The skull of *Monolophosaurus jiangi* (Dinosauria: Theropoda) and its implications for early theropod phylogeny and evolution

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The Middle Jurassic was a critical time in the evolution of theropod dinosaurs, highlighted by the origination and initial radiation of the large-bodied and morphologically diverse Tetanurae. Middle Jurassic tetanurans are rare, but have been described from Europe, South America and China. In particular, China has yielded a number of potential basal tetanurans, but these have received little detailed treatment in the literature. Chief among these is *Monolophosaurus jiangi*, known from a single skeleton that includes a nearly complete and well-preserved skull characterized by a bizarre cranial crest. Here, we redescribe the skull of *Monolophosaurus*, which is one of the most complete basal tetanuran skulls known and the only quality source of cranial data for Middle Jurassic Chinese theropods. The cranial crest is atomized into a number of autapomorphic features and several characters confirm the tetanuran affinities of *Monolophosaurus*. However, several features suggest a basal position within Tetanurae, which contrasts with most published cladistic analyses, which place *Monolophosaurus* within the more derived Allosauroidea. Cranial characters previously used to diagnose Allosauroidea are reviewed and most are found to have a much wider distribution among Theropoda, eroding an allosauroid position for *Monolophosaurus* and questioning allosauroid monophyly. The use of phylogenetic characters relating to theropod cranial crests is discussed and a protocol for future use is given. The systematic position of *Guanlong wucaii* is reviewed, and a basal tyrannosauroid affinity is upheld contrary to one suggestion of a close relationship between this taxon and *Monolophosaurus*.

INTRODUCTION

The Middle Jurassic was a critical interval in the evolution of theropod dinosaurs, but much about theropod anatomy, phylogeny and diversity during this time period remains poorly understood. Up until this time, theropod faunas had been dominated by coelophysoids, primitive and mostly small-bodied carnivores that were abundant and widespread until their extinction in the Early Jurassic (Carrano, Hutchinson & Sampson, 2005; Ezcurra & Novas, 2007). Subsequently, derived theropod clades characterized by a larger body size and more diverse

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morphology originated and radiated in the Early to Middle Jurassic (Sereno, 1999; Rauhut, 2003; Allain *et al.*, 2007; Smith *et al.*, 2007; Carrano & Sampson, 2008). The most diverse and most important of these clades, Tetanurae, included the largest carnivorous dinosaurs in most post-Early Jurassic ecosystems, and later gave rise to birds.

The early evolution of Tetanurae is poorly understood, which is largely the fault of a meager Early to Middle Jurassic theropod fossil record (Rauhut, 2003). Most recent phylogenetic hypotheses imply that this clade originated in the latest Early Jurassic (for example, Rauhut, 2003; Smith *et al.*, 2007; Carrano & Sampson, 2008). The oldest known unequivocal tetanurans are found in slightly younger beds, and include the fragmentary *Magnosaurus nethercomensis* and *Duriavenator* from the Bajocian (early Middle Jurassic) of England (Waldman, 1974). Far more complete are several Middle Jurassic theropods from China (X.-J. Zhao *et al.*, unpubl. data), which unfortunately have only been briefly described (Dong, 1984; Dong & Tang, 1985; Gao, 1993; Zhao & Currie, 1993). As a result, these taxa are frequently excluded from studies of theropod phylogeny and evolution, despite representing a lion's share of available data from this crucial time period.

The most complete of these taxa is *Monolophosaurus jiangi*, a large-bodied theropod represented by a partial skeleton from the Middle Jurassic Shishugou Formation of the Junggar Basin. The skull of *Monolophosaurus* is essentially complete and well preserved, rendering it not only the sole source of quality cranial data for early Middle Jurassic Chinese theropods, but also one of the best-known skulls of any basal theropod dinosaur. The skull is also highly autapomorphic, as it is characterized by a bizarre and heavily pneumatized midline crest. However, despite the completeness and uniqueness of the skull, *Monolophosaurus* has only been briefly described, thus hampering a more complete study of its phylogenetic and evolutionary importance. This crested theropod was originally described in a short publication by Zhao & Currie (1993), who noted a strange mosaic of primitive and derived theropod features. They classified it as a 'megalosaur-grade' theropod closely related to *Allosaurus*. Subsequent cladistic studies supported this determination, often placing *Monolophosaurus* within Allosauroidea, a clade of basal tetanurans including *Allosaurus*, *Sinraptor* and other Late Jurassic to Early Cretaceous theropods (Sereno *et al.*, 1994, 1996; Currie & Carpenter, 2000; Holtz, 2000; Rauhut, 2003; Holtz, Molnar & Currie, 2004). However, recent work has suggested that the affinities of this taxon may lie elsewhere, perhaps closer to the base of Tetanurae (Smith *et al.*, 2007; Brusatte & Sereno, 2008). The

evaluation of these alternatives hinges on a better understanding of *Monolophosaurus* anatomy.

Here, we describe the cranial anatomy of *Monolophosaurus*. A redescription of the postcranial anatomy will be published elsewhere (X.-J. Zhao *et al.*, unpubl. data). This redescription is used to address the phylogenetic position of the taxon, as well as the higher level relationships of *Guanlong wucaii*, a supposed basal tyrannosauroid from higher in the Shishugou Formation (Xu *et al.*, 2006). This is primarily intended to be a thorough and rigorous description of the cranial osteology of a single theropod taxon. Together with similar recent monographs (Madsen, 1976; Welles, 1984; Currie & Zhao, 1993; Charig & Milner, 1997; Harris, 1998; Madsen & Welles, 2000; Brochu, 2002; Sampson & Krause, 2007; Brusatte, Benson & Hutt, 2008), we aim to provide primary descriptive data that can be incorporated into wider studies of theropod evolution, especially phylogenetic analyses, many of which have hitherto scored *Monolophosaurus* based solely on the short original description, or excluded it entirely despite its completeness and phylogenetic importance.

ABBREVIATIONS

FMNH, Field Museum of Natural History, Chicago, IL, USA; IVPP, Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, China; MUCP, Museo de la Universidad Nacional del Comahue, El Chocón Collection, El Chocón, Argentina; OMNH, Sam Noble Oklahoma Museum of Natural History, Norman, OK, USA; OUMNH, Oxford University Museum of Natural History, Oxford, UK; UCMP, University of California Museum of Paleontology, Berkeley, CA, USA; UC OBA, University of Chicago Department of Organismal Biology, Chicago, IL, USA; UMNH, Utah Museum of Natural History, Salt Lake City, UT, USA.

SYSTEMATIC PALAEONTOLOGY

DINOSAURIA OWEN, 1842

SAURISCHIA SEELEY, 1888

THEROPODA MARSH, 1881

TETANURAE GAUTHIER, 1986

MONOLOPHOSAURUS JIANGI ZHAO & CURRIE, 1993

Holotype: IVPP 84019, a complete skull and partial postcranial skeleton comprising the pelvis and axial column from the atlas to the sixth caudal vertebra.

Type locality and horizon: Middle Jurassic Shishugou Formation (Eberth *et al.*, 2001), 34 km northeast of Jiangjunmiao in the Jiangjunmiao Depression within

the Junggar Basin, Xinjiang, China. *Monolophosaurus* was collected from low in the Shishugou Formation section north of the now-abandoned village of Jiangjunmiao and east of Gui Hua Mu Yuan (Silicified Wood Park). Based on radiometric ages from overlying tuffs and biostratigraphic data from within and below the Shishugou Formation, *Monolophosaurus* is regarded as no younger than late Callovian (D. A. Eberth, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada, pers. comm., 2009).

