random variation or a phylogenetically informative signal is difficult to determine in the small samples for most theropod taxa. Furthermore, the final foramen of the conjoined row also opens into a deep groove in *Eocarcharia* (Sereno & Brusatte 2008). Unfortunately, this region of the maxilla is missing in many closely related taxa, precluding comparison. Finally, the primary row of *Shaochilong*, like those of other allosauroids, is positioned several millimetres above the tooth row, not immediately above the alveolar margin as in abelisaurids (Sereno & Brusatte 2008).

The antorbital fossa is not extensive on the lateral surface of the maxilla, although this appearance is partially exaggerated by breakage. As preserved, the fossa only extends for approximately 7 mm ventral to the antorbital fenestra across most of the main body. However, the dorsal edge of the fossa is a broken surface, which is quite thick in mediolateral width. It is possible to link this broken surface with original bone on the dorsal margin of a small flange that projects dorsally at the anteroventral corner of the antorbital fenestra. This was not a flange in life, but rather is a preserved flake of bone, completely covered by the smooth fossa, that remains in isolation after the rest of the bone in this area has been broken away. Furthermore, the original dorsal surface of this flange can be linked to original bone surface on the posterior margin of the ascending ramus, giving a complete and fairly accurate reconstruction of the true dimensions of the antorbital fossa (Fig 2). In life, the fossa extended only 10-15 mm ventrally from the antorbital fenestra along the main body of the maxilla. Similar ventral reduction is present in other carcharodontosaurids such as *Carcharodontosaurus* (Brusatte & Sereno 2007), *Giganotosaurus* (MUCPv-CH-1), and *Mapusaurus* (Coria & Currie 2006), as well as abelisaurids (e.g., Bonaparte *et al*. 1990; Sereno & Brusatte 2008) and the megalosaurid *Torvosaurus* (Britt 1991). In contrast, *Allosaurus* (Madsen 1976), *Sinraptor* (Currie & Zhao 1993a), and the basal carcharodontosaurians *Acrocanthosaurus* (Currie & Carpenter 2000; Eddy 2008), *Eocarcharia* (Sereno & Brusatte 2008), and *Neovenator* (Brusatte *et al.* 2008) have a ventrally extensive antorbital fossa.

The antorbital fossa extends anteriorly onto the ascending ramus of the maxilla, but only excavates approximately 15% of the width of the base of the ramus (Table 1). In most allosauroids, including basal carcharodontosaurians such as *Acrocanthosaurus*, *Eocarcharia*, and *Neovenator*, this proportion is 50-65%. A more extreme condition, an extensive fossa along the entire ascending ramus, is a synapomorphy of Coelurosauria (Sereno *et al.* 1996; Rauhut 2003a; Holtz *et al*. 2004). In *Carcharodontosaurus* and other carcharodontosaurines the fossa is reduced on the ascending ramus (Table 1), but not to the extent seen in *Shaochilong*. Thus, the extremely limited antorbital fossa on the ascending ramus is an autapomorphy of *Shaochilong* among allosauroids.

TABLE 1. Proportion of the base of the ascending ramus of the maxilla excavated by the antorbital fossa. Measurements are taken along an anteroposterior line, parallel with the tooth row, beginning from the anteroventral corner of the antorbital fenestra and continuing until the anterior margin of the maxilla.

Taxon	Ratio	Source
Shaochilong	0.15	IVPP V2885.4
Acrocanthosaurus	0.50	Eddy 2008
Allosaurus	0.60	Madsen 1976
Carcharodontosaurus	0.29	SGM-Din-1
Eocarcharia	0.64	MNN GAD2
Giganotosaurus	0.40	MUCPv-CH-1
Mapusaurus	0.40	Coria & Currie 2006
Neovenator	0.65	MIWG 6348
Sinraptor	0.62	Currie & Zhao 1993

The antorbital fossa and the subcutaneous surface of the main body of the maxilla are not separated by a sharp rim or a swollen ridge (as in *Carcharodontosaurus saharicus*: Sereno *et al.* 1996; Brusatte & Sereno 2007), but rather by an abrupt change in bone texture. Anteriorly, the rim surrounding the antorbital fossa is rounded, not squared-off as in some carcharodontosaurians (*Eocarcharia*, *Neovenator*: Sereno & Brusatte 2008), as well as megalosaurids (*Afrovenator*: UC OBA 1; *Dubreuillosaurus*: Allain 2002), coelophysids (Rauhut 2003a) and *Eoraptor* (Sereno *et al.* 1993). There is a distinct foramen within the fossa, which faces laterally and posteriorly, level with the region between the eighth and ninth alveoli.

No accessory antorbital openings are readily visible within the antorbital fossa. However, as the anteroventral region of the fossa—the location of these openings in other theropods—is broken, this absence is potentially artifactual. Indeed, the broken medial surface of the maxilla shows that the base of the ascending ramus and the promaxillary process were inflated. These two regions are usually inflated by the maxillary and promaxillary fenestrae, respectively (Witmer 1997). Whether both openings were actually present is difficult to assess, since *Carcharodontosaurus* has both inflated internal sinuses but only a single external opening (Sereno *et al.* 1996; Brusatte & Sereno 2007). This single opening has been interpreted as a maxillary fenestra (Sereno *et al.* 1996), but homology with either the promaxillary or maxillary fenestrae of other theropods is difficult to assess (Brusatte & Sereno 2008). Regardless of which fenestra this lone opening is homologous to, both the phylogenetic position of *Carcharodontosaurus* (nested within Tetanurae, most of which possess two openings) and its internal morphology (two sinuses) indicate that one of the fenestrae was lost, as in other carcharodontosaurines (*Giganotosaurus*: MUCPv-CH-1; *Mapusaurus*: Coria & Currie 2006; RBJB pers. obs.). If reduction of the the antorbital fossa correlates with the loss of an accessory pneumatic opening then it is possible that the condition in *Shaochilong* was the same as that in the carcharodontosaurines. Any fenestrae that were present, however, probably penetrated anteriorly into the base of the ascending ramus and were concealed in lateral view, due to the very narrow lateral exposure of the antorbital fossa.

Accessory excavations within the antorbital fossa of the ascending ramus ('excavatio pneumatica' of Witmer 1997) are clearly absent. These structures are present in *Acrocanthosaurus* (Eddy 2008) and *Eocarcharia* (Sereno & Brusatte 2008), as well as *Sinraptor* (Currie & Zhao 1993a), and possibly *Allosaurus* (Witmer 1997), although homology is difficult to assess since some of these structures differ in form, position, and number.

In medial view two separate antorbital sinus chambers are visible at the base of the ascending ramus. It is unclear whether these chambers were closed medially by a wall of bone in life; if so, this wall has broken away to expose the chambers. The more posterior chamber, which corresponds to the maxillary antrum of Witmer (1997), has several concave depressions on its floor that correspond to the tooth crypts. These depressions are referred to as the interalveolar pneumatic recesses by Witmer (1997), and indicate that the tooth replacement crypts extend far dorsally.

The interdental plates are fused into a single lamina, as is the case in all allosauroids more derived than sinraptorids (Currie & Zhao 1993a), ceratosaurs (*sensu* Carrano & Sampson 2008), and the megalosaurid *Torvosaurus* (Britt 1991). This lamina is highly ossified: individual plates are only distinguished by shallow depressions between them and no replacement tooth foramina are present.

Chure (1998) described the interdental plates as "very small" and stated that they could "only be differentiated from the maxilla by their texture." He considered this an "unusual feature" of *Shaochilong*, and in his 2000 thesis described the size and form of the interdental plates as autapomorphic. In particular, Chure (1998, 2000) considered the interdental plates to be restricted to the ventral margin of the tooth row, since there is an approximately 15 mm deep strip of bone above the tooth row that is especially rugose and punctured by a preponderance of small foramina. Small interdental plates such as these, which are difficult to distinguish from the remainder of the maxilla, have also been described in *Dromaeosaurus* (Currie 1995) and were an important featuring linking *Shaochilong* with derived maniraptorans in Chure's (2000) discussion of characters.

However, the discovery and description of new comparative material has helped clarify the anatomy of this region. Importantly, the interdental plates are not small but in fact relatively large. As *Shaochilong* lacks a

maxillary paradental groove (groove for the dental lamina) that cleanly demarcates the interdental plates dorsally in other theropods, their size is not immediately apparent. However, although it is true that the plates are heavily textured ventrally, a similar form of surface texturing that differs only in strength extends approximately 40 mm above the tooth row. This form of texturing, composed of random pits and fine lineations, is characteristic of the interdental plates in other carcharodontosaurids (e.g., Brusatte & Sereno 2007) and not the smooth lingual surface of the maxilla dorsal to the paradental groove. Thus, it is reasonable to consider this entire 40-mm-deep region to represent the heavily fused interdental plates.

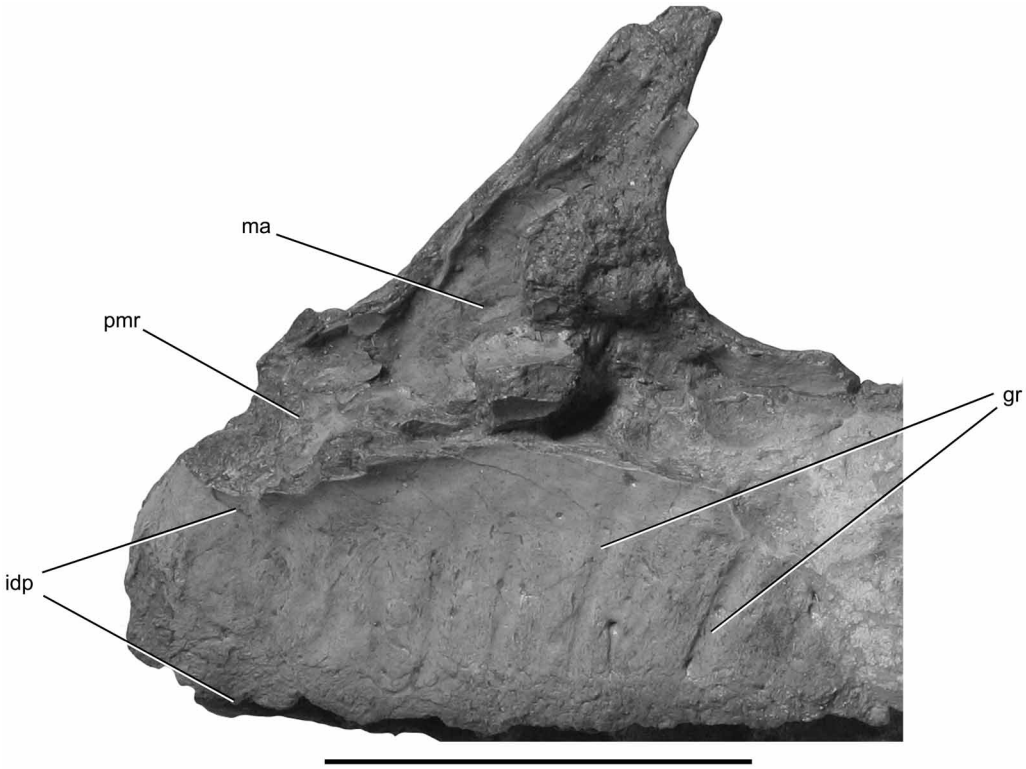

FIGURE 3. Photograph of the right maxilla of *Shaochilong maortuensis* (IVPP V2885.4) in medial view. Abbreviations: **gr**, groove; **idp**, interdental plates; **ma**, maxillary antrum; **pmr**, promaxillary recess. Scale bar equals 5 cm.l plates; **ma**, maxillary antrum; **pmr**, promaxillary recess. Scale bar equals 5 cm.

Two autapomorphies of the interdental plates are present in *Shaochilong*. First, the paradental groove (groove for the dental lamina) is absent, and the interdental plates and lingual surface of the maxilla are not cleanly separated but contact directly so that their junction is only discernable by a subtle textural change. Second, the medial surfaces of the interdental plates are excavated dorsally by several deep, elongate, dorsoventrally oriented grooves. These are broader and deeper than the numerous fine, cut-like lineations that are present in abelisaurids (Rauhut 2004b; Sereno & Brusatte 2008), as well as the less sharp, less dense, and more random array of lineations in carcharodontosaurids. Indeed, these "carcharodontosaurid-type" lineations are present ventrally on the interdental plates of *Shaochilong*, and are present but more widely scattered and less dense dorsally, where they are located alongside and even within the autapomorphic grooves.

Systematically important characters of the interdental plates are also present. The anterior plates are more than twice as deep as wide, a phylogenetically informative character seen in most carcharodontosaurids (*Carcharodontosaurus*, *Giganotosaurus*, *Mapusaurus*: Brusatte & Sereno 2008; *Acrocanthosaurus*: contra Brusatte & Sereno 2008, Sereno & Brusatte 2008). In contrast, the basal carcharodontosaurian *Neovenator* (Brusatte *et al.* 2008) and other allosauroids (*Allosaurus*: Madsen 1976; *Sinraptor*: Currie & Zhao 1993a) have anterior plates that are smaller and shallower, as in other basal tetanurans (e.g., Bonaparte 1986; Sadlier *et al.* 2008). The basal carcharodontosaurid *Eocarcharia* has plates that are less than twice as deep as long, but

are intermediate in size between those of more derived carcharodontosaurids and other allosauroids (Sereno & Brusatte 2008). Additionally, in *Shaochilong*, the line of contact between the plates and the lingual surface of the maxilla is approximately straight across most of the bone, but curves anteroventrally at the second alveolus. This is seen in carcharodontosaurians (*Acrocanthosaurus*, *Carcharodontosaurus*, *Eocarcharia*, *Mapusaurus*, *Neovenator*) and some megalosaurids (Britt 1991; Benson 2008a), but not in *Allosaurus* (Madsen 1976) and *Sinraptor* (Currie & Zhao 1993a), in which the contact (formed in these taxa by the paradental groove) is straight across its entire length.

The tooth row is complete, consisting of 12 alveoli, a low number among basal tetanurans. Tooth number for other allosauroids is as follows: *Acrocanthosaurus* (15), *Allosaurus* (15), *Carcharodontosaurus* (~14), *Giganotosaurus* (12+), *Eocarcharia* (15), *Mapusaurus* (12), *Neovenator* (15+), *Sinraptor* (15). In *Shaochilong* the labial wall of the alveoli, formed by the lateral wall of the maxilla, extends further ventrally than the lingual wall, formed by the interdental plates, as in *Neovenator* (Brusatte *et al.* 2008) and the megalosaurid *Torvosaurus* (Britt 1991). In ventral view the alveoli are ovoid to subrectangular in shape. The seventh alveolus is the largest and more posterior alveoli become progressively smaller (Table 2).

TABLE 2. Measurements (in millimeters) of the maxillary alveoli of *Shaochilong maortuensis* (IVPP V2885.4). Mesiodistal and labiolingual measurements refer to the alveoli, following the terminology of Smith & Dodson (2003).

Alveolus	Mesiodistal	Labiolingual
1	27	17
2	27	17
3	27	16
4	28	18
5	30	18
6	25	17
7	32	20
8	27	15
9	26	15
10	25	13
11	21	12
12	15	13

Only a single partially erupted tooth, situated in the eighth alveolus, is observable. This tooth is very similar in overall morphology (shape, thickness, and surface texture) to an unerupted tooth described for *Eocarcharia* (Sereno & Brusatte 2008), but in the absence of quantitative metrics it is difficult to assess whether such similarity is phylogenetically informative. This tooth is thick labiolingually as in *Eocarcharia*, not thin and blade-like as in derived carcharodontosaurids (Sereno *et al.* 1996). Enamel wrinkles are not visible and if present must have been subtle; the distinct, high-relief, marginal wrinkles of *Carcharodontosaurus* and other derived carcharodontosaurids are absent (Brusatte *et al.* 2007). Both mesial and distal carinae are placed slightly labially, and they are continuous across the tip of the tooth as is usual for theropods (contra Harris 1998).

Nasal. Only a small portion of the nasal is present in *Shaochilong*: a fragment of the posterior end of the right nasal that remains articulated with the nasal prong of the frontal (Figs 4, 5; IVPP V2885.2). This fragment was not discussed by Hu (1964) although it is clearly visible in his figures (Hu 1964: pl. 2). It was described by Chure (2000:252), who noted that it has a "weak ornamentation not found on other skull bones of [*Shaochilong*]." This suggested to Chure (2000) that the fragment might be a displaced element that was later glued onto the holotype frontal. However, Chure (2000) also listed several features consistent with its identification as a nasal, and proceeded to describe the fragment as such. Our observations agree with this

assessment: the fragment clearly articulates with the nasal prong of the frontal, and although its dorsal surface does appear to have a weak array of pits not seen on the frontal, this is likely an artefact of erosion.

This nasal piece is fragmentary (38 mm long anteroposteriorly, 32 mm wide mediolaterally). It is clear that the nasal was not fused to its left counterpart, as its medial surface is well-defined. The opposing nasals would have met each other at a straight, smooth, parasagittal suture along their medial surfaces. Posteriorly, the nasal-frontal articulation is expressed as a nearly transverse contact in dorsal view. Separate medial and lateral projections of the nasal are not apparent here, and if present must have been small. A similar condition is seen in *Allosaurus* (Madsen 1976), *Carcharodontosaurus* (Sereno *et al.* 1996; Sereno & Brusatte 2008), and *Neovenator* (Brusatte *et al.* 2008), whereas in *Acrocanthosaurus* (Currie & Carpenter 2000) and *Sinraptor* (Currie & Zhao 1993a) the nasal-frontal suture is "W" shaped due to an extensive lateral projection of the posterior end of the nasal.

The nasal fragment is extensively pneumatic. The broken anterior and dorsal surfaces of the fragment expose a large pneumatic internal recess that almost completely hollows out the posterior region of the nasal. This recess is divided into two cavities: a posterior pocket and a more anterior region that also extends ventral to the posterior pocket. These pockets are separated by a thick and stout web of bone. The posterior fossa extends much further medially than laterally: here the medial wall of the nasal is only 5 mm thick whereas the lateral wall is 17 mm thick. However, the anterior pocket is wider mediolaterally and the lateral wall of the nasal is only 2 mm thick (the medial wall is not preserved here).

Nasal pneumaticity is a rare feature in theropods and is often considered a synapomorphy of Allosauroidea (e.g., Holtz 2000; Rauhut 2003a; Holtz *et al.* 2004). Indeed, nasal pneumatic foramina are present in all known allosauroids (other than *Acrocanthosaurus*: NCSM 14345) and are generally unknown in other basal theropod dinosaurs (e.g., *Ceratosaurus*, *Cryolophosaurus*, *Zupaysaurus*: see review in Brusatte *et al.* in press). Nasal pneumaticity is present in the basal tetanuran *Monolophosaurus* (Currie & Zhao 1993a; Brusatte *et al.* in press) and the abelisaurid *Majungasaurus* (Sampson & Witmer 2007). However, the nasal morphology of these taxa differs from that of *Shaochilong* in detail: both have fused nasals and *Monolophosaurus* possesses an elaborate cranial crest that is mostly formed by the nasals. Furthermore, the posterior region of the nasal recess of *Majungasaurus* is a single conjoined cavity, shared between the fused nasals, which lacks even a rudimentary midline septum (Sampson & Witmer 2007: fig. 6). In *Shaochilong*, in contrast, there were clearly separate pneumatic recesses in each nasal that were separated medially by the medial surfaces of each unfused nasal.

The morphology of the pneumatic recess of *Shaochilong* is also unique among allosauroids. Other allosauroid taxa have nasal pneumatic recesses anteriorly, but the posterior regions of the nasal are thin, plate-like, and apneumatic where they contact the frontal. This condition is suggested by external morphology (e.g., Currie & Zhao 1993a) and verified by high resolution CT scans of *Allosaurus* (Snively *et al.* 2006: fig. 5). The nasals of derived carcharodontosaurids bear pneumatic excavations anteriorly within the nasal portion of the antorbital fossa, and as these are shallow relative to their width in *Giganotosaurus* (MUCPv-CH 1) and *Mapusaurus* (MCF-PVPH-108.1; Coria & Currie 2006) they do not result in extensive hollowing of the bone. In *Carcharodontosaurus* (SGM-Din 1) the nasals are broken posteriorly and do not show internal pneumatic chambers. Therefore, the posteriorly extending pneumatic internal chambers of the nasal in *Shaochilong* are autapomorphic among allosauroids.

Frontal. The left and right frontals are preserved in articulation (IVPP V2885.2), with fragments of the nasal (see above) and parietal appressed to them (Figs 4–6). The opposing frontals appear to be fused in dorsal view, as each rises up at the midline to contribute to a tall and thin sagittal crest (see below). Chure (2000) considered the frontals to be unfused, noting apparent gaps between the left and right halves of the sagittal crest, but the only well preserved and complete section of the dorsal edge of the crest is sharp and firmly fused. However, the line of fusion between the frontals is visible and partially open in ventral view. This form of coossification is similar to that in a referred specimen of *Eocarcharia* (Sereno & Brusatte 2008: fig. 16). Frontal fusion in derived carcharodontosaurids (e.g., *Carcharodontosaurus*: Brusatte & Sereno 2007) is more extensive and the suture is almost entirely obliterated in ventral view. However, the degree of fusion clearly

changes throughout ontogeny, as shown by the smaller, unfused holotype frontals and larger, fused referred frontals of *Eocarcharia* (Sereno & Brusatte 2008). Thus, we hesitate to subdivide characters relating to frontal fusion into separate states, and instead regard all of these carcharodontosaurids (but not the allosauroids *Allosaurus* and *Sinraptor*) as possessing fused frontals.

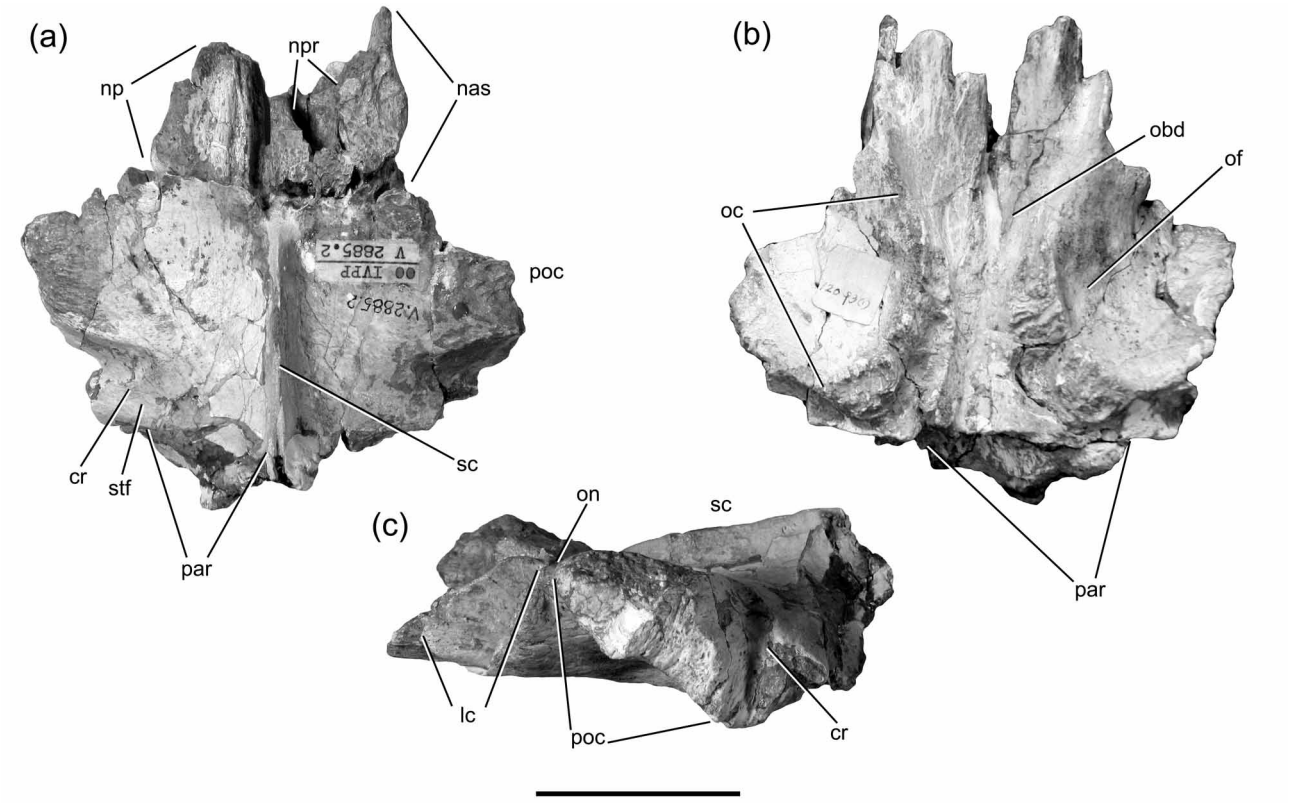

FIGURE 4. Photograph of the skull roof (right nasal, frontals, parietals) of *Shaochilong maortuensis* (IVPP V2885.2) in dorsal (a), ventral (b), and left lateral (c) views. Abbreviations: **cr**, crest within supratemporal fossa; **lc**, lacrimal contact; **nas**, nasal; **np**, nasal process; **npr**, nasal pneumatic recess; **obd**, olfactory bulb depressions; **oc**, orbitosphenoid contact; **of**, orbital fossa; **on**, orbital notch; **par**, parietal; **poc**, postorbital contact; **sc**, sagittal crest; **stf**, supratemporal fossa. Scale bar equals 5 cm.

The frontals of *Shaochilong* are mediolaterally broad and anteroposteriorly short, and a single frontal is approximately 67% as broad as long. Similar ratios are seen in carcharodontosaurids (Sereno & Brusatte 2008), which possess frontals that are 60–70% as long as broad, as well as in *Allosaurus* (Madsen 1976). *Sinraptor* has proportionally longer frontals (52%) and abelisaurids often have frontals that are broader than long (ratios over 100%: Sampson & Witmer 2007). Dromaeosaurids are characterized by ratios of approximately 75% (e.g., Barsbold & Osmólska 1999), due to their enlarged postorbital articular processes which projects far laterally, an autapomorphy of the group (Norell & Makovicky 2004). In *Shaochilong* an individual frontal is 62.5 mm wide mediolaterally at its greatest extent, where it contacts the postorbitals immediately posterior to the nasal prongs. The prongs are discrete processes, one on each frontal, that keep a relatively constant width as they extend anteriorly.

The most remarkable feature of the frontals is a sharp and tall sagittal crest that trends across the entire dorsal surface of the frontal posterior to the nasal prongs. The crest is formed by contributions from both frontals, which appear to be fused along this contact. It is broken in places and some regions have been reconstructed with plaster, but the reconstructed shape appears to be approximately accurate. One exception, however, is that the crest is reconstructed as slightly bifurcating posteriorly, but there is no evidence for this morphology on the specimen itself. The crest is extremely thin: it is only 2 mm in mediolateral width in the

one well preserved and non-reconstructed region at its midpoint. Here, it rises approximately 10 mm above the dorsal surface of the frontal. The dorsal edge of the crest appears to trend posterodorsally when seen in lateral view, and thus the crest expands in depth posteriorly. At its posterior end, where it meets a dorsal knob on the parietal, the crest is 18 mm in mediolateral width when viewed posteriorly.

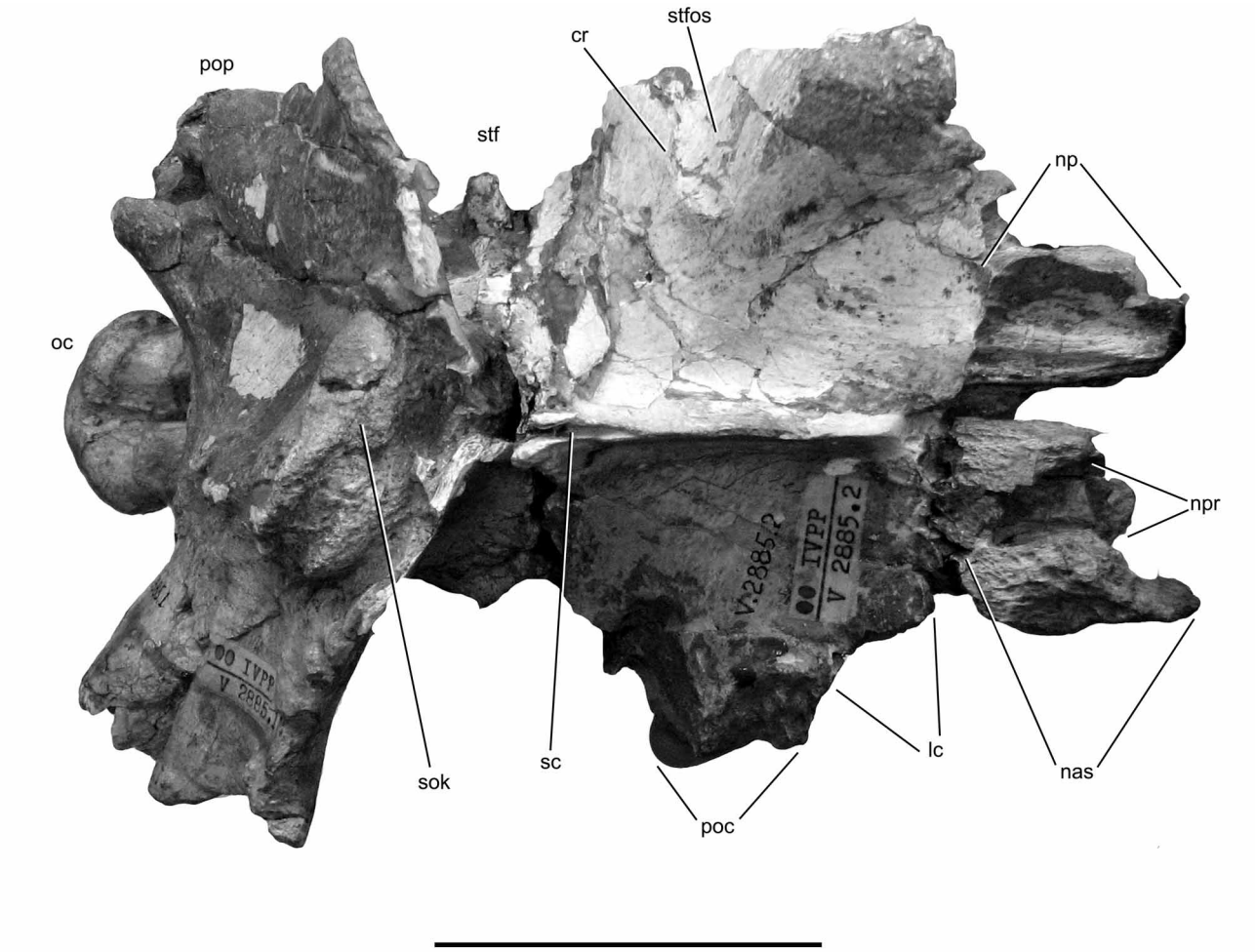

FIGURE 5. Photograph of the skull roof piece (right nasal, frontals, parietals; IVPP V2885.2) articulated with the braincase (IVPP V2885.1) of *Shaochilong maortuensis* in dorsal view. Abbreviations: **cr**, crest within supratemporal fossa; **lc**, lacrimal contact; **nas**, nasal; **np**, nasal process; **npr**, nasal pneumatic recess; **oc**, occipital condyle; **poc**, postorbital contact; **pop**, paroccipital process; **sc**, sagittal crest; **sok**, supraoccipital knob; **stf**, supratemporal fenestra; **stfos**, supratemporal fossa. Scale bar equals 5 cm.

The presence and morphology of the sagittal crest is an autapomorphy of *Shaochilong*. The dorsal surface of the frontal is flat in all other basal tetanurans (e.g., Madsen 1976; Currie & Zhao 1993a; Allain 2002; Sadleir *et al.* 2008), including other carcharodontosaurids such as *Acrocanthosaurus* (Stovall & Langston 1950; Currie & Carpenter; 2000; Eddy 2008), *Carcharodontosaurus* (Sereno *et al.* 1996; Brusatte & Sereno 2007), *Eocarcharia* (Sereno & Brusatte 2008), and *Giganotosaurus* (Coria & Currie 2002). A variety of frontal ornamentation is seen in abelisaurids, including discrete horns and pronounced mound-like eminences (Bonaparte 1985; see review in Sampson & Witmer 2007), and the frontals and parietals narrow posteriorly to form a sharp crest that gives the frontoparietal bridge a triangular outline in dorsal view (Sampson & Witmer 2007: fig. 2; reviewed by Carrano & Sampson 2008: ch. 22). A sharp, narrow crest is also present in coelurosaurs (e.g., Weishampel *et al.* 2004a), formed by constriction of the frontoparietal bridge by the supratemporal fenestrae along its entire length. However, the sagittal crest of *Shaochilong* is unlike the crests of coelurosaurs and abelisaurids because it is located upon the otherwise flat dorsal surface of the

frontoparietal bridge, rather than resulting from narrowing of the bridge itself. Sues *et al.* (2002) noted that the frontals of *Irritator* formed a distinct ridge along their median sutural contact but did not figure the structure. It is possible that this represents dorsal swelling of the bones adjacent to the midline suture, but it may also denote a sagittal crest similar to that of *Shaochilong*. Pending direct examination of the holotype of *Irritator* (SMNS 58022) we consider the unique morphology of the sagittal crest to be an autapomorphy of *Shaochilong*.

Lateral to the sagittal crest the dorsal surface of the frontal is smooth. The supratemporal fossa only extends slightly onto the frontal, and at its longest extent is 34% of the anteroposterior length of the frontal itself. Reduced supratemporal fossae have been described as a synapomorphy of Carcharodontosauridae or a subset of derived members of the group (e.g., Coria & Currie 2002: fossa 'roofed over by a shelf of the frontoparietal'; Brusatte & Sereno 2008). However, a comparative table of measurements has yet to be presented. Among allosauroids, carcharodontosaurids are unique in having a frontal fossa that is less than 35-40% of the length of the frontal (Table 3). The fossa of *Shaochilong* covers a larger portion of the frontal than in any other carcharodontosaurid, but is still much smaller than those of *Allosaurus* and *Sinraptor.* Sereno & Brusatte (2008: character 32) considered the fossae of *Eocarcharia* to be "broadly exposed," as opposed to the "negligible exposure" of *Carcharodontosaurus* and *Giganotosaurus*. However, when measured, all of these carcharodontosaurids have similar ratios (Table 3). With that being said, in *Carcharodontosaurus*, *Giganotosaurus*, and *Shaochilong* the parietal is barely exposed on the dorsal surface of the skull roof posterior to the frontal supratemporal fossa. Therefore, the total length of the supratemporal fossa is longer in *Acrocanthosaurus* and *Eocarcharia*, as it extends posteriorly onto the parietal. In summary, although the proportional length of the frontal portion of the supratemporal fossa is roughly uniform among carcharodontosaurids, the total length of the supratemporal fossa is reduced in *Shaochilong* and carcharodontosaurines, in which the parietal no longer participates.

TABLE 3. Ratio of the longest anteroposterior length of the supratemporal fossa on the frontal to the longest anteroposterior length of the frontal itself. Measurements are taken along an anteroposterior line, parallel to the sagittal axis of the skull.

Taxon	Ratio	Source
Shaochilong	0.34	IVPP V2885.4
Acrocanthosaurus	0.28	Eddy 2008
Allosaurus	0.47	Madsen 1976
Carcharodontosaurus	0.24	SGM-Din-1
Eocarcharia	0.26	MNN GAD2
Giganotosaurus	0.29	Coria & Currie 2002
Sinraptor	0.40	Currie & Zhao 1993

Although proportionally small, the supratemporal fossae of *Shaochilong* are widely exposed in dorsal view. The opposing fossae are widely separated on the midline by a thick margin of the frontals, as in *Acrocanthosaurus* (Stovall & Langston 1950; OMNH 10146), *Carcharodontosaurus* (Brusatte & Sereno 2007; SGM-Din-1), and *Giganotosaurus* (Coria & Currie 2002; MUCPv-Ch 1). In contrast, the fossae of *Eocarcharia* are more extensive and nearly contact medially, and are thus separated by a narrower midline bridge of the frontals (Sereno & Brusatte 2008). The condition in *Eocarcharia* is also present in *Allosaurus* (Madsen 1976) and *Sinraptor* (Currie & Zhao 1993a) and probably represents the plesiomorphic state.

Within the supratemporal fossa of *Shaochilong*, and essentially bisecting it, is a sinuous crest that trends mediolaterally. This has been noted in *Carcharodontosaurus* and described as a possible scar for the attachment of jaw adductor musculature, which filled the fossa in theropods (Brusatte & Sereno 2007). This crest, which differs in shape in different species of *Carcharodontosaurus* (Brusatte & Sereno 2007), has yet to

be described in any other theropod to our knowledge. However, it is also present in *Acrocanthosaurus* (NCSM 14345) and *Giganotosaurus* (MUCPv-CH 1), and its absence in *Eocarcharia* may be due to erosion (Sereno & Brusatte 2008: fig. 14). It is clearly absent in *Allosaurus* (Madsen 1976: fig. 11) and *Sinraptor* (Currie & Zhao 1993: fig. 7), and thus may be a synapomorphy of carcharodontosaurids or a less inclusive subgroup.

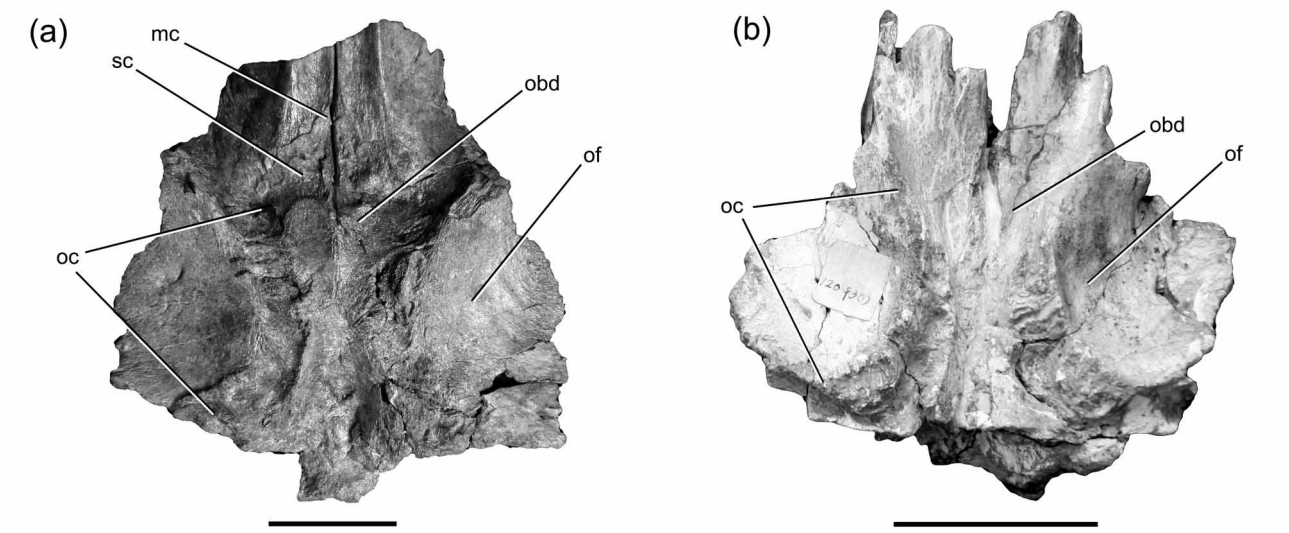

FIGURE 6. Photograph of the frontals of *Carcharodontosaurus iguidensis* (a: MNN IGU3) and *Shaochilong maortuensis* (b: IVPP V2885.2) in ventral views. Abbreviations: **mc**, mesethmoid contact scar; **obd**, olfactory bulb depressions; **oc**, orbitosphenoid contact; **of**, orbital fossa; **sc**, sphenethmoid contact scar. Scale bars equal 5 cm.

The nasal prongs are tongue-like and underlie the nasals ventrally. The articular surface of the prong slopes anteroventrally and is covered with a series of robust grooves that would have strongly interlocked with the nasal, resulting in a firm and immobile contact.

The lateral surface of the frontal is almost completely covered by the extensive articulations for the lacrimal/prefrontal and postorbital. The former articulation is deep and funnel-like, and faces laterally and anteriorly. This contact is 30 mm long anteroposteriorly and 23 mm deep dorsoventrally at its midpoint. It occupies the entire lateral surface of the nasal prong and is deepest at the corner where the prong meets the body of the frontal. Here, the deep, smooth, and rounded internal socket of the funnel faces mostly anteriorly. This socket is obscured in lateral view by a thick lip of bone that trends anteriorly. However, the lip terminates far posterior to the medial edge of the funnel, thus exposing the funnel in lateral view for most of its length. It is unclear if a separate prefrontal articulated here, as the prefrontal and lacrimal are firmly fused into a single element in carcharodontosaurids (Sereno *et al.* 1996; Sereno & Brusatte 2008). However, if present, the prefrontal did not articulate with the frontal across a rugose and interdigitating suture like that seen in *Eocarcharia* (Sereno & Brusatte 2008), *Allosaurus* (Madsen 1976), and *Sinraptor* (Currie & Zhao 1993a).

The postorbital articulation is notably large in lateral view. It trends posteroventrally-anterodorsally, and has a 47 mm long axis and 22 mm perpendicular minor axis at its greatest extent. Posterior to this articulation there is a small notch on the frontal for the laterosphenoid. The anterior part of the postorbital articulation forms a small but discrete process that faces anteriorly, not laterally. This process is present in other carcharodontosaurids, and is well figured in *Eocarcharia* (Sereno & Brusatte 2008: figs. 14, 15), but is absent in *Allosaurus* (Madsen 1976) and *Sinraptor* (Currie & Zhao 1993a). In carcharodontosaurids this region smoothly lines up with an anteriorly facing articular surface on the postorbital, and together they contact the lacrimal to exclude the frontal from the orbital rim. Exclusion of the frontal from the orbital rim is a synapomorphy of carcharodontosaurids (Brusatte & Sereno 2008), and is clearly present in *Shaochilong*. Not only is the small anterior process of the postorbital articulation present, but the region between the lacrimal and postorbital contacts, which corresponds to the orbital rim in other theropods, is essentially absent. It is reduced to a tiny, 4 mm long notch that faces mostly anteriorly, not laterally as does the orbital rim of most

theropods. Furthermore, this notch is not smooth, as is characteristic of the orbital rim, but houses a discrete rugose tuberosity. This narrow margin would not have contributed to the rim of the orbit in *Shaochilong*.

The ventral surface of the conjoined frontals is marked by two large, crescentric scars for the orbitosphenoid (Figs 4, 6). In between them, and extending parasagitally along the midline of the frontals, is a groove for the olfactory tract. This groove, which forms the endocranial surface of the frontal, terminates anteriorly in two small (approximately 25 mm long by 10 mm wide), teadrop-shaped depressions for the olfactory bulbs. These begin at approximately midlength of the frontal and extend anteriorly nearly to the point where the nasal prongs diverge from the body of the frontal. The orbitosphenoid scars terminate near the midpoint of the olfactory bulb depressions and clearly do not enclose the olfactory bulbs anteriorly. Thus, the sphenethmoid was not ossified. This condition is also seen in *Eocarcharia*, *Allosaurus*, *Sinraptor*, and most theropods (Sereno & Brusatte 2008), but an ossified sphenethmoid is present in *Acrocanthosaurus*, *Carcharodontosaurus*, and *Giganotosaurus* (e.g., Stovall & Langston 1950; Coria & Currie 2002); this character is further discussed and reviewed below.

The proportions and shape of the endocranial surface are similar to those of other allosauroids. Importantly, the surface is not extremely narrow as is autapomorphic for *Eocarcharia* (Sereno & Brusatte 2008). However, the endocranial surface is much broader in many coelurosaurs (e.g., Currie 1985: fig. 3), especially posteriorly, and only narrows as it terminates at the olfactory bulbs. In *Shaochilong* and other allosauroids the endocranial surface is narrow across its entire length and actually expands at the olfactory bulbs. Additionally, the endocranial surface and olfactory bulb depressions are shallow in *Shaochilong*, which is characteristic for basal theropods but contrasts with the deeper and more heavily vascularized depressions in most coelurosaurs (e.g., Currie 1985; Osmólska 2004; Kirkland *et al.* 2005).

Parietal. The parietals are nearly complete but are broken in half, with the anterior regions fused to the frontals (IVPP V2885.2) and the posterior regions conjoined with the braincase (IVPP V2885.1) (Figs 4, 5). These two regions match up, providing irrefutable evidence that the frontal/nasal piece and the braincase belong to the same individual. The opposing parietals are fused on the midline, where they are 22 mm long anteroposteriorly.

The conjoined parietals are hourglass shaped in dorsal view, due to the medially extensive supratemporal fenestrae. The fenestrae are only separated by a 20 mm width of parietal at their greatest expansion. In comparison, the posterior edge of the parietal is 123 mm wide, meaning that this bone is constricted to only 16% of its maximum width between the supratemporal fenestrae. This constriction is proportionally greater than in other carcharodontosaurids (*Acrocanthosaurus*: Stovall & Langston 1950; *Carcharodontosaurus*: Sereno *et al.* 1996; Sereno & Brusatte 2008; *Giganotosaurus*: Coria & Currie 2002). Interestingly, in these carcharodontosaurids the narrow extent of the supratemporal fossae on the frontal (in both anteroposterior and mediolateral dimensions) corresponds with a small degree of parietal constriction. However, in *Shaochilong* the frontal fossae are not extensive but the parietal is still strongly hourglass shaped.

Unfortunately, the parietal is eroded dorsally, and thus it is unclear whether *Shaochilong* possessed the tall dorsal parietal eminence that is seen in some carcharodontosaurids (Coria & Currie 2002). Similarly, it is unclear whether the supraoccipitals or parietals overlapped each other dorsally. However, based on the thickened anterior margin of the parietals where they meet the frontals, it appears as if the frontal sagittal crest did continue onto at least the anterior region of the parietals. The frontals and parietals are heavily fused where they contact, a condition seen in all carcharodontosaurids except for *Eocarcharia* (Brusatte & Sereno 2008; Sereno & Brusatte 2008). In posterior view the parietal is exposed broadly on the occiput and rises to the same level as the supraoccipital. A foramen for the dorsal head vein pierces the occipital plate of each parietal where it meets the exoccipital-opisthotic and presumably the supraoccipital, although sutures in this region are not entirely clear.

Quadrate. Both left and right quadrates are known (IVPP V2885.3) (Fig. 7). The right element is complete and well preserved, whereas the left is broken into several pieces. The right quadrate is 143 mm tall dorsoventrally along its posterior margin (the “shaft” region). Anteriorly the shaft gives rise to a plate-like

flange that articulates with the pterygoid. This flange is 47 mm long anteroposteriorly at its midpoint and 104 mm deep at its tallest extent posteriorly.