Diagnosis: Basal tetanuran theropod possessing the following autapomorphies of the cranium: nasal process of premaxilla bifurcating posteriorly at its contact with the nasal; lateral surface of premaxilla with deep groove leading from the subnarial foramen to a foramen on the base of the nasal process; raised crest on nasal with straight dorsal margin that is nearly parallel to the alveolar margin of the maxilla; two enlarged and equal-sized pneumatic fenestrae in the nasal; lacrimal with discrete tab-like process projecting dorsally above the preorbital bar; associated frontals that are rectangular and much wider than long (width to length ratio of 1.67).

ANATOMICAL DESCRIPTION

The type and only known specimen of *Monolophosaurus* is deeply embedded in hard foam for travelling exhibition, permitting only detailed observation of the right lateral surface of the skull, as well as limited views of the dorsal, ventral, anterior and posterior surfaces of some elements. Observation of the medial surfaces of skull bones is not possible, and detailed observation of articular contacts and certain surfaces is precluded by the articulated nature of the skull.

The cranium (Fig. 1) is 800 m long anteroposteriorly (from the anteroventral corner of the premaxilla to the posteroventral corner of the quadratojugal/quadrate). Its most unique feature is a bizarre midline crest comprising the premaxillae, nasals, lacrimals, prefrontals and frontals (Figs 1–4), which is atomized into several autapomorphic characters as described below. In addition, *Monolophosaurus* differs from most other theropods in the possession of a greatly enlarged external naris, which is 168 mm long anteroposteriorly, 43 mm deep dorsoventrally at its midpoint and 65 mm deep posteriorly. The naris is subrectangular and approximately horizontally inclined, with a greatest dimension of 200 mm that trends slightly anteroventrally. The ratio of the greatest dimension of the naris to the skull length is 0.25, much greater than in other basal theropods (Table 1) and most coelurosaurs. Therizinosaurs (for example, *Erlikosaurus*: Clark,

Table 1. External naris size in theropods

Taxon	Ratio	Source
Monolophosaurus	0.25	IVPP 84019
Acrocanthosaurus	0.12	Currie & Carpenter (2000)
Allosaurus	0.17	Madsen (1976)
Ceratosaurus	0.14	Sampson & Witmer (2007)
Citipati	0.21	Clark *et al.* (2002)
Compsognathus	0.14	Peyer (2006)
Dilophosaurus	0.15	Welles (1984); Tykoski & Rowe (2004)
Erlikosaurus	0.25	Clark *et al.* (1994)
Guanlong	0.26	Xu *et al.* (2006)
Majungasaurus	0.09	Sampson & Witmer (2007)
Ornithomimus	0.13	Makovicky, Kobayashi & Currie (2004)
Sinraptor	0.13	Currie & Zhao (1993)
'*Syntarsus*'	0.14	Tykoski & Rowe (2004)
Tyrannosaurus	0.15	Holtz (2004)
Velociraptor	0.12	Barsbold & Osmolska (1999)

Ratio of the greatest dimension of the naris to the cranium length, measured from the anterior margin of the premaxilla to the posterior margin of the quadratojugal. Only those taxa with nearly complete, articulated skulls are included.

Perle & Norell, 1994) and oviraptorosaurs (for example, *Citipati*: Clark, Norell & Rowe, 2002) also possess enlarged nares, but these differ from those in *Monolophosaurus* in shape and orientation. The nares of therizinosaurs are anteroposteriorly elongate and shallow dorsoventrally, whereas those of oviraptorosaurs are more circular with a long axis inclined strongly anteroventrally, and even nearly vertical in some taxa (for example, *Conchoraptor*: Osmolska, Currie & Barsbold, 2004). The basal tyrannosauroid *Guanlong* (Xu *et al.*, 2006) also has an elongate naris very similar to that of *Monolophosaurus*, as discussed below, as does the basal coelurosaur *Proceratosaurus* (BMNH R 4860).

The antorbital fenestra is 162 mm long and somewhat triangular in shape, with a depth of 106 mm at the posterior margin, which is reduced to only 40 mm anteriorly. The keyhole-shaped orbit is 130 mm deep and 90 mm long anteroposteriorly at its greatest extent, but is constricted to a length of only 12 mm ventrally by the highly convex margins of the lacrimal and postorbital. The lateral temporal fenestra is 143 mm deep, 80 mm long ventrally and 54 mm long dorsally. It is narrowest at the midpoint, where anteriorly oriented processes of the squamosal and quadratojugal constrict the fenestra to a length of 50 mm. The supratemporal fenestra is 78 mm transversely wide, 32 mm anteroposteriorly long at its
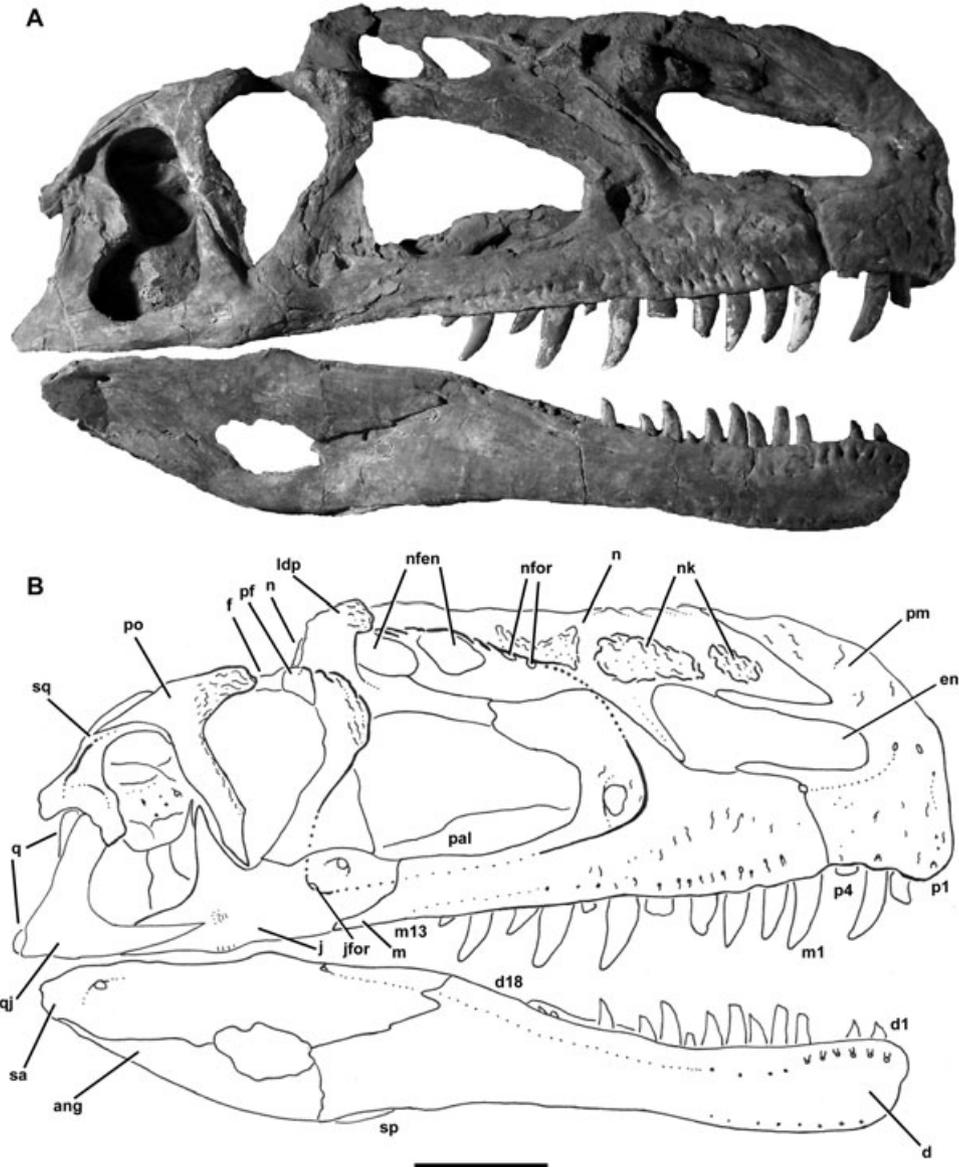
Figure 1. Skull of *Monolophosaurus jiangi* in right lateral view: A, photograph; B, line drawing. Abbreviations: ang, angular; d, dentary; en, external naris; f, frontal; j, jugal; jfor, jugal foramen; ldp, dorsal projection of the lacrimal; m, maxilla; n, nasal; nfen, nasal fenestrae; nfor, nasal foramina; nk, nasal knobs; pal, palatine; pf, prefrontal; pm, premaxilla; po, postorbital; q, quadrate; qj, quadratojugal; sa, surangular; sp, splenial; sq, squamosal. Numerals (e.g. p1) refer to premaxillary, maxillary and dentary tooth positions. Scale bar represents 100 mm.