The lateral surface of the quadrate is marked by an elongate, laterally-facing, rugose articular scar for the quadratojugal. This scar extends along the dorsal half of the shaft and expands in anteroposterior length dorsally before eventually reaching the quadrate cotylus. The cotylus, or head, is a smoothly rounded ovoid structure, which is 24 mm long anteroposteriorly by 18 mm wide mediolaterally in proximal view. Further ventrally, the lateral surface of the lateral condyle is entirely excavated by a rugose articulation for the quadratojugal. This sutural surface is roughly triangular, 24 mm tall by 20 mm long anteroposteriorly, and faces laterally and dorsally. Thus, the quadratojugal articulates with both the lateral surface of the shaft dorsally and the lateral condyle ventrally, as is usual for basal theropods.

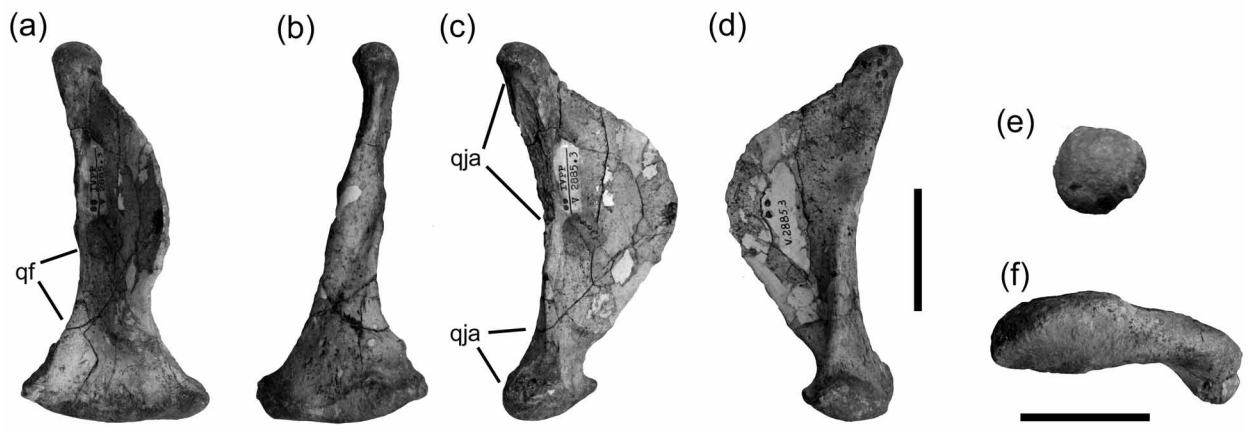

FIGURE 7. Photograph of the right quadrate of *Shaochilong maortuensis* (IVPP V2885.3) in anterior (a), posterior (b), lateral (c), medial (d), dorsal (e), and ventral (f) views. Abbreviations: **qf**, quadrate foramen; **qja**, quadratojugal articulation. Scale bar equals 5 cm.

Between the two articular surfaces for the quadratojugal is a smooth, 34 mm deep nonarticular margin. Approximately 18 mm of this margin is indented as a slight concavity, which is the medial edge of the quadrate foramen. Chure (2000) could not locate the quadrates during the course of his study, but suggested that the quadrate foramen was absent based on an interpretation of Hu's (1964) published figures. However, the smooth, concave margin for the foramen is visible between the two articular surfaces for the quadratojugal in Hu's (1964: fig. 9) illustration. This margin is subtle and suggests that the quadrate foramen was a small structure in life. It must have been extensively enclosed by the quadratojugal, which would have formed its lateral, dorsal, and ventral margins. Small foramina are also present in other allosauroids (e.g., Madsen 1976; Currie & Zhao 1993a; Coria & Currie 2006; Eddy 2008), and the carcharodontosaurids *Acrocanthosaurus* (Eddy 2008), *Giganotosaurus* (MUCPv-CH-1), and *Mapusaurus* (Coria & Currie 2006) also possess foramina that are broadly enclosed by the quadratojugal. In other allosauroids the foramen is primarily enclosed by the quadrate (e.g., *Sinraptor*: Currie & Zhao 1993a). *Allosaurus* is often considered to possess a foramen fully or almost entirely enclosed by the quadrate (Madsen 1976), but this condition is variable among specimens (UMNH VP specimens, RBJB pers. obs.). In posterior view a shallow groove leads into the quadrate foramen, as is characteristic for theropods (e.g., Brusatte *et al.* in press).

The quadrate flange is thin and plate-like. It projects anteriorly and medially relative to the transversely straight condyles and its lateral surface is smooth and flat. In contrast, the medial surface of the flange is flat dorsally but deeply concave ventrally, where there is a smooth pocket that excavates the corner where the flange meets the medial condyle. However, this pocket does not enclose any pneumatopores or other external signs of pneumaticity. Indeed, the quadrate appears to be apneumatic, similar to the condition in *Allosaurus* (Madsen 1976) and *Sinraptor* (Currie & Zhao 1993a). In contrast, all known carcharodontosaurid quadrates are pneumatized (e.g., *Acrocanthosaurus*, *Giganotosaurus*, *Mapusaurus*), as are those of tyrannosaurids (e.g.,

Brochu 2003). Such pneumaticity is usually expressed in two regions of the quadrate in carcharodontosaurids. First, some specimens possess a discrete pneumatopore, which sometimes is fenestra-like, on the posterior surface of the quadrate (e.g., Coria & Currie 2006: fig. 7; Eddy 2008). This structure is also seen in the neovenatorid carcharodontosaurian *Aerosteon* (Alcober *et al.* 1998; Sereno *et al.* 2008). Second, many specimens possess a deep pneumatopore, which leads into an internal chamber, at the corner of the medial surface where the flange meets the medial condyle (e.g., MUCPv-CH-1; Coria & Currie 2006; Eddy 2008). The presence of a smooth pocket in this region in *Shaochilong* suggests that a precursor of pneumaticity may be present. However, many other theropods also possess a smooth fossa on the medial surface of the quadrate flange, which often extends ventrally into the region of the pocket in *Shaochilong*. This is usually described as a shallow pneumatic feature, associated with the paratympanic system, which does not penetrate the quadrate internally (e.g., Currie 2003a).

Separate lateral and medial condyles are present ventrally. Chure (2000) interpreted Hu's (1964) figures as illustrating a single, undivided distal condyle, which was an important feature linking *Shaochilong* with the enigmatic *Labocania* (Molnar 1974) in Chure's (2000) discussion of characters. However, although the groove separating them is subtle, separate condyles are clearly present. The lateral condyle is 37 mm wide mediolaterally by 15 mm long anteroposteriorly. Its ventral articular surface is highly convex anteriorly and concave posteriorly, and in distal view it is seen to continue laterally and posteriorly as a thin flange. This flange develops into the laterally-facing articulation for the quadratojugal, and defines its ventral margin. The medial condyle has a long axis (40 mm) oriented slightly anterolaterally-posteromedially, with a 24 mm perpendicular minor axis, and its ventral articular surface is less convex than the lateral condyle. In fact, the convex region of the lateral condyle continues onto the anterior margin of the articular surface of the medial condyle. This upraised margin, which thins and sharpens as it continues medially, defines the anterior edge of the trochlear surface for the jaw articulation. The posterior edge of the trochlea is demarcated by a slighter upraised bulge along the posterior margin of the medial condyle.

Braincase. The braincase (IVPP V2885.1) is well preserved and substantially complete, making it one of the best known basal tetanuran braincases (Figs 5, 8–12). However, only the bases of both paroccipital processes are currently represented; Hu (1964) figured much of the left paroccipital process, but this piece could not be located during the course of our study. Other missing regions include the right basal tuber, most of the funnel-shaped basisphenoid recess ventrally, and the anterior regions of the laterosphenoids and orbitosphenoids. Most of the sutures between individual bones have been obliterated, and thus the shape and extent of some bones are reconstructed based on landmarks and raised ridges that we consider the fused remnants of original sutures. This degree of fusion suggests that the individual was an adult at its time of death, an assessment supported by the heavily fused interdental plate apron on the maxilla and the fused neurocentral sutures of the axis and most caudal vertebrae.

In general, the braincase is very similar to those of *Acrocanthosaurus* (Stovall & Langston 1950; Franzosa & Rowe 2005; Eddy 2008), *Carcharodontosaurus* (Sereno *et al.* 1996; Brusatte & Sereno 2007), and *Giganotosaurus* (Coria & Currie 2002). As in these carchardontosaurids, the braincase of *Shaochilong* is extremely pneumatic: it is penetrated by numerous pneumatopores and excavated by deep pneumatic fossae, and broken regions show the presence of several internal chambers. Additionally, as in carcharodontosaurids, the braincase of *Shaochilong* as preserved is short anteroposteriorly and extremely deep dorsoventrally. However, the latter dimension is underestimated since much of the basisphenoid funnel is missing, and thus it would have been even deeper in life. In contrast, proportionally longer braincases are seen in other allosauroids (e.g., *Allosaurus*: Madsen 1976; *Sinraptor*: Currie & Zhao 1993a), as well as basal tetanurans (e.g., *Piatnitzkysaurus*: Rauhut 2004a) and basal theropods (e.g., *Cryolophosaurus*: Smith *et al.* 2007; *Dilophosaurus*: Welles 1984; *Majungasaurus*: Sampson & Witmer 2007; *Zupaysaurus*: Ezcurra 2007) in general. The braincases of derived tyrannosaurids (e.g., *Tyrannosaurus*: Brochu 2003) and spinosaurids (e.g., *Baryonyx*: Charig & Milner, 1997; *Irritator*: Sues *et al.* 2002) are also short and deep, but basal members of each clade (spinosauroids: *Dubreuillosaurus*, Allain 2002; tyrannosauroids: *Dilong*, IVPP V14243; *Guanlong*, IVPP V14531) have proportionally longer braincases similar to those of most other theropods.

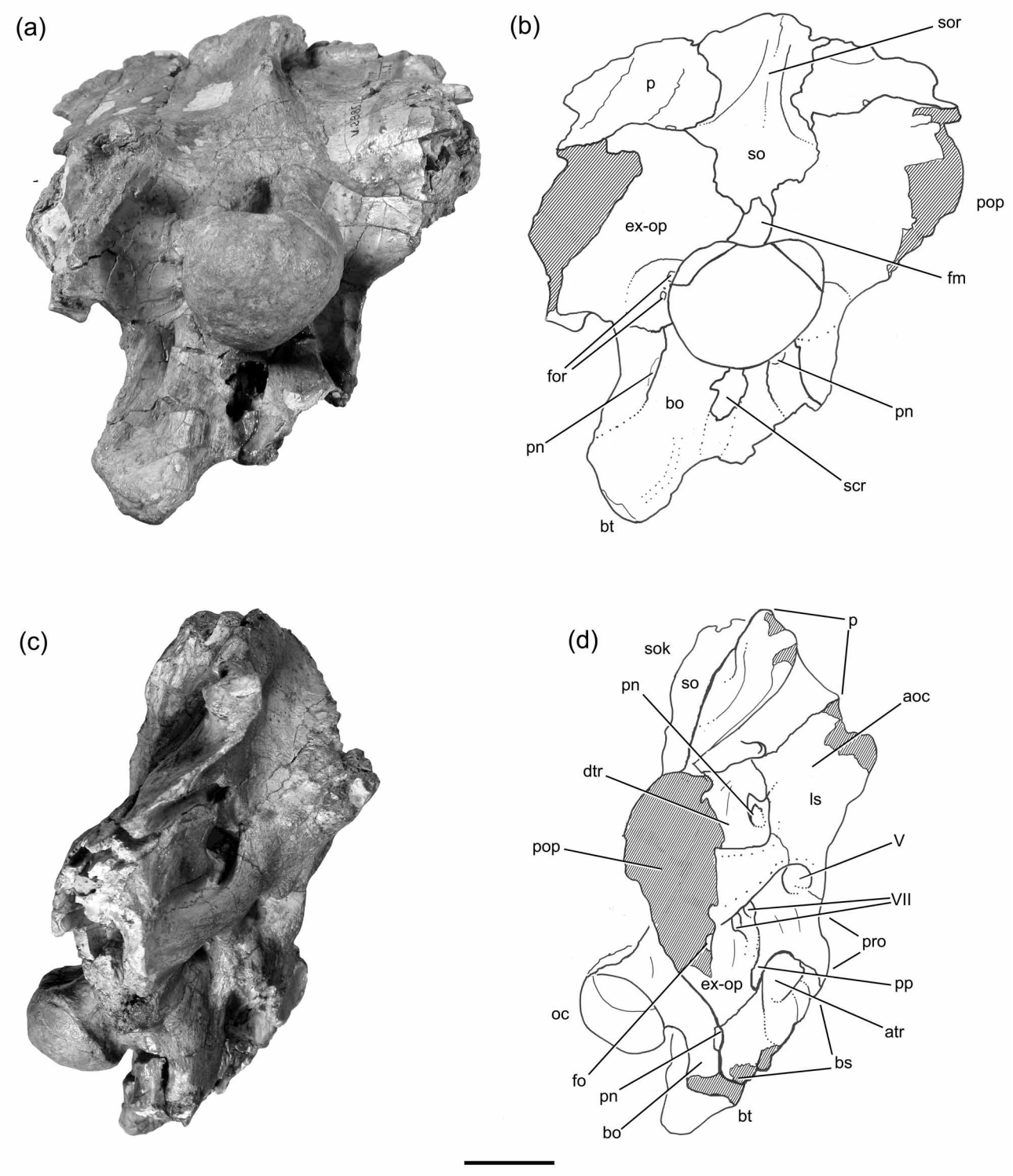

FIGURE 8. Photographs and line drawings of the braincase of *Shaochilong maortuensis* (IVPP V2885.1) in posterior (a, b) and right lateral (c, d) views. Abbreviations: **aoc**, antotic crest; **atr**, anterior tympanic recess; **bo**, basioccipital; **bs**, basisphenoid; **bt**, basal tuber; **dtr**, dorsal tympanic recess; **ex-op**, exoccipital-opisthotic; **fm**, foramen magnum; **fo**, fenestra ovalis; **for**, paracondylar openings representing jugal foramen and foramen for nerve XII; **ls**, laterosphenoid; **oc**, occipital condyle; **p**, parietal; **pn**, pneumatic foramen (pneumatopore); **pop**, paroccipital process; **pp**, preotic pendant; **pro**, prootic; **scr**, subcondylar recess; **so**, supraoccipital; **sok**, supraoccipital knob; **sor**, supraoccipital ridge. Roman numerals refer to cranial nerves. Scale bar equals 5 cm.

Supraoccipital. The supraoccipital is complete and well preserved. It is widely exposed on the occiput and is inclined posteroventrally. Visible sutures clearly show that this bone contributes to the dorsal rim of the foramen magnum. However, it does not extend ventrally to form the lateral margins of the foramen magnum and contribute to the dorsal surface of the occipital condyle, as has been described in *Giganotosaurus* (Coria & Currie 2002). The posterior surface of the supraoccipital is ornamented by a robust midline crest, which thickens in mediolateral dimension as it expands dorsally. The crest becomes confluent with a large dorsal expansion of the supraoccipital, the "pronounced nuchal process" described by Coria & Currie (2002). This process, which is often referred to as the supraoccipital "knob" or "tuberosity" (Sampson & Witmer 2007), is extremely rugose, thickened mediolaterally and anteroposteriorly when viewed dorsally, and is greater than twice the width of the foramen magnum in the derived carchardontosaurids *Acrocanthosaurus* (Stovall & Langston 1950), *Carcharodontosaurus* (Sereno *et al.* 1996), and *Giganotosaurus* (Coria & Currie 2002). A less pronounced and mediolaterally narrower structure is seen in *Allosaurus* (Madsen 1976) and *Sinraptor* (Currie & Zhao 1993a) and more generally among theropods (e.g., Taquet & Welles 1977; Sampson & Witmer 2007). In *Shaochilong* the knob is especially prominent: it is more than three times the width of the foramen magnum, 1.3 times the width of the ventral region of the supraoccipital where it roofs the endocranial cavity, and is slightly wider than the occipital condyle. The knob joins with the occipital plate of the parietal to form a tall nuchal crest, which is striking in posterior view. This crest comprises the posterior edge of the supratemporal fenestrae and thus delimits the chamber for the temporal musculature posteriorly.

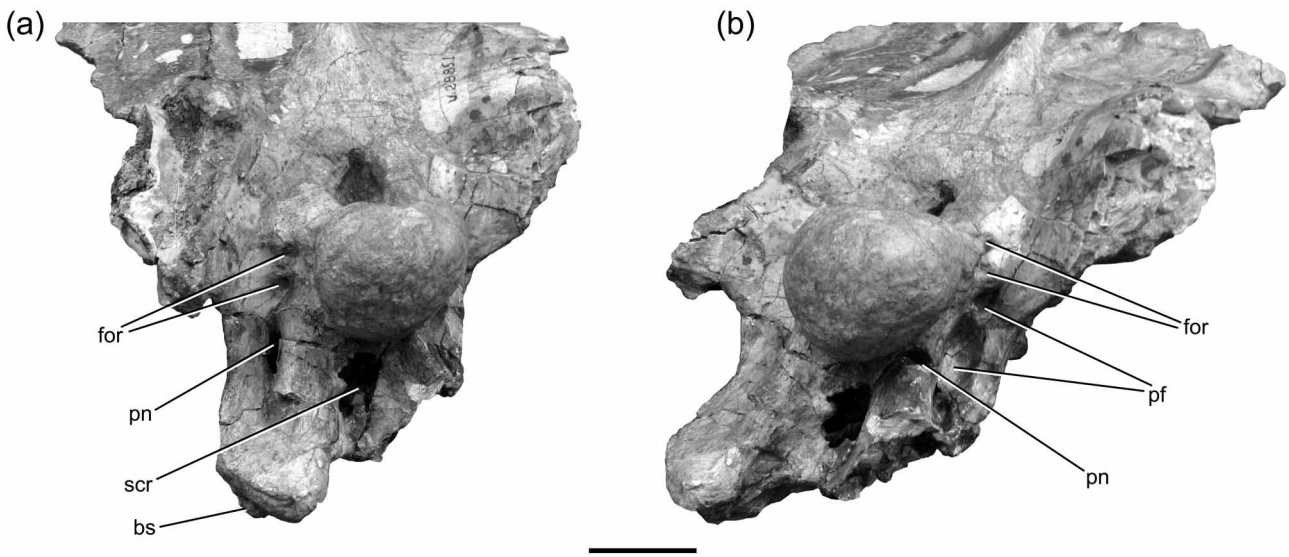

FIGURE 9. Photographs of the braincase of *Shaochilong maortuensis* (IVPP V2885.1) in oblique left posterior (a) and oblique right posterior (b) views. Abbreviations: **bs**, basisphenoid; **for**, paracondylar openings representing jugal foramen and foramen for nerve XII; **pf**, pneumatic fossa; **pn**, pneumatic foramen (pneumatopore); **scr**, subcondylar recess. Scale bar equals 5 cm.

Basioccipital. The basioccipital forms the majority of the occipital condyle and basal tubera. The occipital condyle is subspherical and projects posteroventrally when the frontals are held horizontally. The basioccipital clearly forms the floor of the foramen magnum above the condyle, as the pedicels of the exoccipital-opisthotic only form the dorsolateral corner of the condyle and do not join across the midline. This latter condition, in which the basioccipital is completely separated from the foramen magnum, has been suggested for *Carcharodontosaurus*, but based upon unclear sutures (MNN IGU3; Brusatte & Sereno 2007).

A stout 'neck' of bone supports the occipital condyle and connects the condyle with the exoccipital-opisthotic and remainder of the basioccipital anteriorly and laterally. Ventrolateral to the occipital condyle, the posterior surface of the basioccipital dorsal to the basal tubera is excavated on both sides by deep pneumatic fossae. It is unclear whether the right fossa penetrates the surface due to breakage in this region, but on the left

side there is a large ovoid pneumatopore that leads anteriorly and medially into an extensive recess below the endocranial cavity. Similar 'paracondylar pneumatopores' have been described in carcharodontosaurids (e.g., *Carcharodontosaurus*: Brusatte & Sereno 2007; *Giganotosaurus*: Coria & Currie 2002), and are also present in *Acrocanthosaurus* (OMNH 10146). The presence of these structures has been used as a phylogenetic character (e.g., Coria & Currie 2002; Brusatte & Sereno 2008). Pneumaticity is common in this region in coelurosaurs (e.g., Makovicky & Norell 1998; Currie 2003a; Kirkland *et al.* 2005) and is also present in other basal theropod taxa. Rauhut (2004a) identified small pneumatopores in *Piatnitzkysaurus* that he suggested were associated with the subcondylar recess, whereas Sampson & Witmer (2007) described tiny pneumatic foramina in *Majungasaurus* that lead into an extensive medial cavity underneath the brain, which is confluent with the anterior tympanic recess. However, in neither of these taxa, nor in any other non-avian theropods, are there large pneumatopores entering the posterior surface of the basioccipital ventromedial to the occipital condyle as in carcharodontosaurids. Additionally, the form of the surrounding fossa is different: a distinct fossa is not present in *Majungasaurus*, whereas a shallow fossa that faces directly posteriorly (instead of a deep fossa that faces posterolaterally as in *Shaochilong*) is seen in *Piatnitzkysaurus*. Unfortunately, it is unclear if the median recess underneath the endocranial cavity is associated with the subcondylar or anterior tympanic recesses in *Shaochilong* because of extensive internal breakage.

The basal tubera project posteroventrally relative to the horizontal dorsal surface of the frontals. Combined with the posteroventral sloping of other occipital structures, such as the posterior surface of the supraoccipital, this gives the entire posterior surface of the braincase a posteroventral inclination, as in *Carcharodontosaurus*, *Giganotosaurus*, and *Sinraptor* (Coria & Currie 2002; Brusatte & Sereno 2008). In contrast, the tubera of *Allosaurus* and *Acrocanthosaurus* descend nearly vertically, and thus are perpendicular to a horizontal plane drawn through the occipital condyle (Coria & Currie 2002). In *Shaochilong* the tubera are wider transversely than the occipital condyle as in *Carcharodontosaurus*, *Giganotosaurus*, and indeed most theropods, not narrower as in *Acrocanthosaurus*, *Allosaurus*, and *Sinraptor* (Brusatte & Sereno 2008). The posterior surface of the basioccipitals between the tubera is excavated by a single, deep midline fossa, which continues dorsally underneath the occipital condyle. This depression is an expression of the subcondylar recess, a common structure in theropods (Rauhut 2004a; Sampson & Witmer 2007). A single midline fossa is present in most theropods, but varies in width. In *Allosaurus* (Madsen 1976), *Carcharodontosaurus* (Brusatte & Sereno 2007), *Shaochilong* (Figs 8, 9), and *Sinraptor* (Currie & Zhao 1993a) the fossa is approximately half the width of the occipital condyle and widely separates the pneumatic fossae on the posterior surfaces of the basal tubera. However, in *Acrocanthosaurus* the midline fossa is narrow, forming a deep dorsoventrally oriented groove between the fossae on the basal tubera (NCSM 4345, OMNH 10146). This condition may be related to narrowing of the basal tubera in *Acrocanthosaurus* and seems to be autapomorphic. The condition in *Giganotosaurus* cannot be determined due to incomplete preservation (MUCPv-CH 1). Much of the fossa appears to be open posteriorly in *Shaochilong* and is seen to lead into the large recess underneath the endocranial cavity. However, this opening is not a pneumatopore but simply is broken bone, and thus it is unclear if the external subcondylar fossa communicated with the internal median recess (see above). Only the left basal tuber is complete distally, where it is slightly thickened and rugose for muscle attachment. There clearly was an arched, concave ventral margin between the left and right tubera, which in posterior view appears as a deep notch.

The basal tubera are formed mostly by the basioccipital. The basisphenoid forms the anterior portion of the tuber, as shown by a visible suture at the anterolateral corner of the left tuber. However, this suture is only visible in lateral and anterior views, and the basisphenoid contribution is only seen as a slight ventral projection in posterior view. Only a small region of the basisphenoid contribution is clearly preserved, at the anterolateral margin of the left tuber. Anterior and dorsal to this region the suture between the basisphenoid and basioccipital has been obliterated by fusion. The clear basisphenoid contribution corresponds to the "basisphenoid scar" of Bakker *et al.* (1988), a muscle attachment site. This scar is the only part of the crista ventrolateralis—the web of bone that spans the tuber and basipterygoid process to form the lateral wall of the basisphenoid—that is preserved in *Shaochilong*.

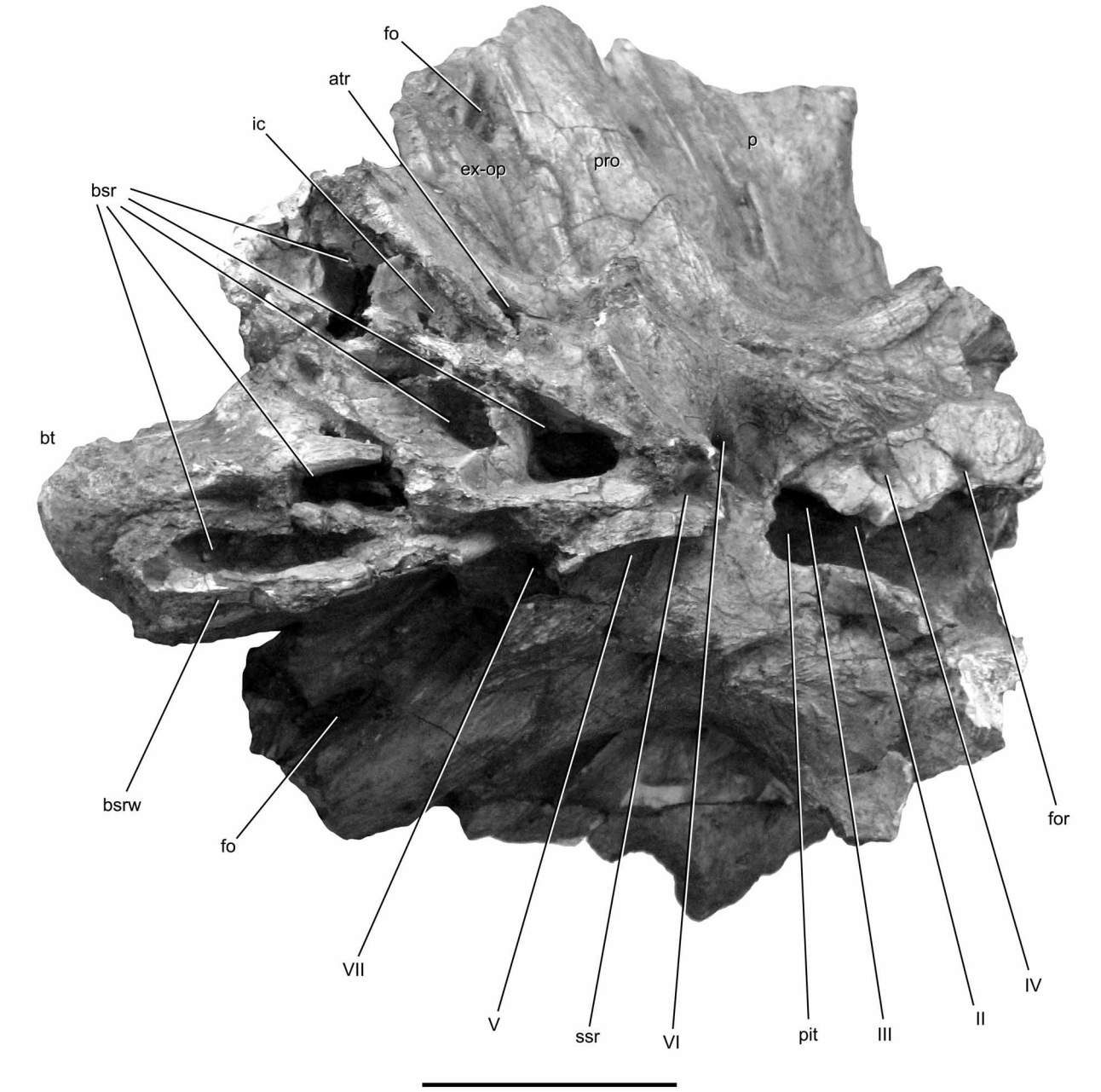

FIGURE 10. Photograph of the braincase of *Shaochilong maortuensis* (IVPP V2885.1) in ventral view. Abbreviations: **atr**, anterior tympanic recess; **bsr**, basisphenoid recess; **bsrw**, basisphenoid recess web; **bt**, basal tubera; **ex-op**, exoccipital-opisthotic; **fo**, fenestra ovalis; **for**, foramen; **ic**, internal carotid entrance; **p**, parietal; **pit**, pituitary fossa; **pro**, prootic; **ssr**, subsellar recess. Roman numerals refer to cranial nerves. Scale bar equals 5 cm.

It is unclear if the exoccipital-opisthotic contributes to the tuber, as the suture between this element and the basioccipital has been obliterated by fusion. In many theropods, including many basal tetanurans, the lateral surfaces of the tubera are formed by descending processes of the exoccipital-opisthotic (Rauhut 2004a). If this is the case in *Shaochilong*, then the two bones are smoothly confluent and not separated by a notch ventrally as in *Allosaurus* (Madsen 1976) and *Acrocanthosaurus* (Stovall & Langston 1950; Eddy 2008). However, other basal theropods (e.g., *Majungasaurus*: Sampson & Witmer 2007) do not exhibit a descending process of the exoccipital-opisthotic, and the entire posterior surface of the tubera is formed by the basioccipital.

Basisphenoid. A large part of the basisphenoid is present, but it is difficult to trace its sutures with other braincase bones (with the exception of the small region of visible suture at the anterolateral corner of the basal

tuber, described above). A large part of the basisphenoid contribution to the lateral wall of the braincase is present, but much of the bone is eroded ventrally in the region of the funnel-like basisphenoid recess. In ventral view the basisphenoid is sheared across a planar surface, exposing a cross sectional view of the pneumatic basisphenoid recess, as well as portions of the anterior tympanic recess and the median recess underneath the endocranial cavity, which appears to be partially enclosed by the basisphenoid. Anteriorly, the basipterygoid processes and most of the crista ventrolateralis linking these processes to the basal tubera are absent. Rauhut (2004a) stated that a basipterygoid recess—a pneumatic depression on the lateral wall of the crista above the basipterygoid process—is present in *Shaochilong*. However, this region of the braincase is not preserved.

The sheared ventral surface of the basisphenoid exposes a number of pneumatic cavities in cross section. A deep, triangular, funnel-like cavity is clearly part of the basisphenoid recess, an enigmatic midline excavation that is hypothesized to be part of the median pharyngeal system (Witmer 1997; Sampson & Witmer 2007). Because the crista ventrolateralis is mostly missing it is not clear if the basisphenoid recess of *Shaochilong* was a deep funnel that occupied approximately 30% of the depth of the braincase as in *Acrocanthosaurus* and *Carcharodontosaurus* (Sereno *et al.* 1996; Brusatte & Sereno 2007; Sereno & Brusatte 2008), a derived condition relative to the smaller and shallower recesses of most theropods. However, the broken walls of the crista ventrolateralis are thick and diverge from each other in a wide, funnel-like shape, suggesting that the recess was extensive, and larger than in most theropods. However, the basal tubera are not nearly as ventrally extensive as they are in *Acrocanthosaurus* (Stovall & Langston 1950; Eddy 2008), where they are extremely deep to form the posterior wall of the deep basisphenoid recess. Thus, we suggest that that the basisphenoid recess was intermediate in size between the shallower recesses in theropods such as *Allosaurus* and *Sinraptor* and the deep funnels of some carcharodontosaurids.

Other cavities visible in ventral view correspond to other recesses. Immediately anterior to the basisphenoid recess is a large, triangular opening that is either an anterior chamber of the basisphenoid recess or the subsellar recess (Rauhut 2004a; Sampson & Witmer 2007). Posterior and lateral to the basisphenoid recess, and well exposed on the better preserved left side, are elongate cavities associated with the median recess underneath the endocranial cavity. Finally, lateral to the basisphenoid recess, and well preserved on the right side, is a smaller funnel-shaped depression that leads into the foramen for the internal carotid. This is the anterior tympanic recess (Rauhut 2004a; Sampson & Witmer 2007), and it is better seen in lateral view where it deeply excavates the lateral wall of the braincase in the region where the prootic and basisphenoid meet. The recess is partially hidden in lateral view by the preotic pendant, which extends posteroventrally as a wing-like structure. Sutures between the prootic and basisphenoid in this area are unclear, but a raised ridge trending anterodorsally across the lateral surface of the pendant may represent this contact. If so, the pendant, as well as the anterior tympanic recess medial to it, is nearly evenly divided between these bones. Unfortunately, after entering the anterior tympanic recess the course of the carotid is not clear. It is not possible to determine whether the paired carotid canals united internally, an unusual feature among theropods (Sampson & Witmer 2007) that has been suggested for *Giganotosaurus* (Coria & Currie 2002).

Whether the various recesses (basisphenoid recess, anterior tympanic recess, medial recess underneath the endocranial cavity) communicated with each other internally is unclear. As preserved, the basisphenoid recess does communicate with the remaining two recesses, but only because of clearly broken surfaces. Therefore, since much of the ventral part of the braincase is missing and the preserved walls are heavily eroded, it is unknown whether the walls of bone between these cavities would have completely separated them in life. This information is probably intractable even with CT data. However, all three recesses are positioned close to one another, and are densely packed within the braincase and only separated by narrow walls of bone. Thus, it is possible that they did communicate in life, since it would only require small foramina between the dividing walls and not complex internal passageways.

Exoccipital-Opisthotic. The exoccipital and opisthotic are indistinguishably fused into a single element as in archosaurs generally (e.g., Currie 1997; Sampson & Witmer 2007). The left and right exoccipitals are separated by the supraoccipital and basioccipital and never come into contact. The exoccipital-opisthotics

form the lateral margins of the foramen magnum and are flat in this region, lacking the depressions seen in many coelurosaurs (e.g., Currie & Zhao 1993b; Currie 1995; Makovicky & Norell 1998; Norell *et al.* 2004). Further ventrally, stout pedicels of the exoccipital-opisthotic contribute to the dorsolateral corners of the occipital condyle, and sutures between the exoccipital-opisthotic and basioccipital are clearly visible on both sides of the condyle.

Ventral to the pedicels, and lateral to the occipital condyle, two large foramina open posterolaterally into a depression, which appears to be mostly present on the exoccipital-opisthotic. This depression is sometimes called the paracondylar pocket (Welles 1984) or the paracondylar recess (Chure 2000); we prefer the former term, since "recess" implies that this region is pneumatic, which is clearly not the case in *Shaochilong* and other large theropod dinosaurs (e.g., Currie & Zhao 1993a; Rauhut 2004a; Brusatte & Sereno 2007; Sampson & Witmer 2007). The two foramina are of equal size, with one placed posterodorsal to the other. A much smaller, ovoid depression between them may represent a third opening that has been filled with matrix. Indeed, three openings in this region—two for the hypoglossal (XII) nerve and one jugular foramen that transmits the jugal vein, vagus (X), and accessory (XI) nerves—is the usual condition in derived theropods. In these taxa, the jugular foramen (= "metotic foramen") is divided from the remainder of the middle ear by an ossified metotic strut, which serves to reposition the jugular foramen on the posterior occipital surface of the braincase, in contrast to its lateral position in more basal archosaurs (e.g., Gower & Weber 1998; Sampson & Witmer 2007). Even if the small depression of *Shaochilong* is not a true third foramen, the presence of only two clear foramina in the paracondylar pocket is not an argument for the primitive condition. First, there is no clear jugular foramen on the lateral wall of the braincase. Second, *Majungasaurus* clearly has a posteriorly-reoriented jugular foramen (as shown by CT data) but only two posterior openings (Sampson & Witmer 2007). Third, several other basal theropod specimens that lack obvious lateral jugular foramina, but have not been subject to rigorous CT study, also only have two openings in the paracondylar pocket (e.g., *Allosaurus*: UMNH VP 16605; *Baryonyx*: Charig & Milner 1997; *Ceratosaurus*: BYU 128930; *Giganotosaurus*: MUCPv-CH 1; *Irritator*: Sues *et al.* 2002). Thus, like *Majungasaurus* and presumably these other basal theropods, *Shaochilong* may have only a single, larger opening for both branches of the hypoglossal nerve within the paracondylar pocket. Whether the number of hypoglossal foramina is phylogenetically informative or randomly variable awaits further study, although it was employed as a phylogenetic character by Benson (in press).

Anteriorly and laterally to the paracondylar pocket, a bony web separates the jugular foramen from the fenestra ovalis. Although this web is usually referred to as the metotic strut (see review in Sampson & Witmer 2007), we prefer the term crista tuberalis, since the web in extinct reptiles cannot be positively associated with the embryonic metotic cartilage that forms the strut in extant taxa (Gower & Weber 1998; Sampson & Witmer 2007). The crista tuberalis is a thick and extensive web that connects the paroccipital process dorsally with the basal tubera ventrally, and in doing so separates the posterior and lateral walls of the braincase. The crista is formed completely by the exoccipital-opisthotic with no contribution from the prootic; the latter condition, which is abnormal for basal theropods, has been described in *Carcharodontosaurus*, but based on equivocal broken bone surfaces (Brusatte & Sereno 2007).

Only the bases of each paroccipital process are preserved on the specimen, although Hu (1964: pls 1, 2) presented photographs showing a nearly complete left paroccipital process. We will use these photographs to augment our description of the paroccipital processes, even though the extensive left paroccipital process (which appears to be preserved as a separate piece based on the photographs) could not be located during the course of our studies, neither by DJC in the 1990s nor SLB in 2009.

The paroccipital processes extend strongly laterally, ventrally, and posteriorly. Their posteriormost extent is unknown and Hu's (1964) images cannot be of help here, since he did not figure the braincase in dorsal view. However, based on the angle and orientation of the broken bases, the processes would have extended far posteriorly as in carcharodontosaurids (Coria & Currie 2002), *Allosaurus* (Madsen 1976), and *Sinraptor* (Currie & Zhao 1993a). The preserved trend of the processes and Hu's (1964) photographs indicate that these structures were approximately planar and did not exhibit the distal twisting of some coelurosaurs (Currie

1995; Norell *et al.* 2004). Hu's (1964) photo of the braincase in posterior view shows that the paroccipital processes were oriented strongly ventrally, such that their tips terminated below the occipital condyle. This is seen in all allosauroids, as well as a few non-allosauroid basal theropods (e.g., *Ceratosaurus*: Madsen & Welles 2000; *Cryolophosaurus*: Smith *et al.* 2007; see review in Brusatte *et al.* in press). However, *Shaochilong* lacks one feature that has been described as an allosauroid synapomorphy: ventral margins of the bases of the paraoccipital processes positioned ventral to the occipital condyle (see review in Brusatte *et al.* in press). This condition is seen in *Acrocanthosaurus*, *Allosaurus*, and *Sinraptor*, whereas other basal theropods have more dorsally positioned paroccipital processes in which the ventral margins of the bases are level with the midpoint of the condyle (Brusatte *et al.* in press). *Shaochilong* clearly possesses the latter condition. Brusatte *et al.* (in press) regarded *Carcharodontosaurus* as possessing the allosauroid condition, but this was based on a reconstruction of the paroccipital processes on two skulls that are broken in this region (SGM-Din-1; MNN IGU3). Similarly, *Giganotosaurus* is also broken in this region (Coria & Currie 2002). Thus, it may be that some carcharodontosaurids have more dorsally positioned paraoccipital processes, unlike the condition in more basal allosauroids in which the paroccipital processes are web-like and extensive in posterior view due to their ventrally-placed bases.

Although the braincase is extensively pneumatized in general, the broken bases of the paroccipital processes exhibit spongy bone texture in cross section, not the large pneumatic cavities of some coelurosaurs (e.g., Kurzanov 1976; Clark *et al.* 1994; Sues 1997; Makovicky & Norell 1998; Brochu 2003; Norell *et al.* 2004). Pneumaticity is also absent in this region in *Carcharodontosaurus*, despite the otherwise extremely pneumatic nature of the braincase.

Anterior to the crista tuberalis, on that part of the exoccipital-opisthotic that contributes to the lateral wall of the braincase, the fenestra ovalis is visible. This opening faces laterally, as is usual for theropods. Coria & Currie (2002) described the fenestra ovalis of *Carcharodontosaurus* and *Giganotosaurus* as being reoriented relative to the normal theropod condition, such that they are exposed on the posterior surface of the braincase due to an enlargement of the jugular foramen and a repositioning of the crista tuberalis. Brusatte & Sereno (2007) reassessed the braincase of *Carcharodontosaurus* and identified the broken base of the crista tuberalis, which is in the usual position for theropods. They noted that heavy erosion in the fenestra ovalis region makes it appear as if this fenestra faced posteriorly, but that in life the crista tuberalis would have separated it from the occiput as is normal for theropods. Brusatte & Sereno (2007) did not discuss the braincase of *Giganotosaurus*, but the fenestra ovalis region, the base of the paroccipital process, and the crista tuberalis are heavily eroded on both sides, thus making interpretation difficult (MUCPv-CH 1).

However, although Coria & Currie (2002) were incorrect in placing the fenestra ovalis on the occiput in *Carcharodontosaurus* and possibly *Giganotosaurus*, they did correctly and astutely observe that the fenestra ovalis region of carcharodontosaurids is heavily modified relative to other theropods. *Shaochilong* helps clarify the anatomy of this region. In most theropods the fenestra ovalis opens almost entirely laterally, between the exoccipital-opisthotic and prootic, and immediately posterior to the opening for the facial (VII) nerve. This is seen in *Allosaurus* (Madsen 1976) and *Sinraptor* (Currie & Zhao 1993a), along with a range of other theropods (e.g., Welles 1984; Currie 1985, 1995; Charig & Milner 1997; Allain 2002; Sues *et al.* 2002; Xu *et al.* 2002; Brochu 2003; Rauhut 2004a; Sampson & Witmer 2007; Smith *et al.* 2007). In *Shaochilong*, on the other hand, the fenestra ovalis is located entirely within the exoccipital-opisthotic and is placed on the base of the crista tuberalis itself, at the region where the crista and paroccipital process meet. Thus, the fenestra ovalis in *Shaochilong* faces strongly anteriorly as well as laterally, although it is still technically located on the lateral wall of the braincase because it is anterior to the crista. Remarkably, the fenestra ovalis is placed far lateral (approximately 22 mm) to the endocranial cavity, and the two are linked via an elongate, anteromedially-trending bony canal that is completely enclosed by the exoccipital-opisthotic and perhaps medially by the prootic.

It is not clear that this condition is present in *Carcharodontosaurus* and *Giganotosaurus*, but the pattern of breakage in both taxa and the clear lack of a laterally facing fenestra ovalis posterior to the facial nerve opening is strong evidence that this is the case. Indeed, the fenestra ovalis of *Giganotosaurus*, as figured by

Coria & Currie (2002: figs 3, 8) is clearly broken posteriorly, and this broken margin is seen in posterior view as a rounded surface that does appear to open onto the occiput (Coria & Currie 2002: fig. 5). Therefore, it is apparent that the fenestra ovalis of *Giganotosaurus* trends strongly anterior-posterior, instead of medial-lateral as in most theropods. However, the broken surfaces delimit a missing section of the braincase, which appears as a notch in posterior view, between the crista tuberalis and the paroccipital process. Coria & Currie (2002:fig. 5) reconstruct this notch as open, and as a posterior continuation of the fenestra ovalis. However, this notch corresponds exactly to the position of the anteriorly-facing fenestra ovalis in *Shaochilong*. The only difference is that the posterior wall of the fenestra—that section of the braincase linking the crista and the paroccipital process—is completely preserved in *Shaochilong* whereas it is broken in *Giganotosaurus*. We suggest that *Shaochilong* and *Giganotosaurus* have the same condition, and that the fragile posterior wall of the fenestra ovalis has simply been broken in *Giganotosaurus*. This broken wall has been interpreted as a real, posteriorly exposed opening in *Giganotosaurus*, but in life the fenestra would have only opened anteriorly. Thus, Coria & Currie (2002) were correct in noting that the fenestra ovalis is reoriented in carcharodontosaurids, such that it now trends primarily anterior–posterior instead of medial–lateral. However, it is not actually exposed posteriorly. *Carcharodontosaurus* may have a similar condition, but both known braincases are too eroded in this region to be certain. Similarly, the condition in *Acrocanthosaurus* deserves further assessment.

Prootic. The prootic is nearly complete on both sides of the braincase but is somewhat crushed and eroded posteriorly on the left side. Sutures with the laterosphenoid, basisiphenoid, supraoccipital, and, if present, the basioccipital, are obscured by partial fusion. However, the prootic clearly overlaps the exoccipital-opisthotic posteriorly and extends slightly onto the paroccipital process, and the shape of this suture is apparent on both sides. Similarly, the prootic-parietal contact within the dorsal tympanic recess is also clear. The prootic does not participate in the margin of the fenestra ovalis, but rather extends posteriorly to terminate immediately anterodorsal to this opening. This relationship is better seen on the right side, which has been less affected by crushing.

Foramina for the trigeminal (V) and facial (VII) nerves are some of the most conspicuous features of the prootic. The openings are not set into the same fossa, but rather are divided by a stout bar of bone. The trigeminal foramen is positioned anterodorsal to the facial nerve fossa, and both openings are posterior to the level of the apex of nuchal wedge of the supraoccipital and parietal when the braincase is oriented with the frontals held horizontal. This is also seen in *Carcharodontosaurus* and *Giganotosaurus* (Coria & Currie 2002; Brusatte & Sereno 2007, 2008) and may be a result of the posteroventrally sloping occiput that these taxa share with *Shaochilong* and *Sinraptor*. In *Sinraptor* the trigeminal (V) foramen is located approximately ventral to the apex of the supraoccipital tuberosity (Currie & Zhao 1993a: fig. 7B), but in allosauroids that have ventrally sloping occiputs (the usual condition among theropods), such as *Acrocanthosaurus* (Franzosa & Rowe 2005) and *Allosaurus* (Madsen 1976), both openings (V and VII) are positioned anterior to the supraoccipital tuberosity (Coria & Currie 2002).

The prootic forms the anterior, dorsal, and ventral borders of the facial nerve fossa; the posterior border is formed by the exoccipital-opisthotic. There are two separate foramina for the facial nerve, both set into the same triangular fossa and one positioned anterodorsal to the other. The more dorsal opening is for the hyomandibular branch and the ventral foramen is for the palatine branch (Franzosa & Rowe 2005). A series of distinct and deep grooves continues posteriorly and dorsally from the facial fossa. The most dorsal groove of the series is the deepest and most elongate; it trends dorsally, posteriorly, and laterally towards the fenestra ovalis and would have transmitted the hyomandibular branch of the facial nerve after it emerged from the braincase. However, the groove does not enter the fenestra ovalis, but rather is separated from it by the raised anterior rim of the fenestra. The series of grooves is demarcated dorsally by the otosphenoidal crest, a thin ridge of bone that continues posteriorly onto the exoccipital-opisthotic to form the dorsal rim of the fenestra ovalis and, ventral to the facial fossa, curves ventrally and posteriorly to become confluent with the posterior edge of the preotic pendant. Thus, the facial fossa is located within the confines of the otosphenoidal crest, as in other theropods (Sampson & Witmer 2007) and would have been part of the middle ear space. Multiple

openings for the facial nerve are rarely seen in theropods, but have been described in *Acrocanthosaurus* (Franzosa & Rowe 2005). Additionally, they appear to be present in *Giganotosaurus* but were not figured by Coria & Currie (2002: fig. 8), as the region of the second opening, anteroventral to the first, was obscured in anteroventrolateral view (MUCPv-CH 1, RBJB pers. obs.). The two foramina of *Giganotosaurus* and *Shaochilong* are close together and set within the same fossa, whereas they are more widely spaced and apparently located on different bones (the prootic and the basisphenoid) in *Acrocanthosaurus* (Franzosa & Rowe 2005).