medial margin and 71 mm long laterally, not counting a narrow notch that extends posteriorly (see below).

CRANIUM

Premaxilla: The premaxilla (Figs 1–3) is an unusual bone in *Monolophosaurus*. The premaxillary body is longer (112 mm) than high (71 mm), as in *Allosaurus* (Madsen, 1976), *Dracovenator* (Yates, 2005), *Dilophosaurus* (Welles, 1984), *Dubreuillosaurus* (Allain, 2002) and coelophysids (Colbert, 1989), not higher than long as in *Acrocanthosaurus* (Currie & Carpenter, 2000), *Ceratosaurus* (Madsen & Welles, 2000), *Torvosaurus* (Britt, 1991), abelisaurids and several coelurosaurs (for example, tyrannosauroids, oviraptorosaurs). However, the premaxillary body is not as relatively long anteroposteriorly as in *Dracovenator*, *Dilophosaurus*, coelophysids and spinosaurids, in which the external naris begins posterior to the premaxillary tooth row.

The anterior margin of the premaxilla is approximately vertically straight, as in *Allosaurus*, *Cerato-*
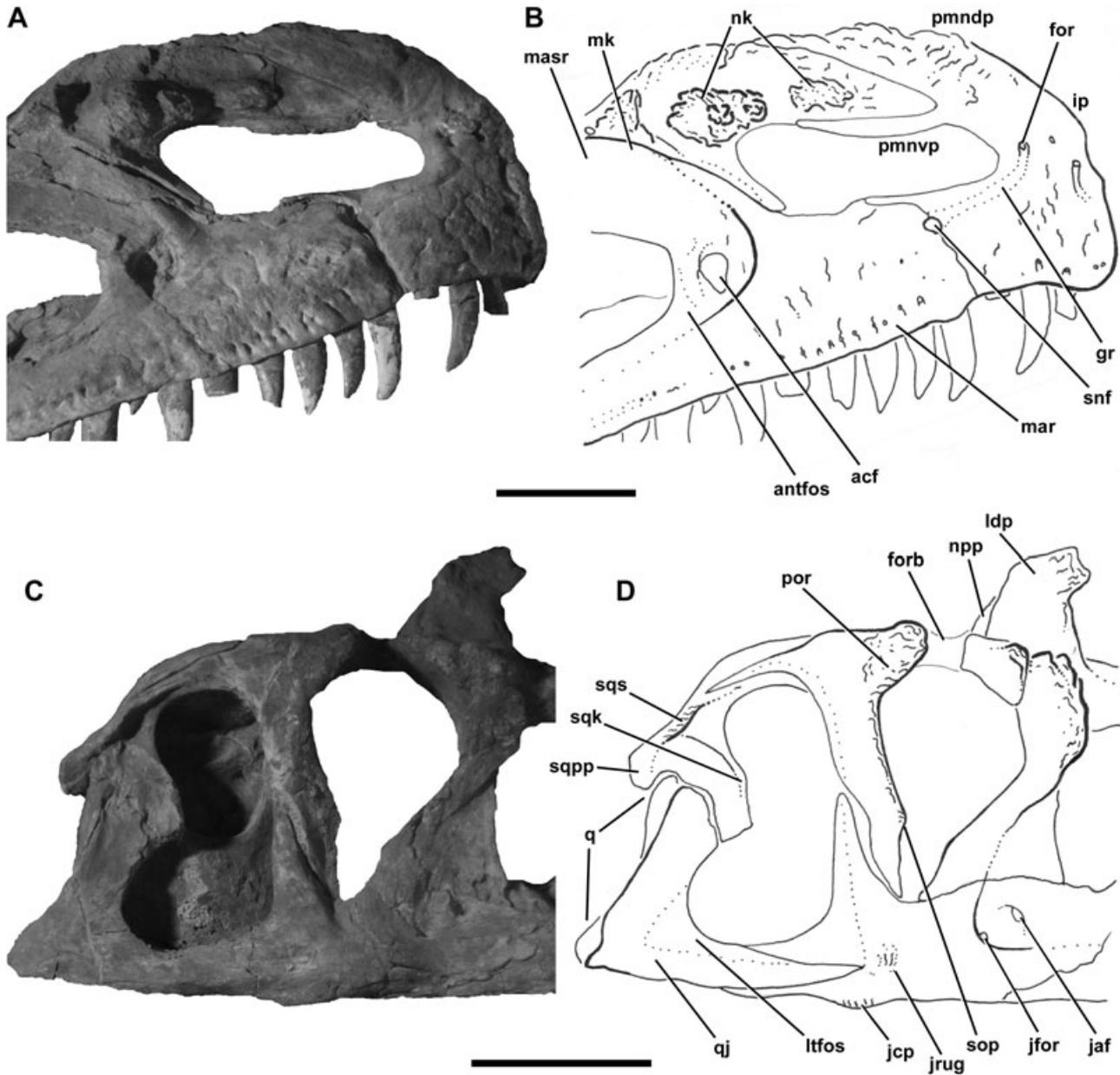
Figure 2. Skull of *Monolophosaurus jiangi* in right lateral view. Anterior region of the snout: A, photograph; B, line drawing. Posterior region of the skull: C, photograph; D, line drawing. Abbreviations: acf, accessory antorbital opening (fossa); antfos, antorbital fossa; for, foramen; forb, orbital rim of the frontal; gr, groove; ip, inflection point; jaf, jugal accessory foramen; jcp, jugal corneal process; jfor, jugal foramen; jrug, rugosity on the jugal; ldp, dorsal projection of the lacrimal; ltfos, lateral temporal fossa; mar, anterior ramus of the maxilla; masr, ascending ramus of the maxilla; mk, kink in the maxilla; nk, nasal knobs; npp, posterior projection of the nasal; pmndp, dorsal projection of the nasal process of the premaxilla; pmnvp, ventral projection of the nasal process of the premaxilla; por, postorbital rugosity; q, quadrate; qj, quadratojugal; snf, subnarial foramen; sop, suborbital projection; sqk, kink in the squamosal; sqpp, posterior process of the squamosal; sqs, squamosal shelf. Scale bar represents 100 mm.