Only a single opening for the trigeminal nerve is present on each side of the braincase. Some allosauroids possess multiple openings, or partially divided foramina, but this may be variable within taxa (Brusatte & Sereno 2007, 2008). In the genus *Carcharodontosaurus*, for instance, *C. saharicus* has a single opening whereas *C. iguidensis* shows a 'binocular'-shaped opening that may indicate incipient division (Brusatte & Sereno 2007). Additionally, Brusatte & Sereno (2008) described a single foramen in one specimen of *Acrocanthosaurus* (OMNH 10146) and two foramina in another specimen (NCSM 14345). However, direct observation of NCSM 14345 reveals that only a single foramen is present, and thus there is no variability within *Acrocanthosaurus*. The trigeminal foramen is usually shared between the prootic and laterosphenoid in most theropods, and this appears to be the case in *Shaochilong*. Although a clear suture is not present, a raised and rugose margin that may represent a heavily fused suture extends dorsally and posteriorly from the posterodorsal corner of the trigeminal foramen. Ventral to this suture, and extending across what is presumably the laterosphenoid, is a deep depression that trends anterodorsally. This is most likely a groove for the ophthalmic branch of the trigeminal nerve, as is common in theropods generally (Sampson & Witmer 2007). Above the groove, and along the presumed prootic-laterosphenoid suture, is a rugose surface that corresponds to the epipterygoid articular facet in *Majungasaurus* and other well described theropod braincases (Sampson & Witmer 2007).

Dorsally, above the facial and trigeminal foramina and separated from them by a thick bar of bone, is a deep dorsal tympanic recess. This structure in *Shaochilong* is remarkably deep and more extensive than in any basal theropod we have ever seen, as well as most coelurosaurs we have examined. It extends onto the parietal and is overhung dorsally by a web of bone that projects ventrally from the parietal. A depression in this region is present in many theropods and is often referred to as a dorsal tympanic recess (Rauhut 2004a), a structure that is present in living birds. However, it is possible that this depression may be apnuematic in some taxa, and instead may house jaw musculature (Sampson & Witmer 2007). Indeed, it is located within the temporal region of the braincase and is separated from the lateral wall of the braincase by the stout bar of the parietal above the trigeminal and facial openings. However, as discussed by Rauhut (2004a), this depression is clearly pneumatic in *Shaochilong*, as its anterodorsal corner is penetrated by an enormous pneumatopore on each side of the braincase. The better preserved right pneumatopore is circular, with a diameter of nine millimetres. Pneumatopores such as these are unknown in other basal theropods, and indeed may only otherwise be present in birds, where they are smaller and less distinct (Rauhut 2004a). Thus, they are considered an autapomorphy of *Shaochilong* among basal, non-coelurosaurian theropods.

Laterosphenoid. Much of the anterior region of the laterosphenoid is missing on both sides, including the capitate process that contacts the postorbital and the far anterior margin that contacts the frontal. However, a good portion of the posterior part of the laterosphenoid is present. This bone likely forms the anterior margin of the trigeminal foramen and contributes to some or all of the more anterior cranial nerve openings (II, III, IV, VI). However, as some or all of these are also formed by the orbitosphenoid, they are discussed in a single section below.

The posterior portion of the antotic crest—a thick ridge that separates the orbital space anteriorly from the temporal musculature space dorsally (Sampson & Witmer 2007)—is preserved. The crest arises anterodorsal to the trigeminal nerve opening, and its presence is persuasive evidence that this part of the braincase pertains to the laterosphenoid, as only this bone forms the antotic crest in other well described theropods (e.g., *Majungasaurus*: Sampson & Witmer 2007). However, unlike *Majungasaurus*, the antotic crest is not essentially continuous with the more posterior otosphenoidal crest. Instead, the two crests are separated by a

smooth and broad fossa that houses the trigeminal foramen. Posterior to this fossa the otosphenoidal crest curves ventrally and posteriorly to become confluent with the posterior margin of the preotic pendant. The base of the antotic crest is thick, suggesting that it was a stout and prominent structure. Prominent crests are also seen in *Acrocanthosaurus* (OMNH 10146), *Carcharodontosaurus* (SGM-Din-1), and *Giganotosaurus* (Coria & Currie 2002), whereas they are thinner and less offset laterally in *Allosaurus* and *Sinraptor* (Sampson & Witmer 2007). This may reflect increased attachment area for jaw adductor musculature more ventrally within the temporal space in carcharodontosaurids, as these taxa have reduced attachment sites on the dorsal surface of the frontal. However, the autapomorphic sagittal crest of *Shaochilong* suggests that the adductors did anchor firmly to the dorsal surface of the frontal, despite the fact that the supratemporal fossa is reduced in size.

Orbitosphenoid. Parts of the orbitosphenoid are clearly present in the vicinity of the pituitary fossa and interorbital region, but sutures with the surrounding bones (laterosphenoid, prootic, basisphenoid) are entirely obliterated. The orbitosphenoids are broken anterior to the openings for the optic (II) nerve but would have extended further anteriorly and dorsally to cup the olfactory bulbs, as shown by rugose attachment scars on the ventral surface of the frontal (see above). The suture with the laterosphenoid probably would have been in the region of the openings for the oculomotor (III) and trochlear (IV) nerves, based on the condition in other theropods (Brusatte & Sereno 2007; Sampson & Witmer 2007). However, the various cranial nerve openings and other foramina and fossae of this region are described together here.

The assorted endocranial structures of this area are divided into two general regions: the pituitary fossa posteriorly (including foramina for nerve VI) and the interorbital region anteriorly (including foramina for nerves II, III, IV). The hypophyseal fenestra itself is not visible since the interorbital septum is unossified (see below), but a depression for the pituitary is present posteriorly. Openings for the abducens (VI) nerve are located within this depression, not lateral to it as in many coelurosaurs (Currie 1997). There is no prominent midline ridge between the left and right abducens foramina; a ridge is present in most theropods, including *Allosaurus* and *Sinraptor*, but is absent in *Carcharodontosaurus* and *Giganotosaurus* (Coria & Currie 2002). Foramina for the optic (II) and oculomotor (III) nerves appear to be similar in size. These are placed next to each other, with the optic foramen anterior to the oculomotor foramen, on the midline. The foramina for the trochlear (IV) nerves are much smaller than those for the optic and oculomotor nerves, and are more widely separated on the midline. Anterior to the trochlear foramen is a small opening whose function is unknown; it has also been identified in *Giganotosaurus* (Coria & Currie 2002: fig. 8). It is not clear if there is a single midline opening for both left and right optic nerves or if there were separate foramina, since the interorbital septum that forms the midline of the braincase here is unossified. This condition is variable in allosauroids and is likely correlated with the ossification of the septum, as carcharodontosaurids with a bony septum have separate openings and those allosauroids with a cartilaginous or membraneous septum have a single foramen (Franzosa & Rowe 2005).

Sphenethmoid, Mesethmoid, and Interorbital Septum. None of these various structures are present as ossified elements in *Shaochilong*. However, as they are frequently discussed in the literature and are an important character in allosauroid phylogeny, they deserve to be discussed further. Furthermore, these structures are often confused in the literature, as different structures are often referred to under the same umbrella term or referred to using misleading or incorrect terms (Ali *et al.* 2008).

The interorbital septum is a parasagittal sheet oriented along the midline of the braincase that connects the cultriform process of parabasisphenoid ventrally to the sphenethmoid dorsally. It is part of a larger sagittal membrane, which stretches to the tip of the snout, and is usually cartilaginous or membraneous in most archosaurs (Sampson & Witmer 2007). This is the case in most theropods, including *Allosaurus* and *Sinraptor* (Currie & Zhao 1993a; Coria & Currie 2002; Brusatte & Sereno 2008). However, *Carcharodontosaurus* and *Giganotosaurus*, as well as some other large theropods (e.g., *Majungasaurus*: Sampson & Witmer 2007), have ossified or otherwise mineralized this sheet. *Acrocanthosaurus* is usually regarded as having an unossified septum (e.g., Coria & Currie 2002; Brusatte & Sereno 2008), but this region of the braincase is more extensively ossified than in other theropods and a bony septum may have been present and subsequently

eroded in the two known braincases, as small parts remain in both specimens, particularly NCSM 14345. The ossified septum is undoubtedly absent in *Shaochilong*, as the region between the optic, oculomotor, and abducens foramina is clearly open on the midline. Although a narrow strut of bone could have divided these foramina on the midline, there is no thick, broken base of the septum, which would be present if the septum was ossified in life but eroded away (e.g., Coria & Currie 2002; Sampson & Witmer 2007).

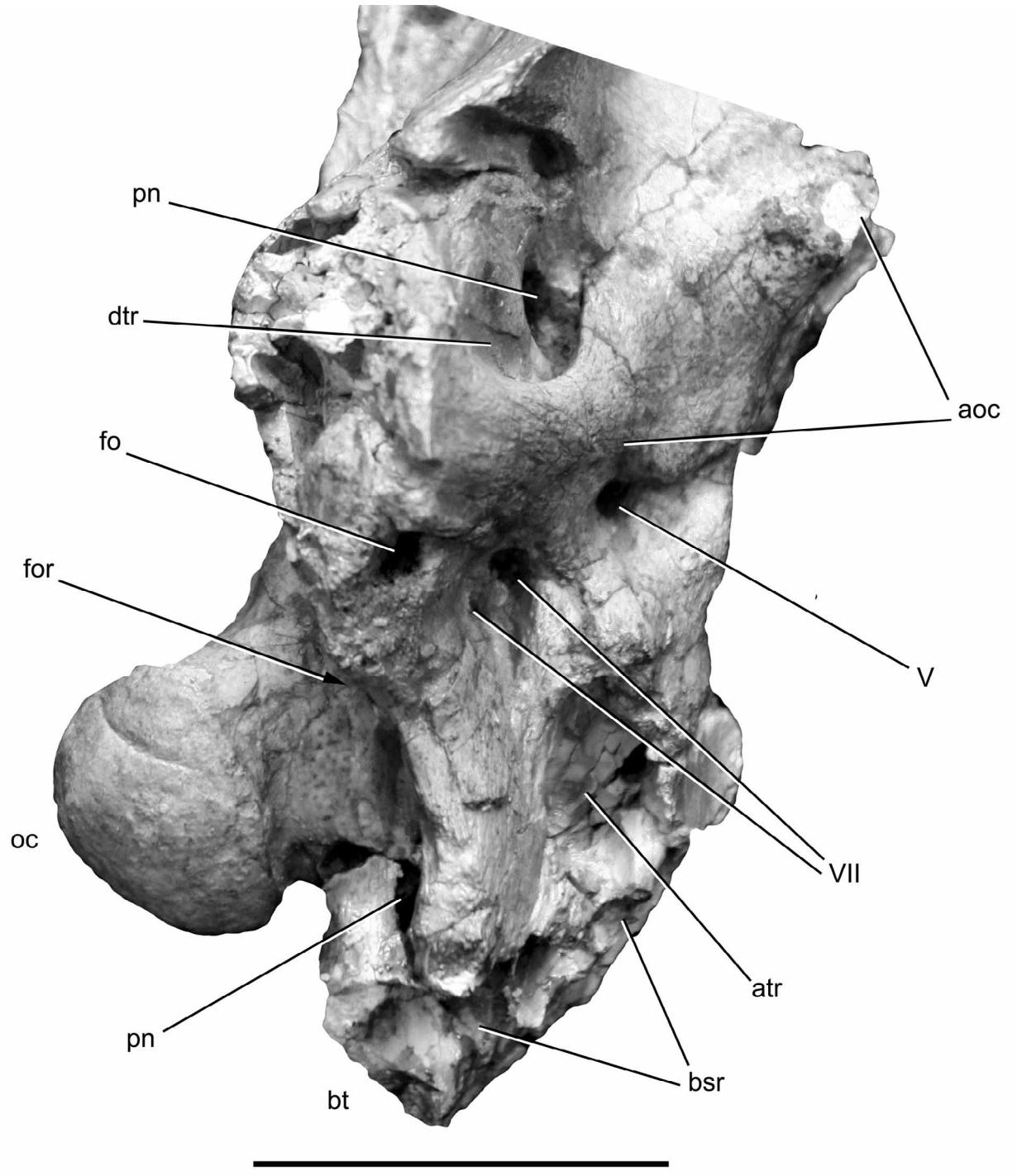

FIGURE 11. Photograph of the braincase of *Shaochilong maortuensis* (IVPP V2885.1) in right lateral view. Abbreviations: **aoc**, antotic crest; **atr**, anterior tympanic recess; **bsr**, basisphenoid recess; **bt**, basal tubera; **dtr**, dorsal tympanic recess; **fo**, fenestra ovalis; **for**, paracondylar openings representing jugal foramen and foramen for nerve XII; **oc**, occipital condyle; **pn**, pneumatic foramen (pneumatopore). Roman numerals refer to cranial nerves. Arrowhead indicates position of foramen (which is hidden in lateral view). Scale bar equals 5 cm.

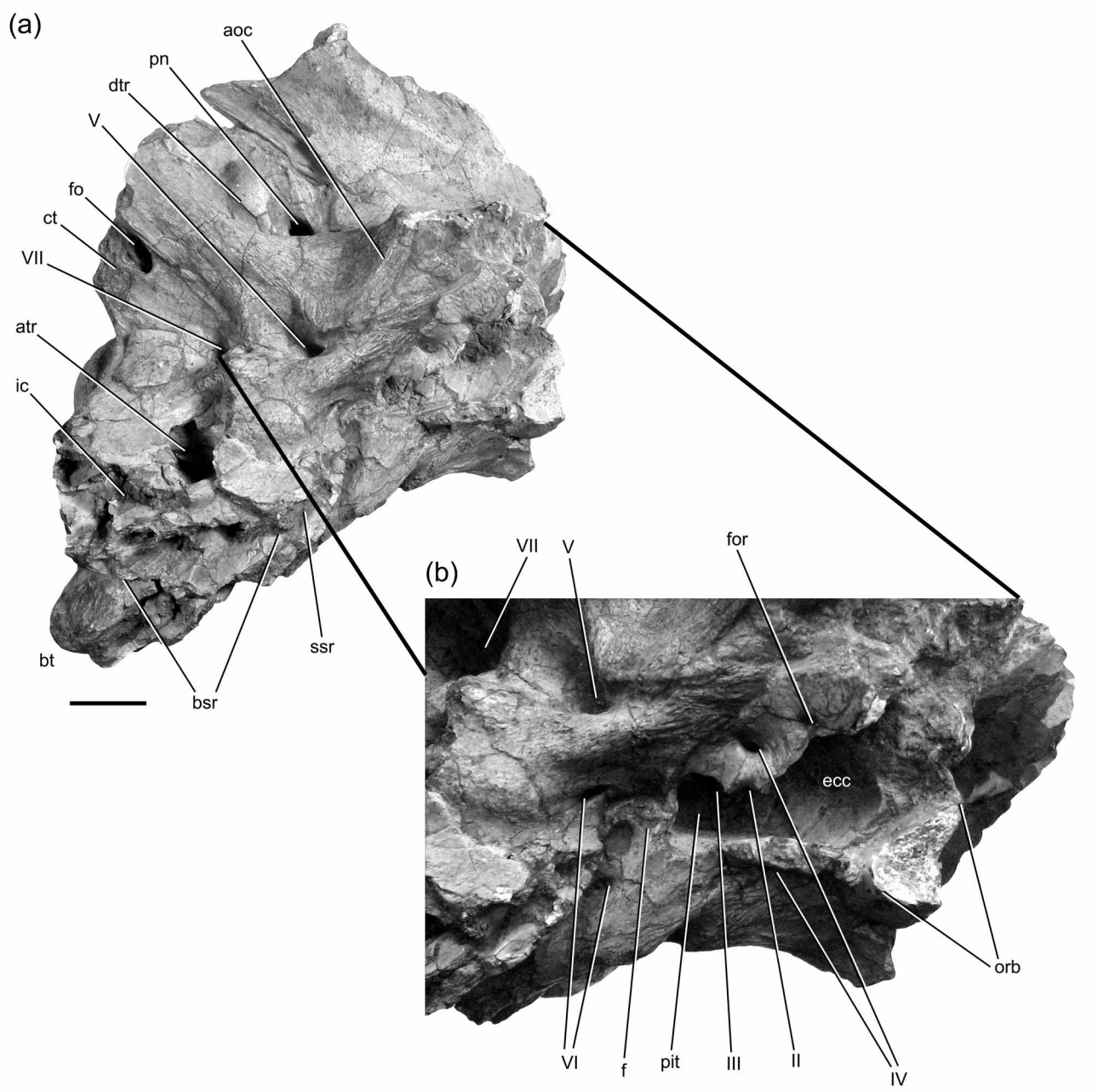

FIGURE 12. Photographs of the braincase of *Shaochilong maortuensis* (IVPP V2885.1) in right lateral oblique views, including a complete photograph (a) and a closeup of the anterior pituitary region (b). Abbreviations: **aoc**, antotic crest; **atr**, anterior tympanic recess; **bsr**, basisphenoid recess; **bt**, basal tubera; **ct**, crista tuberalis (=metotic strut); **dtr**, dorsal tympanic recess; **ecc**, endocranial canal; **f**, fossa; **fo**, fenestra ovalis; **for**, foramen; **ic**, internal carotid entrance; **pit**, pituitary fossa; **pn**, pneumatic foramen (pneumatopore); **orb**, orbitosphenoid articulation scar; **ssr**, subsellar recess. Roman numerals refer to cranial nerves. Scale bar equals 5 cm and refers to image (a) only.

Shaochilong also appears to lack an ossified sphenethmoid (Fig. 6). This bone, located at the junction of the orbital and nasal cavities and usually ventral to the frontal, is a trough-like element that encloses the olfactory bulbs ventrally and anteriorly (Sampson & Witmer 2007; see Ali *et al.* [2008] for review of homologies). It is often associated with a second ossification, termed the mesethmoid, which extends dorsally from the sphenethmoid trough to divide the olfactory tracts and bulbs on the midline (Ali *et al.* 2008). The mesethmoid is sometimes considered to be an extension of the ossified interorbital septum (e.g., Sampson & Witmer 2007), but Ali *et al.* (2008) argue that it is a separate ossification that should be given its own name.

The presence of both the sphenethmoid and mesethmoid can be inferred from the shape of the braincase attachment scars on the ventral surface of the frontal. In particular, a midline scar between the olfactory tracts is strong evidence for an ossified mesethmoid, whereas curved scars that extend lateral and anterior to the olfactory bulb depressions indicate an ossified sphenethmoid. In *Shaochilong* only scars for the orbitosphenoid are present on the frontal; these are crescentic surfaces that extend to only midlength of the olfactory bulb depression. Midline scars or sutural surfaces anterior to the olfactory bulbs are absent. This is also the case in *Allosaurus* and *Sinraptor*, and *Eocarcharia* (Sereno & Brusatte 2008), whereas other carcharodontosaurids (including *Acrocanthosaurus*: Stovall & Langston 1950; Sereno & Brusatte 2008) have ossified sphenethmoids and mesethmoids. This is well shown in *Carcharodontosaurus* (Fig. 6; MNN IGU3), in which a raised midline rim between the olfactory bulb depressions is the attachment site for the mesethmoid, and a large, rugose, C-shaped scar anterior to the bulb depressions is the articular surface for the sphenethmoid.

Axis. The axis (IVPP V2885.5) is generally well preserved but is missing the anterior portion of the centrum, parts of the anterior and dorsal regions of the neural spine, and the lateral edges of the epipophyses (Fig. 13). The entire axis is 145 mm tall dorsoventrally. The centrum is 57 mm long anteroposteriorly along its complete and uneroded dorsal margin, immediately ventral to where the centrum and neural arch are firmly fused, obliterating the neurocentral suture. The anterior articular surface of the centrum is eroded but it appears to have been approximately circular, with a reconstructed diameter of 51 mm. The posterior surface is also eroded but was clearly a dorsoventrally elongate oval, with a reconstructed depth of 53 mm and width of 34 mm. Details of the anterior surface are unclear, but preserved regions of the posterior surface indicate that it was shallowly concave. Some broken surfaces reveal what appears to be camellate internal bone structure, as has been described in other carcharodontosaurians (Harris 1998; Brusatte & Sereno 2008).

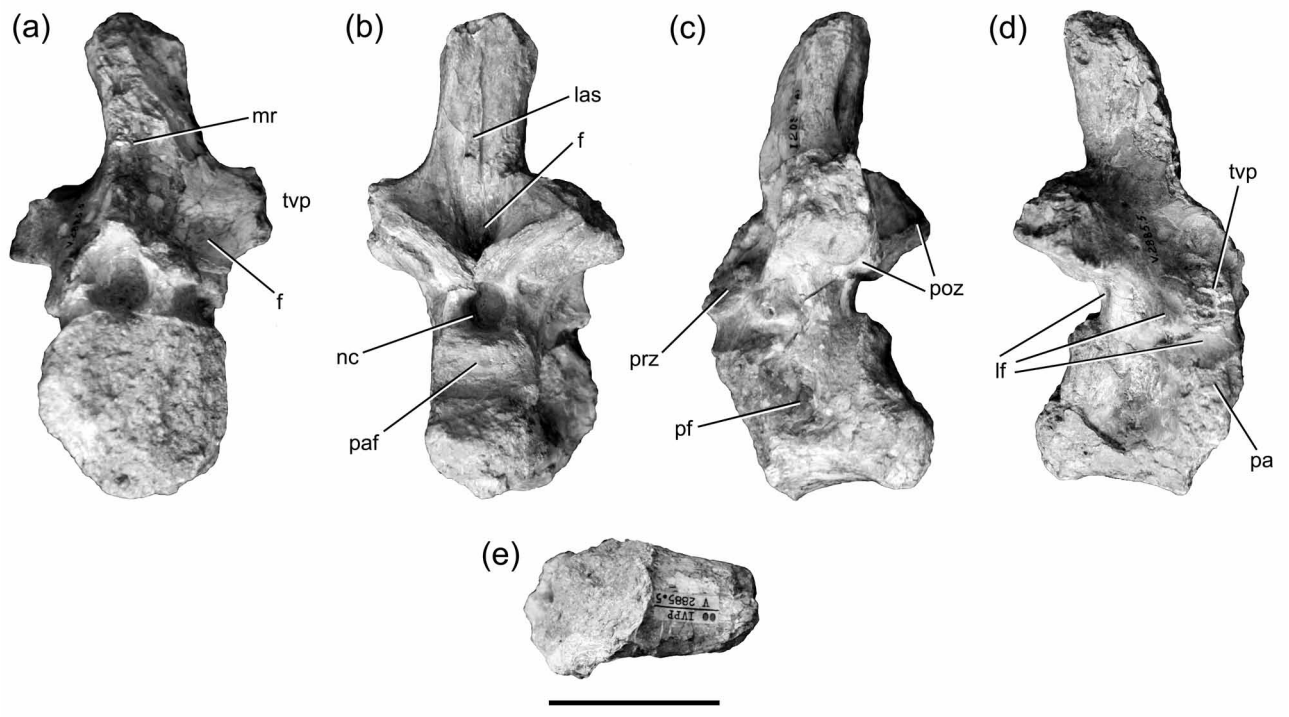

FIGURE 13. Photographs of the axis of *Shaochilong maortuensis* (IVPP V2885.5) in anterior (a), posterior (b), left lateral (c), right lateral (d), and ventral (e) views. Abbreviations: **f**, fossa; **las**, ligament attachment site; **lf**, lateral fossae; **mr**, medial ridge; **nc**, neural canal; **pa**, parapophysis; **paf**, posterior articular surface; **pf**, pneumatic fossa; **poz**, postzygapophysis; **prz**, prezygapophysis; **tvp**, transverse process. Scale bar equals 5 cm.

Two proportional characters of the axial centrum are unusual in *Shaochilong*. First, an ovoid posterior articular surface is rare among allosauroids. *Allosaurus* (Madsen 1976), *Giganotosaurus* (MUCPv-CH-1), and

Sinraptor (Currie & Zhao 1993a) all possess nearly circular posterior surfaces. Brusatte *et al.* (2008: 22) described the posterior articular surface of *Acrocanthosaurus* as "substantially higher…than wide," citing Harris (1998) as justification. However, the table of vertebral measurements provided by Harris (1998) unequivocally shows the posterior surface to be circular. The only other allosauroid with an ovoid posterior surface is the basal neovenatorid carcharodontosaurian *Neovenator* (Brusatte *et al.* 2008). Second, shortened axes, with centra that are approximately as long as tall, are present in the derived carcharodontosaurids *Acrocanthosaurus* (Harris 1998) and *Giganotosaurus* (MUCPv-CH-1), but not *Neovenator* (Brusatte *et al.* 2008) or the basal allosauroids *Allosaurus* (Madsen 1976) and *Sinraptor* (Currie & Zhao 1993a). Molnar *et al.* (1990) suggested, based on this latter character, that *Shaochilong* may belong to Tyrannosauridae, as a shortened axis is seen in *Daspletosaurus*, *Tarbosaurus*, and *Tyrannosaurus*. However, the elongate axes of basal allosauroids and tyrannosauroids (e.g., *Dilong*: IVPP V14243; *Alioramus*: Brusatte *et al*. 2009b) suggests that this character evolved independently in the two groups. It is interesting that a shortened axis is mostly seen in derived, fairly large-bodied members of each clade, and may be related to the biomechanical constraints of large body size.

The ventral surface of the axial centrum is smooth and lacks a ventral keel or ridge. A low ventral axial ridge (often referred to as a "keel") is present in carcharodontosaurids such as *Acrocanthosaurus* (Harris 1998) and *Giganotosaurus* (MUCPv-CH-1), and more prominent keels are present among non-tetanuran theropods (e.g., *Ceratosaurus*, *Dilophosaurus*: see review in Brusatte *et al*. 2008). However, the ventral surface of the axis is rounded in *Allosaurus* and *Sinraptor* (Brusatte & Sereno 2008) and only a subtle ridge is present in the the neovenatorid carcharodontosaurian *Neovenator* (Brusatte *et al.* 2008). The lateral surface of the axial centrum of *Shaochilong* is deeply depressed by a smooth fossa, which is excavated by a single large pneumatic foramen ("pleurocoel") at its midpoint.

The neural arch is well preserved. The neural spine is extensive: it is 85 mm tall dorsoventrally as preserved and 31 mm wide mediolaterally at its base. It is inclined posterodorsally (contra Hu 1964) and appears to maintain a relatively constant width dorsally until it terminates at a broken margin. The dorsal tip of the spine is too eroded to determine the presence or absence of "crown-like" projections that are seen in some theropods, especially tyrannosaurids (e.g., Brochu 2003). The anterior surface of the neural spine is ornamented with a rugose midline ridge, a common feature of theropods that is likely an attachment site for the splenius capitis musculature (Brochu 2003). In *Shaochilong* the ridge is eroded anteriorly but was clearly robust. On either side of this ridge the anterior surface of the neural arch is apneumatic, and lacks the deep pneumatic pockets that are present in some large tyrannosaurids (e.g., Brochu 2003). Similarly, the small pneumatic foramina described in *Acrocanthosaurus* (Harris 1998) and *Neovenator* (Brusatte *et al.* 2008), and also present in *Giganotosaurus* (MUCPv-CH-1), appear to be absent. However, this apparent absence could result from breakage along the anterior portion of the neural arch, as there is a shallow fossa, located anteriorly on the dorsolateral surface of the arch and most clearly visible on the left side, that may be pneumatic. The posterior surface of the neural spine is deeply concave. This concavity is deepest ventrally, where it forms an invaginated pocket, but shallows as it continues dorsally. Within the fossa is a dorsoventrally elongate, thick (5 mm mediolaterally), and rugose ligament attachment scar that trends across the entire height of the neural spine.

Only the left prezygapophysis is preserved. It has a flat, circular (18 mm diameter) articular facet that is barely offset from the remainder of the neural arch. The facet is located at the anteroventral corner of the neural arch and faces laterally but also slightly dorsally and anteriorly. The parapophysis is located at the anterodorsal corner of the lateral surface of the centrum, but is only visible as a heavily eroded region on the right side. The diapophysis is placed at the end of a short and indistinct transverse process, which projects straight ventrally as a small bulge. Ventral and medial to the transverse process, and partially covered by it in lateral view, is a shallow ovoid fossa that trends anterodorsally-posteroventrally. Posterior to this depression is a much deeper, triangular fossa that faces laterally and slightly posteriorly. Posterior to this second fossa, and separated from it by a 10 mm long upraised margin, is a smaller and shallower depression. This third fossa is ovoid, with a transversely oriented long axis, and faces strongly posteriorly and slightly laterally. This fossa is

immediately anteroventral to the postzygapophysis. It is unclear if these fossae are homologous to the infraprezygapophyseal, infradiapophyseal, and infrapostzygapophyseal fossae of other theropods (Wilson 1999), as individual bounding laminae are not clear due to poor preservation.

Each postzygapophysis has a large, flat facet that approximates the shape of a triangle with rounded margins. Each dimension of the rounded triangle is 30 mm long. The facet faces strongly ventrally but also slightly laterally. The base of the epipophysis is preserved on each side. Although both epipophyses are mostly broken it is clear that these structures were robust, pronounced processes that perpendicularly diverged from the neural spine in anterior and posterior views and protruded posteriorly past the postzygapophyses.

Caudal Vertebrae. Hu (1964) stated that six caudal vertebrae were present, three anterior caudals (IVPP V2885.6) and three middle caudals (IVPP V2885.7). Two of these, one anterior caudal and one middle caudal, were figured (Hu 1964: fig. 12). Chure (2000) could only locate five of these during the course of his study, and SLB could only locate four when accessing the specimen again in January 2009 (Figs 14, 15). Strangely, each one of these was labeled as IVPP V2885.7, although one of them (which appears to be an anterior caudal) did not have a label written on it and was simply included in a box with the "middle caudal" (IVPP V2885.7) label. Thus, this is almost certainly one of the anterior caudals (IVPP V2885.6). Therefore, it is clear that the anterior caudal figured by Hu (1964: fig.12a) is missing, as is a second anterior caudal.

The four remaining vertebrae do not form a continuous series but can be placed in a relative sequence based on their size and morphology. The anteriormost caudal (referred to as "caudal A" here), which is the only remaining anterior caudal (IVPP V2885.6), has a centrum that is 72 mm long anteroposteriorly (Fig. 14a–f). The anterior surface is deeper (59 mm) than wide (47 mm), as is the posterior surface (55 mm high, 50 mm wide). Both surfaces are shallowly concave and the centrum is rounded ventrally, lacking a ridge or groove. However, the posterolateral corners of the centrum project somewhat ventrally to articulate with the chevrons. There is a small but discrete depression on each lateral surface of the centrum. On the left side the depression is an ovoid, shallow fossa (15 mm long anteroposteriorly by 6 mm deep dorsoventrally), but whether it contains any foramina is unclear due to weathering. On the right side there is a single, circular (5 mm diameter) opening located within an ovoid fossa. As the depression and foramen are located immediately ventral to the transverse processes, and penetrate the neural arch, they are unlikely to be homologous with the "pleurocoels" (pneumatic foramina) of the cervical and dorsal vertebral centra of most theropods (Sereno *et al.* 2008; O'Connor 2009; Wedel 2009), which are also present in the caudal centra in some allosauroids and other basal theropods (Stromer 1931; Britt 1991; Calvo *et al.* 2004; Sereno *et al.* 2008). However, left-right asymmetry suggests the possibility of a pneumatic origin, perhaps homologous with foramina that are present within the infradiapophyseal fossa of some theropod dorsal vertebrae, which correspond in position. However, this caudal vertebra of *Shaochilong* lacks neural arch laminae ventral to the transverse process that commonly delimit the infradiapophyseal fossa. Furthermore, infraprezygapophyseal and infrapostzygapophyseal fossae, which are usually located anterior and posterior to the infradiapophyseal fossa, are absent. It is possible that the foramen on the right side of IVPP V.2885.6 represents a nutrient foramen, but such non-pneumatic foramina in theropod vertebrae are usually only on the order of 1 mm in diameter (RBJB pers. obs.). Therefore, it is difficult to say with certainty whether the lateral depressions and foramen of IVPP V.2885.6 were formed by pneumatic diverticulae.

The centrum and neural arch are fused but the interdigitating neurocentral suture between them is still partially visible. Only the bases of the transverse processes are preserved, but their thick cross sections (14 mm deep dorsoventrally) indicate that the processes were quite large in life. The trend of the broken base indicates that the processes extended laterally and posteriorly. The dorsal surface of the transverse process, at the point where it diverges from the arch, is indented with a smooth, deep, and broad fossa. None of the zygapophyses are preserved. The neural spine is present and is displaced posteriorly, such that its posterior margin is level with the posterior margin of the centrum but its anterior margin is located 12 mm behind the anterior face of the centrum. The spine is broken dorsally but is 46 mm long anteroposteriorly by 16 mm wide mediolaterally at its base.

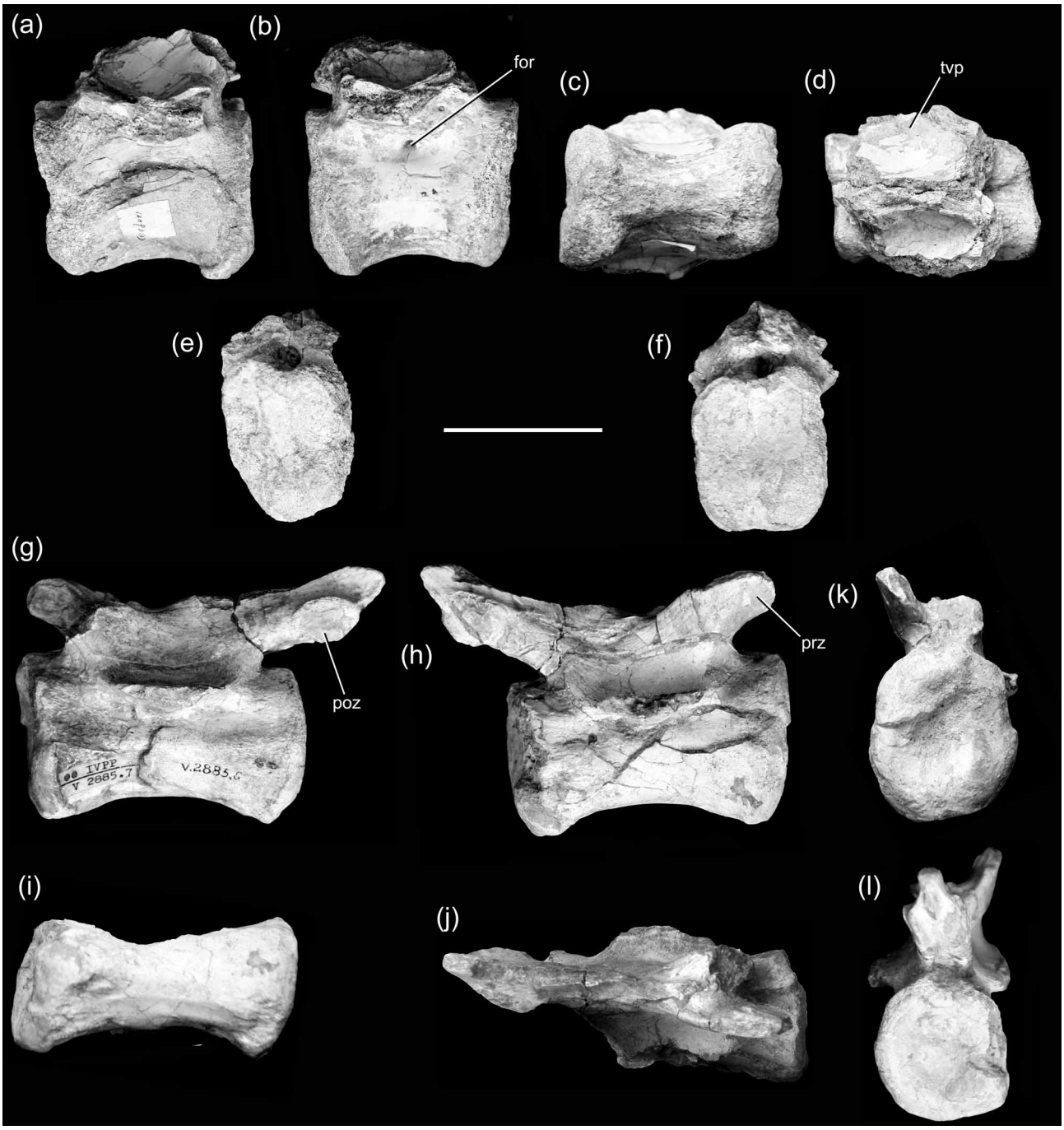

FIGURE 14. Photographs of an anterior caudal vertebra (a–f: caudal A, IVPP V2885.6,) and a posterior caudal vertebra (g–l: caudal B, IVPP V2885.7) of *Shaochilong maortuensis* in left lateral (a, g), right lateral (b, h), ventral (c, i), dorsal (d, j), anterior (e, k), and posterior (f, l) views. Abbreviations: **for**, foramen; **poz**, postzygapophysis; **prz**, prezygapophysis; **tvp**, transverse process. Scale bar equals 5 cm.

The second remaining caudal vertebra ("caudal B") is that figured by Hu (1964: fig. 12b), and belongs to IVPP V2885.7 (Fig. 14g–h). The centrum is 85 mm long, the strongly concave posterior face is deeper (50 mm) than wide (45 mm), and the more shallowly concave anterior face is also deeper (53 mm) than wide (45 mm). The ventral surface is smooth, without any keel or groove, and the lateral surfaces do not contain any fossae or foramina. Only the bases of the transverse processes are preserved, and these are thin (7 mm deep) and project straight laterally. There are no laminae linking the transverse process and centrum ventrally and there is only a shallow fossa on the dorsal surface of the base of the process. The neural spine is centrally

located on the centrum and is reduced to a small bulge between the zygapophyses. The postzygapophyses extend 25 mm past the centrum posteriorly and project posterodorsally. The articular facets are flat, ovoid (20 mm long by 15 mm deep), and face strongly laterally and slightly ventrally. A flange continues past the articular facets posteriorly, and in this region there is a midline ridge between the two facets, which is robust in dorsal view. The prezygapophyses do not extend past the centrum anteriorly, but rather terminate 5 mm posterior to the anterior face. The two prezygapophyses diverge laterally, and together they clasp the postzygapophyses of the preceding vertebrae, which together form a single wedge. The prezygapophyseal facet is only preserved on the right side; is is flat, faces strongly medially and slightly dorsally, and is somewhat smaller than the postzygapophyseal facets.

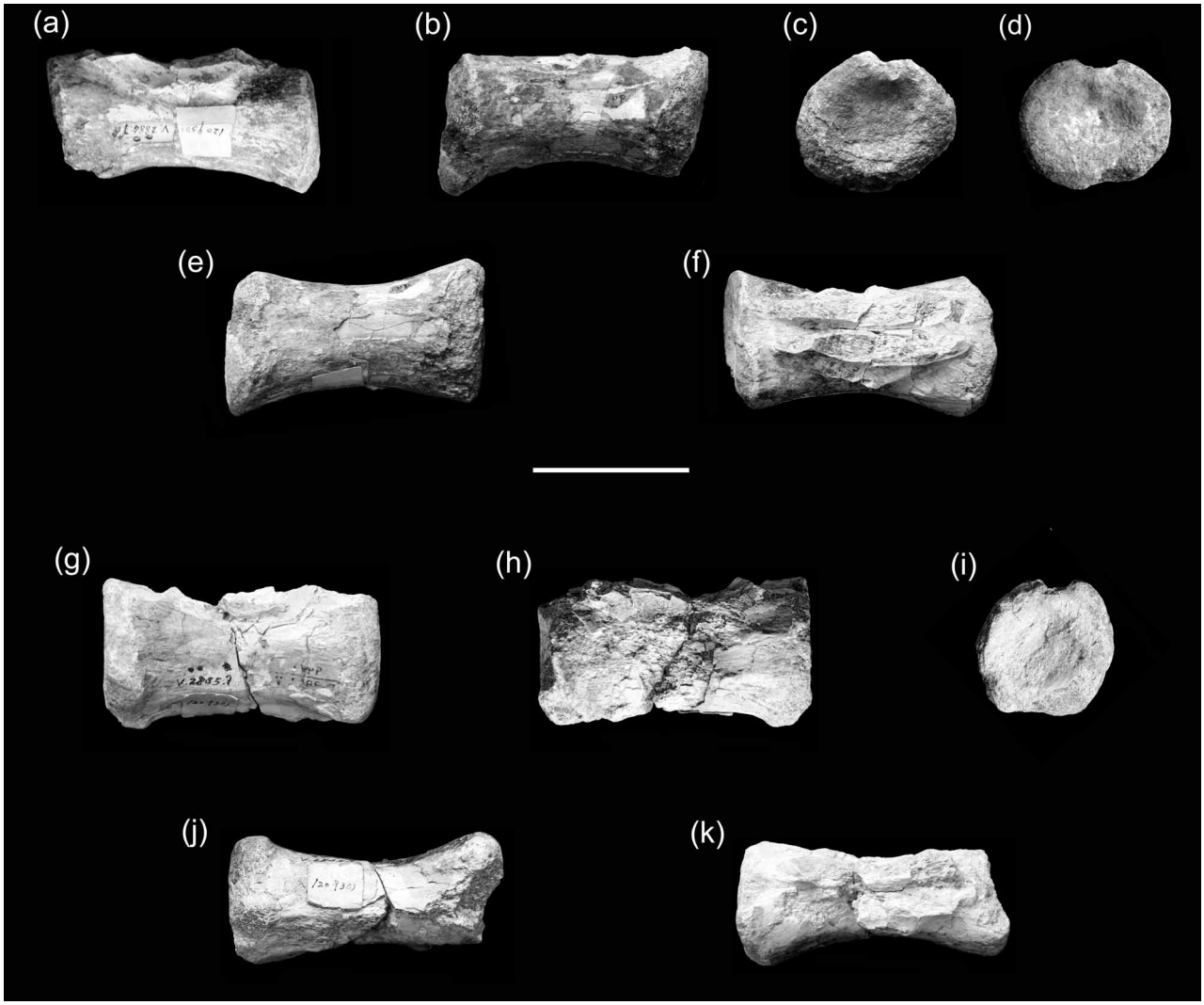

FIGURE 15. Photographs of two posterior caudal vertebrae, caudal C (a–f) and caudal D (g–k), of *Shaochilong maortuensis* (IVPP V2885.7) in left lateral (a, g), right lateral (b, h), anterior (c, i), posterior (d), ventral (e, j), and dorsal (f, k) views. Scale bar equals 5 cm.

Finally, two distal caudals also belong to IVPP V2885.7 (Fig. 15), and are referred to as caudals C and D, respectively. The first is 85 mm long, with shallowly concave anterior (40 mm deep by 47 mm wide) and posterior (40 by 50 mm) faces. The second is 90 mm long, also with shallowly concave anterior (44 by 43 mm) and posterior (44 by 38 mm) faces. The ventral surface of the first centrum is smooth, whereas that of the second has a very slight, anteroposteriorly elongate, rectangular groove. The neural arch is not preserved on either caudal but articular scars for the arch are present on each centrum. Thus, it is unclear whether these vertebrae are anterior or posterior to the "transition point," where theropod caudals lose their transverse

processes and neural spines. The posterior face of each centrum extends ventrally relative to the anterior face to brace the centrum.

Discussion

Body Size and Maturity of the Lectotype. The lectotype series of *Shaochilong* appears to belong to a mature, or near mature, individual. The interfrontal, frontal-parietal, and most braincase sutures are closed and obscured by fusion. However, although this type of fusion is often held as a sign of maturity in dinosaurs (e.g., Sereno & Brusatte 2008), the ontogenetic sequence of theropod cranial suture fusion has yet to be studied in a rigorous manner. Similarly, the caudal vertebrae and axis of *Shaochilong* have fully fused centra and neural arches, which is often considered a sign of maturity in archosaurs (Brochu 1996), although the ontogenetic timing of these changes is variable among taxa (Irmis 2007). Despite this uncertainty, we consider the lectotype series to represent an adult or near-adult individual, but it is possible that the specimen was not fully grown.

It is difficult to estimate the body size (total body length and mass) in *Shaochilong*, as the lectotype series is incomplete and lacks all of the appendicular elements (e.g., femur, tibia, fibula) that are commonly used as body mass estimators (e.g., Anderson *et al.* 1985; Christiansen & Farina 2004). Length of the maxillary tooth row may give a reasonable estimate of body mass, because in other large theropods (tyrannosaurids: Currie 2003b) the tooth row scales isometrically with femur length, which is a confident body mass predictor (Christiansen & Farina 2004). The maxillary tooth row of *Shaochilong* is 255 millimetres in length, approximately 65–75% of the tooth row length in adult specimens of *Allosaurus* (e.g., Madsen 1976) and *Sinraptor* (e.g., Currie & Zhao 1993a), 60% of the length in the carcharodontosaurid *Eocarcharia* (Sereno & Brusatte 2008), and only 40% of the length in the colossal carcharodontosaurid *Acrocanthosaurus* (NCSM 14345; Eddy 2008). Thus, *Shaochilong* was likely about 70% of the total length of *Allosaurus* and *Sinraptor*, both of which are known from complete skeletons in the 7–9 metre range, giving it an estimated length of approximately 5–6 metres. The estimated femur length of *Shaochilong* is approximately 615 mm, resulting in a body mass estimate of 500 kg based on equations presented by Christiansen & Farina (2004). This is substantially smaller than the 1620–1700 kg mass predicted for *Allosaurus* and *Sinraptor*, and much smaller than the masses of monstrous carcharodontosaurids such as *Acrocanthosaurus*, which may have reached over 5000 kilograms (based on femur measurements given by Currie & Carpenter 2000).

The above measurements and estimates indicate that *Shaochilong* was small compared to many of its closest relatives, and along with the neovenatorids *Australovenator* (Hocknull *et al*. 2009) and *Fukuiraptor* (Azuma & Currie 2000) was among the smallest allosauroids. *Shaochilong*, or at least the lectotype specimen, was not the largest carnivore in its fauna, as it lived alongside the colossal *Chilantaisaurus tashuikouensis*. The femur of *C. tashuikouensis* is approximately 1.2 metres long (Benson & Xu 2008)—approximately the same length as the femur of *Tyrannosaurus*—which results in a body size estimate of ca. 6000 kilograms (Christiansen & Farina 2004). However, *Shaochilong* is substantially larger than the best known Early-mid Cretaceous tyrannosauroids of Asia (*Xiongguanlong*: 272 kilograms, Li *et al.* 2009). The recently described tyrannosauroid *Sinotyrannus*, from the Early Cretaceous Jiufotang Formation, has been estimated at 9–10 meters in body length, but it is only known from incomplete fossils, and it is substantially older than *Shaochilong* (Ji *et al*. 2009).