saurus, *Majungasaurus* and *Sinraptor*, not rounded and inclined posteroventrally as in *Acrocanthosaurus*, *Dracovenator*, *Dubreuillosaurus* and *Torvosaurus*. In *Monolophosaurus*, the anterior margin is projected slightly anterodorsally, such that the angle between the alveolar margin and anterior margin ('premaxillary angle' of some authors) is greater than 90°, a condition common in taxa with straight anterior margins. The straight anterior surface extends 92 mm dorsally until an inflection point (Fig. 2, ip),
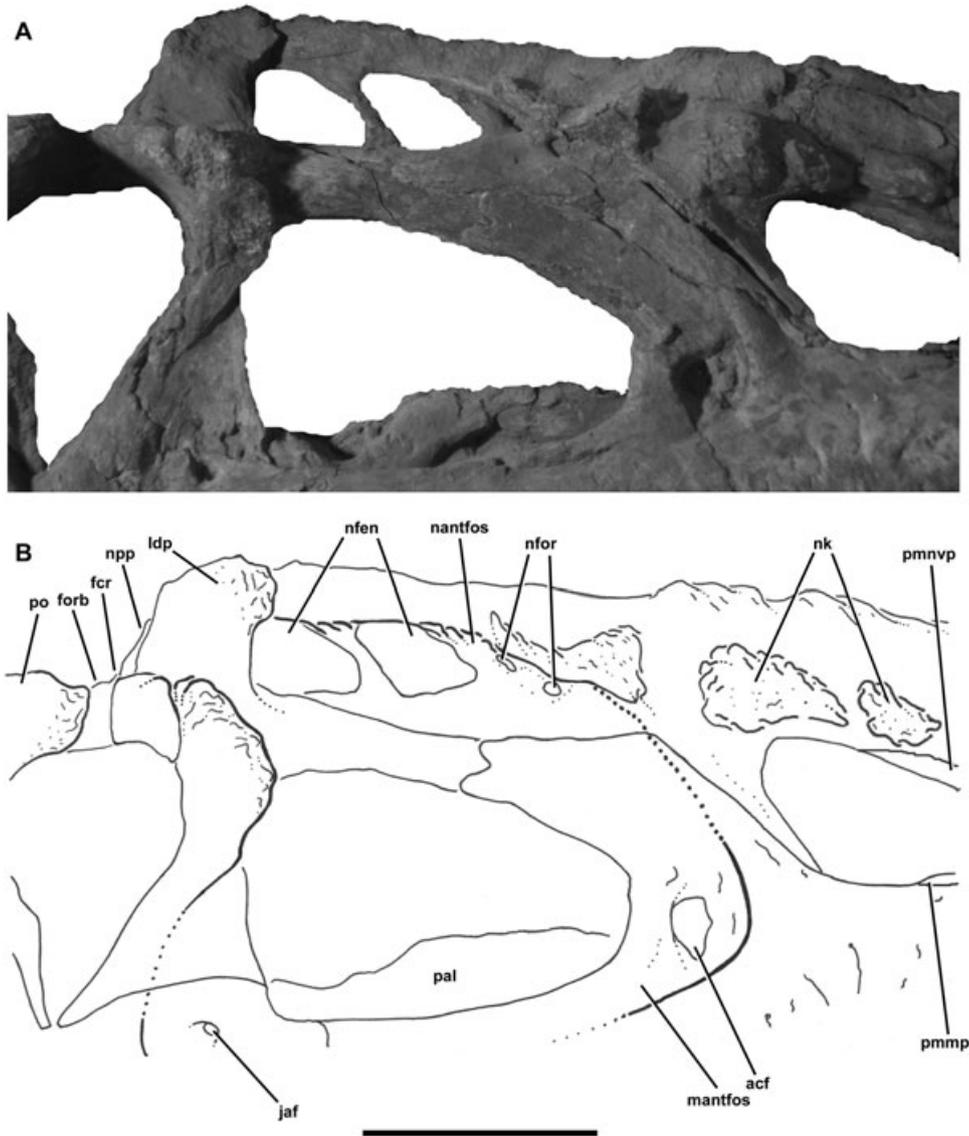
Figure 3. Cranial crest of *Monolophosaurus jiangi* in right lateral view: A, photograph; B, line drawing. Abbreviations: acf, accessory antorbital opening (fossa); fcr, frontal contribution to the crest; forb, orbital rim of the frontal; jaf, jugal accessory foramen; ldp, dorsal projection of the lacrimal; mantfoss, antorbital fossa on the maxilla; nantfoss, antorbital fossa on the nasal; nfen, nasal fenestrae; nfor, nasal foramina; nk, nasal knobs; npp, posterior projection of the nasal; pal, palatine; pmmp, maxillary process of the premaxilla; pmnvp, ventral projection of the nasal process of the premaxilla; po, postorbital. Scale bar represents 100 mm.

level with the midpoint of the external naris, at which the surface curves posterodorsally as it gives rise to the nasal process. Such an extreme dorsal elongation of the straight anterior margin is not seen in other basal theropods with this feature, which instead possess an inflection point located much further ventrally (for example, *Allosaurus*, *Majungasaurus*, *Sinraptor*). However, an extensive straight margin is present in some tyrannosauroids (for example, *Dilong*: Xu *et al.*, 2004; *Eotyrannus*: Hutt *et al.*, 2001;

Guanlong: Xu *et al.*, 2006; *Tyrannosaurus*: Brochu, 2002; Holtz, 2004).

Articulation with the maxilla is complex. Ventrally, a dorsoventrally oriented groove on the posterior surface of the premaxilla abuts the anterior margin of the maxilla. Dorsal to this long contact surface is a posteriorly projecting flange of the premaxilla, the maxillary process, which is visible as a discrete projection in lateral view (Figs 1, 3, pmmp). The elongate ventral contact is slightly posterodorsally inclined,
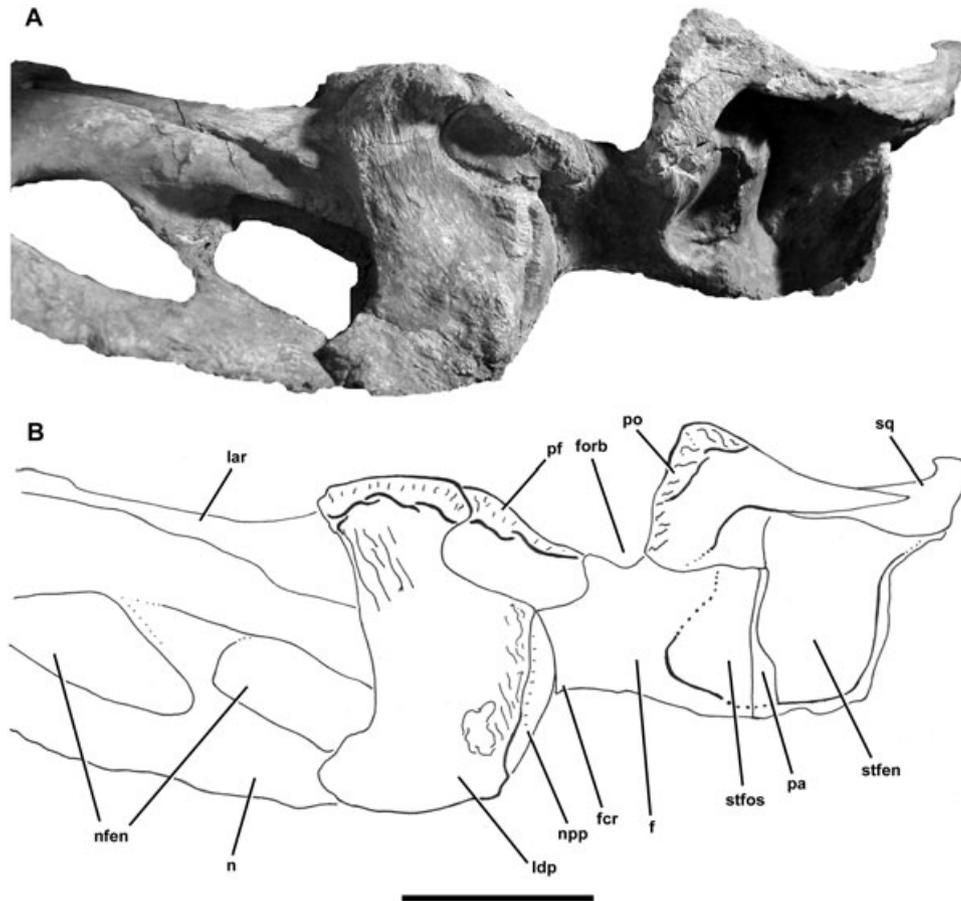
Figure 4. Cranial crest of *Monolophosaurus jiangi* in dorsolateral (dorsal and slightly oblique) view: A, photograph; B, line drawing. Abbreviations: f, frontal; fcr, frontal contribution to the crest; forb, orbital rim of the frontal; lar, lacrimal anterior ramus; ldp, dorsal projection of the lacrimal; n, nasal; nfen, nasal fenestrae; npp, posterior projection of the nasal; pa, parietal; pf, prefrontal; po, postorbital; sq, squamosal; stfen, supratemporal fenestra; stfos, supratemporal fossa. Scale bar represents 50 mm.

although not to the same extent as in most basal theropods (for example, coelophysids: Tykoski & Rowe, 2004; *Ceratosaurus*: Madsen & Welles, 2000; allosauroids: Currie & Carpenter, 2000; Coria & Currie, 2006). Instead, the condition is more similar to *Allosaurus*, in which this articulation is generally straight dorsoventrally (Madsen, 1976). There is no subnarial gap or notch along the tooth row where the premaxilla and maxilla articulate, as is the case in coelophysids (Colbert, 1989) and *Zupaysaurus* (Ezcurra, 2007). The maxillary process is thin and finger-like and slightly wraps around the maxilla medially. It extends 50 mm posterior to the ventral premaxillary–maxillary articulation, is parallel with the alveolar margin and tapers in depth posteriorly.

The nasal process of the premaxilla is unique in *Monolophosaurus*, as it bifurcates posteriorly to receive the anterior portion of the nasal (Fig. 2B, pmndp, pmnvp). The dorsal ramus of this bifurcation

is much larger than the ventral prong. It takes the form of a posteroventrally inclined elongate triangle that is 42 mm dorsoventrally deep at its base. In contrast, the ventral prong is finger-like, keeps a relatively constant depth of approximately 10 mm throughout its length and is oriented nearly parallel to the alveolar row. Both processes extend posteriorly for approximately 120 mm. The ventral prong was not figured by Zhao & Currie (1993: fig. 1), and represents an autapomorphy of *Monolophosaurus*, as it is not present in other basal tetanurans (for example, Madsen, 1976).

The lateral surface of the premaxilla is rugose and ornamented with numerous foramina, many of which are set into shallow grooves. These foramina are especially concentrated near the anterior margin of the bone. A single large foramen is located at the base of the nasal process (Fig. 2B, for) as in many theropods (for example, *Dubreuillosaurus*, *Neovenator*,

Torvosaurus, *Tyrannosaurus*). This foramen resembles a dorsoventrally elongated oval, and is not slot-shaped as in *Dilophosaurus* and *Dracovenator* (Yates, 2005). A large oval-shaped subnarial foramen (17 mm dorsoventrally deep by 11 mm anteroposteriorly long) is present between the premaxilla and maxilla, immediately ventral to the maxillary process of the premaxilla. A shallow groove extends anteriorly from the subnarial foramen, paralleling the ventral border of the external naris (Fig. 2B, gr). The groove curves dorsally to follow the anterior margin of the naris and becomes confluent with the foramen at the base of the nasal process. Such a groove is unknown in other theropods and represents another autapomorphy of *Monolophosaurus*. The lateral surface of the premaxilla around the periphery of the external naris does not bear a shallow fossa as it does in *Acrocanthosaurus*, *Allosaurus*, *Dracovenator*, *Dubreuillosaurus*, *Sinraptor*, and many other basal theropods; instead, this region is slightly rugose. The dorsal prong of the nasal process is also rugose, and is marked by numerous linear striations that are horizontal anteriorly but slightly posterodorsally inclined on the posterior surface of the process. Most of the premaxillary body shows a mottled and irregular pattern of rugosity.

Because the skull is articulated, most details of the medial surface of the premaxilla are concealed. However, it is apparent that the interdental plates are unfused, and resemble dorsoventrally shallow triangles. The labial wall of the alveolar row, comprising the lateral surface of the premaxillary body, extends further ventrally than the lingual wall, which is formed from the interdental plates. Four alveoli are present, and the first is notably smaller than the remaining three (Table 2). There is no *en echelon* overlap of the alveoli as has been described in *Torvosaurus* (Britt, 1991) and is present in other basal theropods (for example, *Dubreuillosaurus*: MNHN 1998-13; *Neovenator*: Brusatte *et al.*, 2008).

Maxilla: The maxilla (Figs 1–3) is 400 mm long anteroposteriorly along the tooth row, and comprises most of the ventral and anterior border of the antorbital fenestra. The maxillary body tapers only slightly in depth posteriorly, thinning from a depth of 65 mm at the anterior margin of the antorbital fenestra to 50 mm at the posterior end of the bone. This contrasts with most basal theropods (for example, *Allosaurus*: Madsen, 1976; *Dubreuillosaurus*: Allain, 2002; *Piatnitzkysaurus*: Bonaparte, 1986; *Sinraptor*: Currie & Zhao, 1993), in which the maxilla extensively tapers posteriorly, and is similar to the condition in *Zupaysaurus* (Ezcurra, 2007) and abelisaurids, which possess maxillae that maintain a relatively constant depth throughout their length.