The generic distinction of *Shaochilong* and *Chilantaisaurus*. *Shaochilong maortuensis* was originally erected within the genus *Chilantaisaurus* by Hu (1964). However, Chure (1998, 2000), Rauhut (2003a), and Benson & Xu (2008) concluded that *Shaochilong* ("*Chilantaisaurus*") *maortuensis* could not be confidently referred to *Chilantaisaurus* due to the lack of overlapping material between the syntype series of *S. maortuensis* and *C. tashuikouensis* (known from a humerus, ilium and hindlimb bones), the type species of *Chilantaisaurus*. The two taxa were also perceived to have disparate phylogenetic positions, as *Shaochilong* was recovered as a derived coelurosaur by Rauhut (2003a; see also Chure 2000) whereas *Chilantaisaurus* was

considered to be a megalosauroid (spinosauroid: Rauhut 2003a), allosauroid, or basal coelurosaur (Benson & Xu 2008; Benson in press). This led to the conclusion that, although the two could not be directly compared, they were unlikely to represent a single genus (Rauhut 2003a; Benson & Xu 2008). The recent analysis of Benson *et al.* (2009) incorporated numerous new data and observations supporting allosauroid affiliation for *Chilantaisaurus* and *Shaochilong*. However, within Allosauroidea *Chilantaisaurus* is a neovenatorid and *Shaochilong* is a carcharodontosaurid. As the basic anatomy of these clades is now well-documented and distinct, it is unlikely that *Chilantaisaurus* and *Shaochilong* represent a single taxon. Additional evidence for this distinction is the notable size difference between *S. maortuensis* (estimated here as 500 kg body mass) and *C. tashuikouensis* (comparable in size to some of the largest theropods such as *Mapusaurus* >5000 kg; Benson & Xu 2008).

Phylogenetic Implications. In their description of *Shaochilong*, Brusatte *et al.* (2009a) provided two cladistic analyses. First, they scored *Shaochilong* for the phylogenetic dataset of Smith *et al.* (2007), a broad-scale theropod phylogenetic analysis that includes representatives of the various disparate groups that *Shaochilong* has previously been allied with (i.e Megalosauridae, Allosauridae, Tyrannosauroidea, Maniraptora). This analysis placed *Shaochilong* deep within the Carcharodontosauridae, and the strict consensus of all most parsimonious trees does not include a monophyletic Allosauroidea (*Allosaurus*, Sinraptoridae, Carcharodontosauridae). A monophyletic allosauroid clade has been recovered in most basal tetanuran cladistic analyses (e.g., Sereno *et al.* 1996; Harris 1998; Holtz 2000; Rauhut 2003a; Holtz *et al.* 2004; Smith *et al.* 2007), but Smith *et al.* (2007) and Brusatte *et al.* (in press) found a wider distribution for many characters once thought to unite allosauroids to the exclusion of other theropods. However, although the revised version of Smith *et al.*'s (2007) analysis does not recover a monophyletic Allosauroidea, it must be kept in mind that character sampling in this part of the tree is somewhat limited. A larger analysis of basal tetanuran phylogeny, which includes much more complete character and taxon sampling for this part of theropod phylogeny, recovers a strongly supported allosauroid clade (Benson in press; Benson *et al*. 2009).

Second, Brusatte *et al.* (2009a) included *Shaochilong* within a modified version of the phylogenetic analysis of Brusatte & Sereno (2008), which focuses completely on allosauroids and incorporates a wealth of character data pertinent to allosauroid ingroup phylogeny that is not included in Smith *et al.*'s (2007) broader study. This analysis also places *Shaochilong* firmly with Carcharodontosauridae, and indeed as a fairly derived member of the clade. The two most parsimonious trees only differ in whether *Shaochilong* or the Early Cretaceous Argentinian genus *Tyrannotitan* are more closely related to Carcharodontosaurinae, the Aptian–Albian Gondwanan clade that includes the African *Carcharodontosaurus* and the South American *Giganotosaurus* and *Mapusaurus*. Thus, the closest relatives of *Shaochilong* are all Gondwanan taxa from the Aptian–Cenomanian.

Several characters support a carcharodontosaurid placement for *Shaochilong*, including a limited antorbital fossa on the lateral surface of the maxilla, deep interdental plates, fused frontal-frontal and frontal-parietal sutures, limited supratemporal fossae on the frontal, a curved muscle crest within the supratemporal fossa, postorbital-lacrimal contact above the orbit, paracondylar pneumatic foramina leading into a midline recess underneath the endocranial cavity, a largely anterior-posterior trending fenestra ovalis, a trigeminal (V) nerve foramen located posterior to the nuchal crest, two foramina for the facial (VII) nerve, and a thickened antotic crest on the laterosphenoid. Some of these features have been dismissed by previous authors as dependent on body size, and thus phylogenetically uninformative. Most notable among these are the postorbital-lacrimal contact and fused skull roof sutures (Currie & Carpenter 2000). The presence of these character states in a small-bodied allosauroid that is smaller than *Allosaurus* and *Sinraptor*, neither of which possesses these states, argues strongly against the hypothesis that carcharodontosaurid features are dependent solely on large body size.

Biogeographic Implications. *Shaochilong* is strongly supported as a member of Carcharodontosauridae, a clade once thought to be restricted to Gondwana (e.g., Allain 2002; Novas *et al.* 2005), but also known from North America during the Early–mid Cretaceous (*Acrocanthosaurus*: Sereno *et al*. 1996; Harris 1998; Brusatte & Sereno 2008). The reinterpretation of *Shaochilong* as a carcharodontosaurid provides the first

definitive evidence of this clade of large-bodied theropods in Asia. One previous claim of an Asian carcharodontosaurid, based on an isolated tooth from Japan (Chure *et al.* 1999), must be considered equivocal since the diagnostic character thought to support a carcharodontosaurid affinity, enamel wrinkles, is widespread among theropods (Brusatte *et al.* 2007; Canale *et al.* 2009). With the identification of a definitive Asian carcharodontosaurid, this clade is now known from Early-mid Cretaceous units of Africa (*Carcharodontosaurus*, *Eocarcharia*), South America (*Giganotosaurus*, *Mapusaurus*, *Tyrannotitan*), North America, and Asia. Indeed, carcharodontosaurids are currently unknown from only Antarctica, Australia and Europe, three poorly sampled landmasses (Weishampel *et al.* 2004b). Thus, it is reasonable to consider the carcharodontosaurid radiation of the Early–mid Cretaceous as a global event. Neovenatorid carcharodontosaurians such as *Neovenator* (Europe), *Chilantaisaurus* and *Fukuiraptor* (Asia), *Megaraptor* (South America) and *Australovenator* (Australia) were also cosmopoliatian in the Early-mid Cretaceous (see review in Benson *et al.* 2009).

This pattern has two important implications for Cretaceous dinosaur biogeography. First, in a geographic sense, it provides evidence that the large-bodied theropod faunas of Early-mid Cretaceous Asia had a cosmopolitan flavour. This trend has previously been noted for large dinosaurian herbivores, including sauropods (Upchurch 1995; Barrett *et al.* 2002) and ornithopods (Norman 1998). Such cosmopolitan Early–mid Cretaceous herbivore assemblages contrast with more endemic faunas of the Middle–Late Jurassic, when Asia was largely isolated from the remainder of Laurasia (e.g., Upchurch *et al.* 2002). Increased cosmopolitanism in the Early-mid Cretaceous is thought to reflect increased faunal interchange after the breakdown of oceanic and topographic barriers that had isolated Asia during the Jurassic (Russell 1993; Upchurch *et al.* 2002). However, some authors have argued that the small-bodied theropod faunas of Early Cretaceous Asia were largely endemic, comprised of relicts of once diverse Jurassic clades that were able to survive in isolation in Asia (Luo 1999). Evidence for this hypothesis was based almost exclusively on the small theropods of China's Jehol Biota, but recent faunal reviews and fossil discoveries indicate that there is no systematic pattern of small theropod endemism (e.g., Xu & Norell 2006).

Until this point, the large-bodied theropods of Asia have not entered into this debate, as very few large Asian theropods are known from the Early–mid Cretaceous. Prior to this gap, Asia was largely populated by endemic basal tetanuran theropods, such as *Monolophosaurus* and close kin (Brusatte *et al.* in press; Zhao *et al.* 2009). Indeed, the most recent and comprehensive phylogenetic analyses find support for at least one basal tetanuran clade restricted to the Middle Jurassic of Asia (Benson in press). After the Early–mid Cretaceous gap, Asian ecosystems were dominated by the colossal tyrannosaurids, which were widespread and common across China and Mongolia in the Campanian and Maastrichtian (e.g., Currie 2000; Holtz 2004). The discovery of *Shaochilong* within this gap indicates that Early-mid Cretaceous Asia was home to a cosmopolitan large theropod clade, the carcharodontosaurids (which are part of the larger, cosmopolitan carcharodontosaurian clade). In fact, *Shaochilong* is most closely related to a speciose clade of Gondwanan carcharodontosaurids. The cosmopolitan nature of Asian Early–mid Cretaceous theropod faunas is further supported by other recent discoveries. The two other reasonably complete large Asian theropods from this time are *Fukuiraptor* (Azuma & Currie 2000; Currie & Azuma 2006) and *Siamotyrannus* (Buffetaut *et al.* 1996), both of which appear to belong to Allosauroidea, the diverse basal tetanuran clade that includes carcharodontosaurids (Rauhut 2003a; Holtz *et al.* 2004). More conspicuous, fossils of spinosaurid theropods, previously known from Africa, Europe, and South America, have been described from Asia (Milner *et al.* 2007; Buffetaut *et al.* 2008). Taken together, there is little evidence for endemic Asian large-bodied theropods during the Early-mid Cretaceous, but copious evidence for cosmopolitan faunas.

The second important biogeographic pattern suggested by the reinterpretation of *Shaochilong* is specific to allosauroid theropods. The revised version of the Brusatte & Sereno (2008) phylogenetic analysis indicates that the closest relatives of *Shaochilong* are Gondwanan taxa. This finding may cast serious doubt on one of the most prominent Mesozoic biogeographic scenarios: the hypothesis that allosauroids evolved vicariantly in association with the breakup of Pangaea (e.g., Harris 1998; Sereno 1999; Brusatte and Sereno 2008). This scenario has been suggested based on a literal reading of the fossil record, as well as quantitative cladistic

biogeographic analysis that reconstructs an area tree based on the taxonomic cladogram of allosauroids (three-area analysis: Brusatte & Sereno 2008). Although quantitative, the latter method does have some drawbacks, most notably sensitivity to sampling bias (reviewed by Brusatte & Sereno 2008), as well as lack of temporal control (time slicing: Upchurch & Hunn 2002) and statistical randomization tests to compensate for temporal and topological biases. Although useful as a first approximation of which areas are united by the possession of shared, derived taxa, three-area analysis has little power to describe the biogeographic history of a clade such as allosauroids, which contain a limited number of taxa spanning a long duration. Unfortunately, none of the other cladistic biogeographic methods are any better for the analysis of a single extinct clade (Brusatte & Sereno 2008).

With these caveats in mind, it is still useful to use the allosauroid cladogram as a framework for biogeographic prediction and hypothesis testing. For instance, the hypothesis that allosauroids evolved vicariantly in concert with Pangaean fragmentation predicts that Asian allosauroids should be positioned basally on the cladogram, as Asia was the first landmass to break away from Pangaea. However, the affinities of *Shaochilong* may instead suggest that allosauroid clades originated prior to major continental breakup events, and thus that allosauroids did not speciate in response to continental breakup but were rather "along for the ride." Alternatively, a large vicariant model may still hold, with *Shaochilong* as an outlier that made its way to Asia via northern-southern interchange after landmasses had separated. This type of interchange has been hypothesized to explain striking faunal similarities between Early Cretaceous assemblages in Africa and Europe, and has been envisioned as "island hopping" across the Tethys (Gheerbrant & Rage 2006). As discussed above, authors have long found support for Asian interchange during the Early Cretaceous. However, most previous work has noted similarities between Asia, Europe, and North America, as opposed to Asia and Gondwana (e.g., Russell 1993). Unfortunately, the current allosauroid dataset is not suitable for distinguishing between many possible hypotheses of allosauroid distribution and biogeography. Indeed, the most reasonable interpretation based on current fossils and an understanding of sampling bias is that allosauroids, especially carcharodontosaurians, were essentially cosmopolitan during the Early–mid Cretaceous, and that their distribution does not strongly support any specific biogeographic scenario (Benson *et al*. 2009). Ultimately, as large theropods and other dinosaurs become better understood, it is hoped that congruent patterns in many groups may point to a consensus scenario.

Large-bodied Theropod Faunas of the Cretaceous. *Shaochilong* also increases understanding of the pace and tempo of large theropod turnover during the Cretaceous. As discussed above, there was previously a large, mostly unsampled gap in the Early–mid Cretaceous large-bodied theropod fossil record of Asia. This is also true of Laurasia as a whole, as little is known about the large theropods that lived in North America and Europe between the Albian–Campanian (Cifelli *et al.* 1997). It is now known that carcharodontosaurians (and other allosauroids) were present on each Laurasian landmass in the Early–mid Cretaceous, and that Campanian–Maastrichtian ecosystems in North America and Asia were dominated by the colossal tyrannosaurids (the Late Cretaceous of Europe is poorly sampled: Weishampel *et al.* 2004b). However, the gap between the hitherto youngest allosauroids (*Acrocanthosaurus*: 125–100 Ma) and oldest large-bodied tyrannosaurids (Campanian: ca. 83.5 Ma) is substantial. This large missing record, up to 41.5 million years, makes it difficult to understand the pace of large-bodied theropod evolution during the Cretaceous. Did large tyrannosaurids originate much earlier than the Campanian, did carcharodontosaurids persist until later in the Cretaceous, or were there other clades that filled the large predator niche during this time?

Shaochilong, as well as the contemporary *Chilantaisaurus tashuikouensis*, help fill this gap and provide some of the only concrete data for analyzing large theropod turnover during the mid Cretaceous. The putative allosauroids *Fukuiraptor* and *Siamotyrannus*, as well as the Asian spinosaurid material mentioned above, are insufficient in this context, as they come from the much older Barremian–Albian. Similarly, the tyrannosaurid *Alectrosaurus*, although sometimes regarded as Cenomanian (e.g., Holtz 2004), has been conclusively re-dated as Campanian (Van Itterbeeck *et al.* 2005). The recently described tyrannosauroid *Sinotyrannus*, known from fragmentary fossils from the Early Cretaceous of China, may have reached 9–10 meters in body length (Ji *et al*. 2009). However, this taxon also is from the Barremian–Aptian, and the fact that it shares several

unusual features with the basal tyrannosauroids *Guanlong* and *Proceratosaurus* (e.g., enlarged external naris, anterior ramus of maxilla, midline nasal crest, dentary primary neurovascular foramina set into sharp groove) indicates that it is a basal taxon that evolved large body size independently of, and long before, the tyrannosaurids of the Campanian–Maastrichtian.

Therefore, this leaves *Shaochilong* and *C. tashuikouensis* as the only substantially complete large-bodied theropods from the mid Cretaceous of Laurasia that are well understood in a phylogenetic context. Importantly, both *Shaochilong* and *C. tashuikouensis* are carcharodontosaurian theropods, and neither is a tyrannosaurid. Although only two data points from a single formation, the presence of large carcharodontosaurians in the Turonian of Asia (ca. 92 Ma) suggests that basal tetanurans still occupied the large predator role in Laurasia at this time, and that the ascent of tyrannosaurids was a delayed event that occurred towards the end of the Cretaceous. If true, this is an interesting pattern, as the more inclusive tyrannosauroid clade originated during or before the Middle Jurassic (Rauhut & Milner 2008) and was represented by several small-medium bodied taxa throughout the Late Jurassic and Early Cretaceous of the northern continents (e.g., Hutt *et al.* 2001; Rauhut 2003b; Benson 2008b), including Asia (Xu *et al.* 2004, 2006; Li *et al.* 2009). Thus, it appears as if large-bodied tyrannosaurid evolution followed a "long fuse" pattern, in which the tyrannosauroid clade originated long before it reached large body size and ecological dominance. Like any evolutionary scenario reconstructed from the fossil record, this hypothesis awaits testing with further large theropod discoveries from the mid Cretaceous.

Acknowledgments

SLB first and foremost thanks XX for the opportunity to study the specimen and D. Hone and C. Sullivan for hospitality while visiting Beijing. S. Gallagher took most of the photos used in the figures, B. Booth provided the excellent skull reconstruction, and D. Hone provided the line drawings for Figure 8. We thank numerous curators and researchers for access to specimens in their care: R. Allain (MNHN), P. Barrett (NHM), J. Canale (MUCPv-CH), S. Chapman (NHM), R. Coria (MCF), M. Getty (UMNH), S. Hutt (MIWG), C. Mehling (AMNH), A. Milner (NHM), M. Munt (MIWG), L. Murray (TMM), M. Norell (AMNH), J. Person (OMNH), O. Rauhut (BSPG), T. Rowe (TMM), V. Schneider (NCSM), D. Schwarz-Wings (HMB), P. Sereno (UCRC), and X.-J. Zhao (IVPP). SLB is supported by a NSF Graduate Research Fellowship at Columbia University and his visit to Beijing was supported by the American Museum of Natural History (NSF to M. Norell). RBJB's research is supported by Trinity College, Cambridge. XX is supported by the Chinese Academy of Sciences and National Natural Science Foundation of China.

References

Alcober, O., Sereno, P.C., Larsson, H.C.E., Martinez, R. & Varricchio, D. (1998) A Late Cretaceous carcharodontosaurid (Theropoda: Allosauroidea) from Argentina. *Journal of Vertebrate Paleontology*, 15 (suppl.), 16A.

Ali, F., Zelenitsky, D.K., Therrien, F. & Weishampel, D.B. (2008) Homology of the 'ethmoid complex' of tyrannosaurids and its implications for the reconstruction of the olfactory apparatus of non-avian theropods. *Journal of Vertebrate Paleontology*, 28, 123–133.

Anderson, J.F., Hall-Martin, A. & Russell, D.A. (1985) Long-bone circumference and weight in mammals, birds and dinosaurs. *Journal of Zoology*, 207, 53–61.

Allain, R. (2002) Discovery of megalosaur (Dinosauria, Theropoda) in the Middle Bathonian of Normandy (France) and its implications for the phylogeny of basal Tetanurae. *Journal of Vertebrate Paleontology*, 22, 548–563.

Azuma, Y. & Currie, P.J. (2000) A new carnosaur (Dinosauria: Theropoda) from the Lower Cretaceous of Japan. *Canadian Journal of Earth Sciences*, 37, 1735–1753.

Bakker, R.T., Williams, M. & Currie, P.J. (1988) *Nanotyrannus*, a new genus of pygmy tyrannosaur, from the latest Cretaceous of Montana. *Hunteria*, 1, 1–30.

Barrett, P.M., Hasegawa, Y., Manabe, M., Isaji, S. & Matsuoka, H. (2002) Sauropod dinosaurs from the Lower

Cretaceous of eastern Asia: taxonomic and biogeographical implications. *Palaeontology*, 45, 1197–1217.
Barsbold, R. & Osmólska, H. (1999) The skull of *Velociraptor* (Theropoda) from the Late Cretaceous of Mongolia. *Acta Palaeontologica Polonica*, 44, 189–212.
Benson, R.B.J. (2008a) A redescription of '*Megalosaurus*' *hesperis* (Dinosauria, Theropoda) from the Inferior Oolite (Bajocian, Middle Jurassic) of Dorset, United Kingdom. *Zootaxa*, 1931, 57–67.
Benson, R.B.J. (2008b) New information on *Stokesosaurus*, a tyrannosauroid (Dinosauria: Theropoda) from North America and the United Kingdom. *Journal of Vertebrate Paleontology*, 28, 732–750.
Benson, R.B.J. (In press) A description of *Megalosaurus bucklandii* (Dinosauria: Theropoda) from the Bathonian of the United Kingdom and the relationships of Middle Jurassic theropods. *Zoological Journal of the Linnean Society.*
Benson, R.B.J. & Xu, X. (2008) The anatomy and systematic position of the theropod dinosaur *Chilantaisaurus tashuikouensis* Hu, 1964 from the Early Cretaceous of Alanshan, People's Republic of China. *Geological Magazine*, 145, 778–789.
Benson, R.B.J., Carrano, M.T. & Brusatte, S.L. (2009) A new clade of archaic large-bodied predatory dinosaurs (Theropoda: Allosauroidea) that survived to the latest Mesozoic. *Naturwissenschaften* (published online, doi:10.1007/s00114-009-0614-x).
Bonaparte, J.F. (1985) A horned Cretaceous carnosaur from Patagonia. *National Geographic Research*, 1, 149–151.
Bonaparte, J.F. (1986) Les dinosaurs (carnosaures, allosauridés, sauropodes, cétiosauridés) du Jurassic moyen de Cerro Cóndor (Chubut, Argentina). *Annales de Paléontologie*, 72, 247–289.
Bonaparte, J.F., Novas, F.E. & Coria, R.A. (1990) *Carnotaurus sastrei* Bonaparte, the horned, lightly built carnosaur from the Middle Cretaceous of Patagonia. *Contributions in Science, Natural History Museum of Los Angeles County*, 416, 1–41.
Britt, B.B. (1991) Theropods of Dry Mesa Quarry (Morrison Formation, Late Jurassic), Colorado, with emphasis on the osteology of *Torvosaurus tanneri*. *Brigham Young University, Geology Studies*, 37, 1–72.
Brochu, C.A. (1996) Closure of neurocentral sutures during crocodilian ontogeny: implications for assessment of maturity in fossil archosaurs. *Journal of Vertebrate Paleontology*, 16, 49–62.
Brochu, C.A. (2003) Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. *Society of Vertebrate Paleontology Memoir*, 7, 1–138.
Brusatte, S.L. & Sereno, P.C. (2007) A new species of *Carcharodontosaurus* (Dinosauria: Theropoda) from the Cenomanian of Niger and a revision of the genus. *Journal of Vertebrate Paleontology*, 24, 902–916.
Brusatte, S.L. & Sereno, P.C. (2008) Phylogeny of Allosauroidea (Dinosauria: Theropoda): comparative analysis and resolution. *Journal of Systematic Palaeontology*, 6, 155–182.
Brusatte, S.L., Benson, R.B.J & Hutt, S. (2008) The osteology of *Neovenator salerii* (Dinosauria: Theropoda) from the Wealden Group (Barremian) of the Isle of Wight. *Monograph of the Palaeontographical Society*, 162(631), 1–166.
Brusatte, S.L., Benson, R.B.J., Carr, T.D., Williamson, T.E. & Sereno, P.C. (2007) The systematic utility of theropod enamel wrinkles. *Journal of Vertebrate Paleontology*, 27, 1052–1056.
Brusatte, S.L., Carr, T.D., Erickson, G.M., Bever, G.S. & Norell, M.A. (2009b) A long-snouted, multi-horned tyrannosaurid from the Late Cretaceous of Mongolia. *Proceedings of the National Academy of Sciences (USA)*, 106, 17261–17266.
Brusatte, S.L., Benson, R.B.J., Chure, D.J., Xu, X., Sullivan, C. & Hone, D.E.W. (2009a) The first definitive carcharodontosaurid (Dinosauria: Theropoda) from Asia and the delayed ascent of tyrannosaurids. *Naturwissenschaften*, 96, 1051–1058.
Brusatte, S.L., Benson, R.B.J, Currie, P.J. & Zhao, X.–J. (In press) The skull of *Monolophosaurus jiangi* (Dinosauria: Theropoda) and its implications for early theropod phylogeny and evolution. *Zoological Journal of the Linnean Society.*
Buffetaut, E., Suteethorn, V. & Tong, H. (1996) The earliest known tyrannosaur from the Lower Cretaceous of Thailand. *Nature*, 381, 689–691.
Buffetaut, E., Suteethorn, V., Tong, H. & Amiot, R. (2008) An Early Cretaceous spinosaurid theropod from southern China. *Geological Magazine*, 145, 745–748.
Calvo, J.O., Porfiri, J.D., Veralli, C., Novas, F. & Poblete, F. (2004) Phylogenetic status of *Megaraptor namunhuaiquii* Novas based on a new specimen from Neuquén, Patagonia, Argentina. *Ameghiniana*, 41, 565–575.
Canale, J.I., Scanferla, C.A., Angolin, F.L. & Novas, F.E. (2009) New carnivorous dinosaur from the Late Cretaceous of NW Patagonia and the evolution of abelisaurid theropods. *Naturwissenschaften*, 96, 409–414.
Carrano, M.T. & Sampson, S.D. (2008) The phylogeny of Ceratosauria (Dinosauria: Theropoda). *Journal of Systematic Palaeontology*, 6, 183–236.
Charig, A.J. & Milner, A.C. (1997) *Baryonyx walkeri*, a fish–eating dinosaur from the Wealden of Surrey. *Bulletin of the Natural History Museum London (Geology)*, 53, 11–70.
Chatterjee, S. (1978) *Indosuchus* and *Indosaurus*, Cretaceous carnosaurs from India. *Journal of Paleontology*, 52, 570–580.
Christiansen, P. & Farina, R.A. (2004) Mass prediction in theropod dinosaurs. *Historical Biology*, 16, 85–92.