Table 2. Measurements of the alveoli and erupted teeth

Element	Alveolus	Mesiodistal	Labiolingual	CBL	CBW
Premaxilla	1	11	9	–	–
	2	15	11	–	–
	3	18	11	–	–
	4	17	14	–	–
Maxilla	1	22	12	–	–
	2	20	10	–	–
	3	21	10	–	–
	4	20	10	–	–
	5	22	12	–	–
	6	23	12	–	–
	7	18	10	–	–
	8	24	12	–	–
	9	18	9	–	–
	10	21	8	–	–
	11	15	5	–	–
	12	10	5	–	–
	13	7	4	–	–
Dentary	1	6	5	–	–
	2	8	6	–	–
	3	10	6	9	5
	4	10	6	–	–
	5	14	9	13	6
	6	16	9	16	6
	7	13	9	13	5
	8	15	10	14	6
	9	15	10	14	6
	10	10	9	7	3
	11	15	10	15	7
	12	12	9	11	4
	13	10	8	–	–
	14	13	8	12	4
	15	14	5	–	–
	16	9	5	–	–
	17	6	4	5	3
	18	5	3	4	2

Mesiodistal and labiolingual measurements refer to the alveoli and CBL (crown base length) and CBW (crown base width) refer to the teeth, following the terminology of Smith & Dodson (2003). Measurements taken from the right skull elements, all measurements in millimetres. Only clear erupted teeth not heavily reconstructed by plaster are included.

As in many other basal tetanurans, there is a distinct anterior ramus that projects from the maxillary body anterior to the ascending ramus (Fig. 2B, mar). In *Monolophosaurus*, this ramus is roughly square-shaped, with a depth of 92 mm and an anteroposterior length of 90 mm. Similar rami are present in *Afrovenator* (Sereno *et al.*, 1994), *Allosaurus* (Madsen, 1976), *Dubreuillosaurus* (Allain, 2002), *Neovenator* (Brusatte *et al.*, 2008), *Torvosaurus* (Britt,

1991) and spinosaurids, many of which exhibit a projection that is longer than deep. In contrast, many basal theropods (for example, *Acrocanthosaurus*: Currie & Carpenter, 2000; *Ceratosaurus*: Madsen & Welles, 2000; *Coelophysis*: Colbert, 1989; *Sinraptor*: Currie & Zhao, 1993; *Zupaysaurus*: Ezcurra, 2007) possess a slight ramus that is much deeper than long, or lack this process altogether.

The surfaces for contact with the premaxilla, nasal, jugal and lacrimal are preserved. The premaxilla is contacted via a nearly vertical margin on the anterior surface of the anterior ramus, and the nasal articulates with the anterior and dorsal surfaces of the ascending ramus. This latter articulation does not reach the posterior margin of the maxilla–premaxilla contact, thus allowing the maxilla to make a 40 mm contribution to the external naris. A maxillary contribution to the external naris is also seen in many other basal theropods, including *Afrovenator*, *Carcharodontosaurus* (Sereno *et al.*, 1996), *Neovenator*, *Torvosaurus* (Britt, 1991) and spinosaurids (Sues *et al.*, 2002). The jugal laterally overlaps the maxilla across a posteroventrally oriented articulation, which results in a thin and tapering posterior process of the maxilla that extends 40 mm posterior to the maxillary body. Finally, the posterior surface of the maxillary ascending ramus is excavated by a shallow notch for articulation with the lacrimal. The maxilla overlaps the lacrimal at this contact.

In lateral view, the surface of the maxilla is marked by numerous foramina, which are especially abundant near the articulation with the premaxilla and along the tooth row. These latter foramina are large, measuring up to 5 mm in diameter, and are located immediately above and parallel to the tooth row for the entire length of the bone. The foramina decrease in size posteriorly, and grade into a groove that continues posteriorly from the level of the 11th alveolus. This sculpturing is broadly similar to that of most theropods, and is not as extensive as in most carcharodontosaurids (Sereno *et al.*, 1996; Brusatte & Sereno, 2007; Brusatte *et al.*, 2008) or abelisaurids (Lamanna, Martínez & Smith, 2002; Sampson & Witmer, 2007), in which elongated grooves and ridges ornament much of the lateral surface.

The ascending ramus of the maxilla (Fig. 2B, masr) rises posterodorsally from the maxillary body at an angle of approximately 45°. It maintains a posterodorsal trend for 102 mm, reaches an inflection point and continues as a horizontal process for 64 mm before articulating with the lacrimal (Fig. 2B, mk). A similar inflection is seen in *Neovenator* (Brusatte *et al.*, 2008), and is not as pronounced as the distinct kink seen in spinosauroids, such as *Afrovenator* (UC OBA 1) and *Dubreuillosaurus* (Allain, 2002). The lateral lamina of the ascending ramus slightly over-

hangs the anterior margin of the antorbital fossa, thins as it continues dorsally and merges with the medial lamina at the inflection point. Posterior to the inflection point, the medial lamina articulates with the lacrimal and nasal, and all three elements are excavated by the antorbital fossa.

The antorbital fossa excavates the lateral surfaces of the posterior region of the ascending ramus and the dorsal region of the maxillary body. On the ascending ramus, the fossa extends 46 mm posteriorly before reaching the antorbital fenestra. Thus, it is not elongated anteroposteriorly as in coelurosaurs (Holtz *et al.*, 2004). The fossa has limited exposure on the maxillary body, extending 18 mm ventrally immediately anterior to the antorbital fenestra and tapering to a depth of 8 mm in the region of the jugal articulation. This contrasts with the more extensive fossa on the maxillary body of coelophysids, some spinosauroids (*Afrovenator*, *Dubreuillosaurus*: Allain, 2002), *Zupaysaurus* (Ezcurra, 2007), *Ceratosaurus* (Madsen & Welles, 2000) and some allosauroids (Madsen, 1976; Currie & Zhao, 1993), as well as the total lack of the antorbital fossa on the maxillary body of most abelisaurids (Sampson & Witmer, 2007). Anteriorly, the rim surrounding the antorbital fossa is rounded, not squared-off as in *Afrovenator*, *Dubreuillosaurus*, *Zupaysaurus*, some carcharodontosaurids (*Eocarcharia*, *Neovenator*: Sereno & Brusatte, 2008) and coelophysids (Colbert, 1989; Ezcurra, 2007). The rim along the ventral margin of the fossa is sharply defined anteriorly, but becomes less prominent posteriorly, such that posterior to the eighth alveolus the antorbital fossa is only demarcated by a slight change in bone texture. Again, this contrasts with the condition in coelophysids and *Zupaysaurus*, which are characterized by a sharp rim paralleling the tooth row throughout its length.

A single accessory antorbital opening pierces the antorbital fossa in *Monolophosaurus* (Figs 2B, 3, acf). The identification of this opening is unclear: Witmer (1997: 44) describes it as ambiguous, but regards it as 'occupying the position of the promaxillary fenestra.' As its relationships to the internal antorbital sinuses are unknown, we do not assign this opening a name. Although broken margins preclude an exact measurement, apparently this opening was quite large and deep. The opening on the right side appears to be closed medially, not open as reconstructed on the left side by Zhao & Currie (1993), and therefore forms a fossa rather than a fenestra. The pillar separating this opening from the antorbital fenestra is thin, measuring only 20 mm in anteroposterior length. There is no pneumatic excavation on the ascending ramus as in *Acrocanthosaurus* (NCSM 14345), *Eocarcharia* (Sereno & Brusatte, 2008) and *Sinraptor* (Currie & Zhao, 1993), and, to a lesser extent,

Ceratosaurus (Madsen & Welles, 2000) and some specimens of *Allosaurus* (Witmer, 1997). Finally, there is no smaller anterior opening concealed by the lateral lamina, as is sometimes the case in theropods (Witmer, 1997).

In medial view, the interdental plates are dorsoventrally shallow and appear to be unfused, although exact measurements were not possible. As in the premaxilla, the labial wall of the alveoli extends further ventrally than the lingual wall. The tooth row contains 13 alveoli. The teeth were heavily reconstructed for exhibition, but functional teeth are present and visible in alveoli 2, 4, 7 and 9 on the right side. Low, band-like enamel wrinkles are present on the labial surfaces of exposed crowns. These are similar in morphology to the enamel wrinkles of many basal tetanurans (Brusatte *et al.*, 2007) and differ from the more pronounced wrinkles of some carcharodontosaurids, which are especially distinct marginally near the serrations.

Nasal: The nasal of *Monolophosaurus* is a distinctive bone, as it is expanded and greatly modified to form the major component of the cranial crest (Figs 1–4). This element is 435 mm long anteroposteriorly and is broadly exposed in lateral view throughout its length, in contrast with most other basal theropods. Such exposure is the result of extreme dorsal expansion, which is also the case in the crested *Dilophosaurus* (Welles, 1984), but not *Cryolophosaurus* (Smith *et al.*, 2007). *Zupaysaurus* was originally described as possessing a similar crest comprising dorsoventrally expanded and laterally exposed nasals (Arcucci & Coria, 2003), but the holotype was recently reinterpreted as lacking any sort of cranial ornamentation (Ezcurra, 2007). In addition, the anterior region of the nasal of *Ceratosaurus* is expanded dorsoventrally (Madsen & Welles, 2000), but this localized, horn-like structure is clearly different from the crest of *Monolophosaurus*, which involves the entire nasal.

In *Monolophosaurus*, the nasals are also anteroposteriorly expanded, such that they extend posterior to the lacrimals and prefrontals (Figs 2D, 3, 4, npp). This is not the case in *Dilophosaurus* (Welles, 1984) or *Cryolophosaurus* (Smith *et al.*, 2007). The dorsal margin of the nasal contribution to the crest is nearly straight in *Monolophosaurus*, and is approximately parallel to the alveolar margin of the maxilla throughout its entire length (~5° angle). This is an autapomorphy, and differs from the condition of other basal theropods, which generally exhibit an angle of 30–40° (for example, *Allosaurus*, *Ceratosaurus*, *Majungasaurus*, *Sinraptor*) or a rounded dorsal margin (for example, *Dilophosaurus*, *Guanlong*: Xu *et al.*, 2006).

The nasal articular surfaces for the premaxilla, maxilla, lacrimal, frontal and prefrontal are preserved. The maxilla and lacrimal are contacted by the ventral surface of the nasal, and thus any details of this contact are obscured by the articulated nature of the skull. The dorsal expansion of the lacrimal also makes contact with the lateral surface of the nasal, but crushing obscures further details. The prefrontal articulates with the posterolateral corner of the nasal immediately dorsal to the orbital rim, and the frontal meets the posterior end of the nasal in an approximately transverse contact near the posterior termination of the crest. The nasals are not separated posteriorly by a wedge of the frontals as in *Cryolophosaurus* (Smith *et al.*, 2007). Contact with the premaxilla takes the form of a large, elongate, triangular-shaped process that extends 125 mm anterior to the nasal body. This process is oriented approximately horizontally for most of its length, demarcating the dorsal rim of the external naris. However, it curves slightly ventrally as it tapers anteriorly, and meets the premaxilla along an anteroventrally trending suture. Ventral to this process, the ascending ramus of the maxilla is contacted by a much smaller, finger-like process. This 53-mm-long process is angled strongly anteroventrally, tapers as it continues ventrally and forms the posterior margin of the external naris.

Dorsally, the opposing nasals are co-ossified, but the midline suture is still visible. The nasal crest rises into a thick sheet dorsally, similar to the condition in *Dilophosaurus* and *Guanlong* (Xu *et al.*, 2006), although the crests of these taxa are much thinner. Thus, the nasal is not flat dorsally as in most basal theropods (for example, *Zupaysaurus*: Ezcurra, 2007; coelophysids: Tykoski & Rowe, 2004) or vaulted and broadly convex dorsally as in other taxa with fused nasals (for example, *Majungasaurus*: Sampson & Witmer, 2007; tyrannosauroids: Snively, Henderson & Phillips, 2006). The nasals of *Ceratosaurus* are flat posterior to the nasal horn (Madsen & Welles, 2000) and those of abelisaurids are convex (Bonaparte, Novas & Coria, 1990). *Allosaurus* (Madsen, 1976), *Cryolophosaurus* (Smith *et al.*, 2007) and *Neovenator* (Brusatte *et al.*, 2008) exhibit an interesting condition in which robust lateral ridges give the nasal a somewhat concave appearance in dorsal view. Nevertheless, this morphology is broadly similar to that of most basal theropods, which are characterized by extensively exposed nasals in dorsal view, and differs from *Monolophosaurus*. However, *Monolophosaurus* shares with *Cryolophosaurus* nasals that become pinched between the lacrimals in dorsal view (Smith *et al.*, 2007: fig. 6), although the morphology is different in detail. In *Cryolophosaurus*, the nasals terminate underneath the lacrimal crest and do not greatly

expand posterior to the pinched region. In contrast, the nasals of *Monolophosaurus* extend posterior to the expanded lacrimal contribution to the crest (Figs 2D, 3, 4, npp), and expand in width posterior to the constriction, such that the width of the posterior margin is nearly identical to the width of the nasal body anteriorly.

The lateral surface of the nasal is heavily rugose, except for the region excavated by the antorbital fossa (Figs 1, 3, nantfos). The premaxillary process and anterior region of the nasal body exhibit a swollen and knobbly texture, which includes a series of discrete swellings (Figs 2B, 3, nk). The right nasal is marked by two knobs on the premaxillary process and one immediately posterior to the process on the nasal body. The most anterior knob is located directly dorsal to the midpoint of the external naris. Posterior to this is a much larger swelling positioned dorsal to the posterodorsal corner of the external naris. This rugosity is 35 mm deep dorsoventrally and 70 mm long anteroposteriorly at its widest extent, and overhangs the nasal 24 mm laterally. Finally, posterior to this knob is a 70-mm-long 'V'-shaped knob dorsal to the inflection point on the maxillary ascending ramus. This knob has a maximum depth of 20 mm and projects 14 mm laterally. The posterior wing of the swelling demarcates the anterodorsal border of the antorbital fossa, and is essentially continuous with the edge of the lateral lamina of the maxilla. This wing forms a ridge that pinches out posteriorly and, in this region, the antorbital fossa is only demarcated by a gentle change in bone texture.