Chure, D.J. (1998) "*Chilantaisaurus*" *maortuensis*, a large maniraptoran theropod from the Early Cretaceous (Albian) of Nei Mongol, PRC. *Journal of Vertebrate Paleontology*, 18 (suppl.), 33A–34A.

Chure, D.J. (2000) *A new species of* Allosaurus *from the Morrison Formation of Dinosaur National Monument (UT–CO) and a revision of the theropod family Allosauridae*. Unpublished Ph.D. dissertation, Columbia University, New York, 964 pp.

Chure, D.J., Manabe, M., Tanimoto, M. & Tomida, Y. (1999) An unusual theropod tooth from the Mifune Group (Late Cenomanian to Early Turonian), Kumamoto, Japan. *In*: Tomida, Y., Rich, T.H. & Vickers–Rich, P. (Eds.) *Proceedings of the Second Gondwanan Dinosaur Symposium*. National Science Museum Monographs, Tokyo, 15, pp. 291–296.

Cifelli, R.L., Kirkland, J.I., Weil, A., Deino, A.L. & Kowallis, B.J. (1997) High-precision $^{40}Ar/^{39}Ar$ geochronology and the advent of North America's Late Cretaceous terrestrial fauna. *Proceedings of the National Academy of Sciences (USA)*, 94, 11163–11167.

Clark, J.M., Perle, A. & Norell, M.A. (1994) The skull of *Erlicosaurus andrewsi*, a Late Cretaceous "segnosaur" (Theropoda: Therezinosauridae) from Mongolia. *American Museum Novitates*, 3115, 1–39.

Coria, R.A. & Currie, P.J. (2002) The braincase of *Giganotosaurus carolinii* (Dinosauria: Theropoda) from the Upper Cretaceous of Argentina. *Journal of Vertebrate Paleontology*, 22, 802–811.

Coria, R.A. & Currie, P.J. (2006) A new carcharodontosaurid (Dinosauria, Theropoda) from the Upper Cretaceous of Argentina. *Geodiversitas*, 28, 71–118.

Coria, R.A. & Salgado, L. (1995) A new giant carnivorous dinosaur from the Cretaceous of Patagonia. *Nature*, 377, 224–226.

Currie, P.J. (1985) Cranial anatomy of *Stenonychosaurus inequalis* (Saurischia, Theropoda) and its bearing on the origin of birds. *Canadian Journal of Earth Sciences*, 22, 1643–1658.

Currie, P.J. (1995) New information on the anatomy and relationships of *Dromaeosaurus albertensis* (Dinosauria: Theropoda). *Journal of Vertebrate Paleontology*, 15, 576– 591.

Currie, P.J. (1997) Braincase anatomy. *In*: Currie P.J. & and Padian, K. (Eds.), *The Encyclopedia of Dinosaurs*. Academic Press, New York, pp. 81–85.

Currie, P.J. (2000) Theropods from the Cretaceous of Mongolia. *In*: Benton, M.J., Shishkin, M.A., Unwin, D.M. & Kurochkin, E.N. (Eds.) *The Age of Dinosaurs in Russia and Mongolia*. Cambridge University Press, Cambridge, pp. 434–455.

Currie, P.J. (2003a) Cranial anatomy of tyrannosaurid dinosaurs from the Late Cretaceous of Alberta, Canada. *Acta Palaeontologica Polonica*, 48, 191–226.

Currie, P.J. (2003b) Allometric growth in tyrannosaurids (Dinosauria: Theropoda) from the Upper Cretaceous of North America and Asia. *Canadian Journal of Earth Sciences*, 40, 651–665.

Currie, P.J. & Azuma, Y. (2006) New specimens, including a growth series, of *Fukuiraptor* (Dinosauria, Theropoda) from the Lower Cretaceous Kitadani Quarry of Japan. *Journal of the Paleontological Society of Korea*, 22, 173–193.

Currie, P.J. & Carpenter, K. (2000) A new specimen of *Acrocanthosaurus atokensis* (Theropoda, Dinosauria) from the Lower Cretaceous Antlers Formation (Lower Cretaceous, Aptian) of Oklahoma, USA. *Geodiversitas*, 22, 207–246.

Currie, P.J. & Zhao, X.–J. (1993a) A new large theropod (Dinosauria, Theropoda) from the Jurassic of Xinjiang, People's Republic of China. *Canadian Journal of Earth Sciences*, 30, 2037–2081.

Currie, P.J. & Zhao, X.–J. (1993b) A new troodontid (Dinosauria, Theropoda) braincase from the Dinosaur Park Formation (Campanian) of Alberta. *Canadian Journal of Earth Sciences*, 30, 2231–2247.

Dong, Z. (1992) *Dinosaurian Faunas of China*. China Ocean Press, Beijing 188 pp.

Eddy, D.R. (2008) A re-analysis of the skull of *Acrocanthosaurus atokensis* (NCSM 14345): implications for allosauroid morphology, phylogeny, and biogeography. Unpublished MSc Thesis, North Carolina State University, Raleigh, North Carolina, 180 pp.

Ezcurra, M.D. (2007) The cranial anatomy of the coelophysoid theropod *Zupaysaurus rougieri* from the Upper Triassic of Argentina. *Historical Biology*, 19, 185–202.

Franzosa, J, & Rowe, T. (2005) Cranial endocast of the Cretaceous theropod dinosaur *Acrocanthosaurus atokensis*. *Journal of Vertebrate Paleontology*, 25, 859–864.

Gauthier, J. (1986) Saurischian monophyly and the origin of birds. *Memoirs of the California Academy of Sciences*, 8, 1–55.

Gheerbrant, E. & Rage, J.-C. (2006) Paleobiogeography of Africa: how distinct from Gondwana and Laurasia? *Palaeogeography, Palaeoclimatology, Palaeoecology*, 241, 224–246.

Gower, D.J. & Weber, E. (1998) The braincase of *Euparkeria*, and the evolutionary relationships of birds and crocodilians. *Biological Reviews*, 73, 367–411.

Harris, J.D. (1998) A reanalysis of *Acrocanthosaurus atokensis*, its phylogenetic status, and paleobiogeographic implications, based on a new specimen from Texas. *New Mexico Museum of Natural History and Science Bulletin*, 13, 1–75.

Hocknull, S.A., White, M.A., Tischler, T.R., Cook, A.G., Calleja, N.D., Sloan, T. & Elliott, D.A. (2009) New mid-

Cretaceous (latest Albian) dinosaurs from Winton, Queensland, Australia. *PLoS ONE*, 4(7), e6190 (doi:10.1371/journal.pone.0006190).
Holtz, T.R. (2000) A new phylogeny of the carnivorous dinosaurs. *Gaia*, 15, 5–61.
Holtz, T.R. (2004) Tyrannosauroidea. *In*: Weishampel, D.B., Dodson, P. & Osmólska, H. (Eds.), *The Dinosauria*, 2nd edn. University of California Press, Berkeley, pp. 111–136.
Holtz, T.R., Molnar, R.E. & Currie P.J. (2004) Basal Tetanurae. *In*: Weishampel, D.B., Dodson, P. & Osmólska, H. (Eds.), *The Dinosauria*, 2nd edn. University of California Press, Berkeley, pp. 71–110.
Hu, S.-Y. (1964) Carnosaurian remains from Alashan, Inner Mongolia. *Vertebrata PalAsiatica*, 8, 42–63.
Hutt, S., Naish, D., Martill, D.M., Barker, M.J. & Newbery, P. (2001) A preliminary account of a new tyrannosauroid theropod from the Wessex Formation (Early Cretaceous) of southern England. *Cretaceous Research*, 22, 227–242.
Irmis, R.B. (2007) Axial skeleton ontogeny in the Parasuchia (Archosauria: Pseudosuchia) and its implications for ontogenetic determination in archosaurs. *Journal of Vertebrate Paleontology*, 27, 350–361.
Ji, Q., Ji, S.-A. & Zhang, L.-J. (2009) First large tyrannosauroid theropod from the Early Cretaceous Jehol Biota in northeastern China. *Geological Bulletin of China*, 28, 1369–1374.
Kirkland, J.I., Zanno, L.E., Sampson, S.D., Clark, J.M. & DeBlieux, D.D. (2005) A primitive therizinosauroid dinosaur from the Early Cretaceous of Utah. *Nature*, 435, 84–87.
Kobayashi, Y. & Lu, J.-C. (2003) A new ornithomimid dinosaurian with gregarious habits from the Late Cretaceous of China. *Acta Palaeontologica Polonica*, 48, 235–259.
Kurzanov, S.M. (1976) Braincase structure in the carnosaur *Itemirus* n. gen. and some aspects of the cranial anatomy of dinosaurs. *Paleontological Journal*, 10, 361–369.
Lamanna, M.C., Martínez, R.D. & Smith, J.B. (2002) A definitive abelisaurid theropod dinosaur from the early Late Cretaceous of Patagonia. *Journal of Vertebrate Paleontology*, 22, 58–69.
Li, D., Norell M.A., Gao, K., Smith, N.D. & Makovicky, P.J. (2009) A longirostrine tyrannosauroid from the Early Cretaceous of China. *Proceedings of the Royal Society B* (published online, doi:10.1098/rspb.2009.0249).
Luo, Z. (1999) A refugium for relicts. *Nature*, 400, 24–25.
Madsen, J.H. (1976) *Allosaurus fragilis*: a revised osteology. *Utah Geological Survey Bulletin*, 109, 1–163.
Madsen, J.H. & Welles S.P. (2000) *Ceratosaurus* (Dinosauria, Theropoda) a revised osteology. *Utah Geological Survey, Miscellaneous Publication*, 00–2, 1–80.
Makovicky, P.J. & Norell, M.A. (1998) A partial ornithomimid braincase from Ukhaa Tolgod (Upper Cretaceous, Mongolia). *American Museum Novitates*, 3247, 1–16.
Marsh, O.C. (1878) Principal characters of American Jurassic dinosaurs. Pt. 1. *American Journal of Science (Series 3)*, 16, 411–416.
Marsh, O.C. (1881) Principal characters of American Jurassic dinosaurs. Part V. *American Journal of* Science (Series 3), 21, 417–423.
Milner, A., Buffetaut, E. & Suteethorn, V. (2007) A tall–spined spinosaurid theropod from Thailand and the biogeography of spinosaurs. *Journal of Vertebrate Paleontology*, 27 (suppl.), 118A.
Molnar, R.E. (1974) A distinctive theropod dinosaur from the Upper Cretaeous of Baja California (Mexico). *Journal of Paleontology*, 48, 1009–1017.
Molnar, R.E., Kurzanov, S.M. & Dong, Z. (1990) Carnosauria. *In*: Weishampel, D.B., Dodson, P. & Osmólska, H. (Eds.), *The Dinosauria*. University of California Press, Berkeley, pp. 169–209.
Norell, M.A. & Makovicky, P.J. (2004) Dromaeosauridae. *In*: Weishampel, D.B., Dodson, P. & Osmólska, H. (Eds.), *The Dinosauria*, 2nd edition. University of California Press, Berkeley, pp. 196–209.
Norell, M.A., Makovicky, P.J. & Clark, J.M. (2004) The braincase of *Velociraptor. In*: Currie, P.J., Koppelhus, E.B., Shugar, M.A. & Wright, J.L. (Eds.), *Feathered Dragons: Studies on the Transition from Dinosaurs to Birds*. Indiana University Press, Bloomington, pp. 133–143.
Norman, D.B. (1998) On Asian ornithopods (Dinosauria: Ornithischia). 3. A new species of iguanodontid dinosaur. *Zoological Journal of the Linnean Society*, 122, 291–348.
Novas, F.E., de Valais, S., Vickers-Rich, P. & Rich, T. (2005) A large Cretaceous theropod from Patagonia, Argentina, and the evolution of carcharodontosaurids. *Naturwissenschaften*, 92, 226–230.
O'Connor, P.M. (2009) Evolution of archosaurian body plans: skeletal adaptations of an air–sac-based breathing apparatus in birds and other archosaurs. *Journal of Experimental Zoology*, 311A, 504–521.
Osmólska, H. (2004) Evidence on relation of brain to endocranial cavity in oviraptorid dinosaurs. *Acta Palaeontologica Polonica*, 49, 321–324.
Owen, R. (1842) Report on British fossil reptiles. *Report of the British Association for the Advancement of Science*, 11 (1841), 60–294.
Rauhut, O.W.M. (2003a) The interrelationships and evolution of basal theropod dinosaurs. *Special Papers in Palaeontology*, 69, 1–213.
Rauhut, O.W.M. (2003b) A tyrannosauroid dinosaur from the Upper Jurassic of Portugal. *Palaeontology*, 46, 903–910.
Rauhut, O.W.M. (2004a) Braincase structure of the Middle Jurassic theropod dinosaur *Piatnitzkysaurus*. *Canadian*

Journal of Earth Sciences, 41, 1109–1122.
Rauhut, O.W.M. (2004b) Provenance and anatomy of *Genyodectes serus*, a large–toothed ceratosaur (Dinosauria: Theropoda) from Patagonia. *Journal of Vertebrate Paleontology*, 24, 894–902.
Rauhut, O. & Milner, A. (2008) Cranial anatomy and systematic position of the Middle Jurassic theropod dinosaur *Proceratosaurus* from England. *Journal of Vertebrate Paleontology*, 28 (suppl.), 130A.
Russell, D.A. (1993) The role of Central Asia in dinosaurian biogeography. *Canadian Journal of Earth Sciences*, 30, 2002–2012.
Sadlier, R.W., Barrett, P.M. & Powell, H.P. (2008) The anatomy and systematics of *Eustreptospondylus oxoniensis*, a theropod dinosaur from the Middle Jurassic of Oxfordshire, England. *Monograph of the Palaeontographical Society*, 627, 1–82.
Sampson, S.D. & Witmer, L.M. (2007) Craniofacial anatomy of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. *Society of Vertebrate Paleontology Memoir*, 8, 32–102.
Seeley, H.G. (1887) On the classification of the fossil animals commonly named Dinosauria. *Proceedings of the Royal Society of London*, 43, 165–171.
Sereno, P.C. (1999) The evolution of dinosaurs. *Science*, 284, 2137–2147.
Sereno, P.C. & Brusatte, S.L. (2008) Basal abelisaurid and carcharodontosaurid theropods from the Elrhaz Formation (Aptian–Albian) of Niger. *Acta Palaeontologica Polonica*, 53, 15–46.
Sereno, P.C., McAllister, S. & Brusatte, S.L. (2005) TaxonSearch: a relational database for suprageneric taxa and phylogenetic definitions. *PhyloInformatics*, 8, 1–21.
Sereno, P.C., Wilson, J.A. & Conrad, J.L. (2004) New dinosaurs link southern landmasses in the Mid–Cretaceous. *Proceedings of the Royal Society B*, 271, 1325–1330.
Sereno, P.C., Forster, C.A., Rogers, R.R. & Monetta, A.M. (1993) Primitive dinosaur skeleton from Argentina and the early evolution of Dinosauria. *Nature*, 361, 64–66.
Sereno, P.C., Wilson, J.A., Larsson, H.C.E., Dutheil, D.B. & Sues, H.-D. (1994) Early Cretaceous dinosaurs from the Sahara. *Science*, 266, 267–271.
Sereno, P.C., Martinez, R.N., Wilson, J.A., Varricchio, D.J., Alcober, O.A. & Larsson, H.C.E. (2008) Evidence for avian intrathoracic air sacs in a new predatory dinosaur from Argentina. *PLoS One*, 3, e3303 (doi:10.1371/journal.pone.0003303).
Sereno, P.C., Dutheil, D.B., Iarochene, M., Larsson, H.C.E., Lyon, G.H., Magwene, P.M., Sidor, C.A., Varricchio, D.J. & Wilson, J.A. (1996) Predatory dinosaurs from the Sahara and Late Cretaceous faunal differentiation. *Science*, 272, 986–991.
Smith, J.B. & Dodson, P. (2003) A proposal for a standard terminology of anatomical notation and orientation in fossil vertebrate dentitions. *Journal of Vertebrate Paleontology*, 23, 1–12.
Smith, N.D., Makovicky, P.J., Hammer, W.R. & Currie, P.J. (2007) Osteology of *Cryolophosaurus ellioti* (Dinosauria: Theropoda) from the Early Jurassic of Antarctica and implications for early theropod evolution. *Zoological Journal of the Linnean Society*, 151, 377–421.
Snively, E., Henderson, D.M. & Phillips, D.S. (2006) Fused and vaulted nasals of tyrannosaurid dinosaurs: implications for cranial strength and feeding mechanics. *Acta Palaeontologica Polonica*, 51, 435–454.
Stovall, J.W. & Langston, W. (1950) *Acrocanthosaurus atokensis*, a new genus and species of Lower Cretaceous Theropoda from Oklahoma. *American Midland Naturalist*, 43, 696–728.
Stromer, E. (1931) Ergebnisse der Forschungsrisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltierreste der Baharije–Stufe (unterstes Cenoman). 10. Ein Skelett–Rest von *Carcharodontosaurus* nov. gen. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch–Naturwissenschaftliche Abteilung, Neue Folge*, 9, 1–23.
Sues, H.-D. (1997) On *Chirostenotes*, a Late Cretaceous oviraptorosaur (Dinosauria: Theropoda) from Western North America. *Journal of Vertebrate Paleontology*, 17, 698–716.
Sues, H.-D., Frey, E., Martill, D.M. & Scott, D.M. (2002) *Irritator challengeri*, a spinosaurid (Dinosauria: Theropoda) from the Lower Cretaceous of Brazil. *Journal of Vertebrate Paleontology*, 22, 535–547.
Taquet, P. & Welles, S.P. (1977) Redescription du crâne de dinosaure de Dives Normandie. *Annales de Paléontologie*, 63, 191–206.
Upchurch, P. (1995) The evolutionary history of the sauropod dinosaurs. *Philosophical Transactions of the Royal Society of London B*, 349, 365–390.
Upchurch, P. & Hunn, C.A. (2002) "Time": the neglected dimension in cladistic biogeography? *Geobios*, 35, 277–286.
Upchurch, P., Hunn, C.A. & Norman, D.B. (2002) An analysis of dinosaurian biogeography: evidence for the existence of vicariance and dispersal patterns caused by geological events. *Proceedings of the Royal Society Series B*, 269, 613–621.
Van Itterbeeck, J., Horne, D.J., Bulynck, P. & Vandenberghe, N. (2005) Stratigraphy and palaeoenvironment of the dinosaur-bearing Upper Cretaceous Iren Dabasu Formation, Inner Mongolia, People's Republic of China. *Cretaceous Research*, 26, 699–725.
Wedel, M.J. (2009) Evidence for bird–like air sacs in saurischian sinosaurs. *Journal of Experimental Zoology*, 311A

(published online, doi: 10.1002/jez.513).
Weishampel, D.B., Dodson, P. & Osmólska, H. (Eds.) (2004a) *The Dinosauria* (2nd Edition). University of California Press, Berkeley 880 pp..
Weishampel, D.B., Barrett, P.M., Coria, R.A., Le Loeuff, J., Xu, X., Zhao, X., Sahni, A., Gomani, E. & Noto, C.R. (2004b) Dinosaur distribution. *In*: Weishampel, D.B., Dodson, P. & Osmólska, H (Eds.), *The Dinosauria*, 2nd edn. University of California Press, Berkeley, pp. 517–606.
Welles, S.P. (1984) *Dilophosaurus wetherilli* (Dinosauria, Theropoda) osteology and comparisons. *Palaeontographica Abteilung A*, 185, 85–180.
Wilson, J.A. (1999) A nomenclature for vertebral laminae in sauropods and other saurischian dinosaurs. *Journal of Vertebrate Paleontology*, 19, 639–653.
Wilson, J.A., Sereno, P.C., Srivastava, S., Bhatt, D.K., Khosla, A. & Sahni, A. (2003) A new abelisaurid (Dinosauria, Theropoda) from the Lameta Formation (Cretaceous, Maastrichtian) of India. *Contributions from the Museum of Paleontology, University of Michigan*, 31, 1–42.
Witmer, L.M. (1997) The evolution of the antorbital cavity of archosaurs: a study in soft–tissue reconstruction in the fossil record with analysis of the function of pneumaticity. *Society of Vertebrate Paleontology Memoir*, 3, 1–73.
Xu, X. & Norell, M.A. (2006) Non-avian dinosaur fossils from the Lower Cretaceous Jehol Group of western Liaoning, China. *Geological Journal*, 41, 419–437.
Xu X., Norell, M.A., Wang, X.-L., Makovicky, P.J. & Wu, X.-C. (2002) A basal troodontid from the Early Cretaceous of China. *Nature*, 415, 780–784.
Xu, X., Norell, M.A., Kuang, X., Wang, X., Zhao, Q. & Jia, C. (2004) Basal tyrannosauroids from China and evidence for protofeathers in tyrannosauroids. *Nature*, 431, 680–684.
Xu, X., Clark, J.M., Forster, C.A., Norell, M.A., Erickson, G.M., Eberth, D.A., Jia, C. & Zhao, Q. (2006) A basal tyrannosauroid dinosaur from the Late Jurassic of China. *Nature*, 439, 715–718.
Zhao, Q., Xu, X., Jia, C. & Dong, Z. (2008) Order Saurischia. *In*: Li, J., Wu, X. & Zhang, F. (Eds.), *The Chinese Fossil Reptiles and their Kin*. Science Press, Beijing, 279–335.
Zhao, X.-J., Benson, R.B.J., Brusatte, S.L. & Currie, P.J. (2009) The postcranial skeleton of *Monolophosaurus jiangi* (Dinosauria: Theropoda) from the Middle Jurassic of Xinjiang, China, and a review of Middle Jurassic Chinese theropods. *Geological Magazine*. (published online, doi:10.1017/S0016756809990240)