The nasal antorbital fossa of *Monolophosaurus* is unique. The nasal contributes to the antorbital fossa in allosauroids; it is broadly exposed in lateral view in *Allosaurus* (Madsen, 1976) and *Sinraptor* (Currie & Zhao, 1993), is reduced laterally in *Neovenator* (Brusatte *et al.*, 2008), and is restricted to the ventral surface in derived carcharodontosaurids (for example, *Carcharodontosaurus*: SGM-Din 1; *Giganotosaurus*: MUCPv-CH-1; *Mapusaurus*: Coria & Currie, 2006). Although often considered a synapomorphy of allosauroids, a nasal antorbital fossa is also present in the basal theropods *Cryolophosaurus* (Smith *et al.*, 2007) and *Dilophosaurus* (Smith *et al.*, 2007). In addition, a narrow fossa contiguous with the maxillary and lacrimal antorbital fossa surrounds a large nasal pneumatopore in the abelisaurid *Majungasaurus* (Sampson & Witmer, 2007). The nasal contribution to the fossa in *Monolophosaurus* is extensive and excavated by several pneumatic openings. Two small pneumatopores are present ventral to the most posterior swelling described above (Figs 1, 3, nfor); the anterior opening is 17 mm long anteroposteriorly and 7 mm deep dorsoventrally, whereas the posterior foramen is 21 mm × 5 mm. These anteroposteriorly elongate foramina are teardrop-shaped, and are overhung dorsally by the swelling. Posterior to these small foramina are two enormous fenestrae that probably opened medially (Zhao & Currie, 1993) and completely pierced the nasal crest (Figs 1, 3, nfen). Both fenestrae are oval-shaped with a posterodorsally oriented long axis (60 mm for the anterior opening, 55 mm for the posterior opening). The posterior fenestra is bounded posteriorly by the upturned and dorsally extended process of the lacrimal. Ventral to these openings, the nasal antorbital fossa is smooth and continuous with the fossa on the maxilla and lacrimal.

The pattern of nasal pneumaticity is similar on both sides of the skull and is autapomorphic for *Monolophosaurus*. Although pneumatopores are apparently absent in *Ceratosaurus* (Madsen & Welles, 2000), *Cryolophosaurus* (Smith *et al.*, 2007) and *Zupaysaurus* (Ezcurra, 2007), some basal theropods exhibit lateral openings penetrating the nasal. The number of pneumatic openings in many theropods is two (for example, *Giganotosaurus*: MUCPv-CH-1; *Mapusaurus*: Coria & Currie, 2006; *Sinraptor*: Currie & Zhao, 1993), whereas *Majungasaurus* and *Neovenator* possess one (Sampson & Witmer, 2007; Brusatte *et al.*, 2008), and *Allosaurus* variably exhibits one, two or three (Currie & Zhao, 1993). Unfortunately, nasals are missing for many basal theropods, precluding broader comparisons. Most importantly, no other theropod possesses the two enlarged and equal-sized fenestrae of *Monolophosaurus*. The most similar condition is seen in *Guanlong*, in which four large fenestrae of varying sizes are present (Xu *et al.*, 2006). The two smaller anterior pneumatopores of *Monolophosaurus* are similar in size, form and location to the pneumatic openings of other theropods, but we hesitate to homologize these structures pending a more detailed study of nasal pneumaticity. Computed tomography (CT) scans briefly discussed by Zhao & Currie (1993) show that the nasals of *Monolophosaurus* are extensively pneumatized, rendering the nasal almost completely hollow internally. However, a median septum is clearly visible, in contrast with *Majungasaurus*, which also exhibits rugose, extensively pneumatized and fused nasals with no median septum (Sampson & Witmer, 2007).

Lacrimal: The lacrimal of *Monolophosaurus* is also modified to participate in the cranial crest (Figs 1–4). This bone does not take the shape of an inverted 'L' in lateral view as in most theropods, but rather resembles a sideways 'T', as a result of an autapomorphic dorsal projection that forms the posterolateral region of the crest (Figs 1–4, ldp). The other processes comprising the lacrimal include anterior and ventral rami that are broadly similar to those of

other theropods. The anterior ramus is 100 mm long, curves ventrally as it continues anteriorly and is marked by a concave ventral margin. The ventral ramus is 95 mm deep dorsoventrally; it is 22 mm long anteroposteriorly at its narrowest constriction at the centre of the orbit, and fans out to a length of 77 mm ventrally where it meets the jugal. The posterior margin is concave for most of its length, but becomes slightly convex ventrally, thus constricting the orbit. This constriction was interpreted as the attachment of ligamentum suborbitale by Currie & Zhao (1993), and probably represents the ventral limit of the eyeball in life. In *Monolophosaurus*, it is less distinct and positioned further ventrally than in many other large theropods (for example, *Acrocanthosaurus*: Currie & Carpenter, 2000; *Cryolophosaurus*: Smith *et al.*, 2007; *Majungasaurus*: Sampson & Witmer, 2007; *Sinraptor*: Currie & Zhao, 1993). The anterior and ventral rami meet at an angle of approximately 70° as in many large theropods, and are not nearly perpendicular as in *Dubreuillosaurus* (Allain, 2002), *Torvosaurus* (Britt, 1991), *Zupaysaurus* (Ezcurra, 2007) and coelophysids.

Articular surfaces with the maxilla, nasal, jugal and prefrontal are partially visible. The anterior ramus is overlapped by the ascending ramus of the maxilla anteriorly and contacts the nasal dorsally via a long suture. The nasal slightly overhangs the lacrimal along this suture, and both elements are smoothly excavated in this region by the antorbital fossa. In addition, the medial surface of the dorsal expansion contacts the lateral surface of the nasal. The ventral ramus expands ventrally to overlap the jugal, resulting in a dorsally convex suture in lateral view. Finally, the prefrontal abuts a notch in the posterior margin of the lacrimal, which arises as a result of the slight posterior expansion of the dorsal sheet-like process relative to the lacrimal body. The prefrontal excludes the lacrimal from contacting the postorbital dorsal to the orbit, as is the case in carcharodontosaurids (for example, Sereno *et al.*, 1996; Sereno & Brusatte, 2008) and abelisaurids (for example, Sampson & Witmer, 2007).

In lateral view, a large rugosity rises from the region immediately anterodorsal to the orbit where the various rami of the lacrimal meet. This rugosity is heavily striated and slightly overhangs the anterior and ventral rami laterally. Anterior to this rugosity, the anterior ramus is excavated by the antorbital fossa, which also envelops much of the anterior margin of the ventral process. However, these regions of the antorbital fossa are not contiguous, and are instead separated by a rugose anterior process of the ventral ramus that projects into the posterodorsal corner of the antorbital fenestra. The portion of the antorbital fossa on the anterior ramus is not pen-

etrated by any visible pneumatic openings. Therefore, *Monolophosaurus* differs from most theropods (for example, *Afrovenator*, *Allosaurus*, *Ceratosaurus*, *Cryolophosaurus*, *Ornitholestes*, *Torvosaurus*, *Sinraptor*, *Zupaysaurus*; see review in Ezcurra & Novas, 2007), but is similar to coelophysids, which lack extensive lacrimal pneumaticity. Abelisaurids (for example, *Majungasaurus*: Sampson & Witmer, 2007) are characterized by a large pneumatopore that is only visible medially. As the medial surface of the lacrimal is not visible in *Monolophosaurus*, this condition cannot be ruled out.

The dorsal tab-like expansion of the lacrimal is an autapomorphy of *Monolophosaurus* (Figs 1–4, ldp). This rectangular, thin process extends 70 mm dorsal to the lacrimal body, is slightly expanded anteriorly at its dorsal tip and slopes medially, such that it is strongly offset medially from the remainder of the lacrimal. The lateral surface of the process is heavily rugose, especially along its posterior margin, and ornamented by numerous dorsoventrally and anteroposteriorly trending striations. This process reaches the top of the crest on the right side, but falls approximately 8 mm short on the left, a feature not likely to be a result of preservation.

Dorsal expansions characterize the lacrimals of many theropods, but differ in detail. Allosauroids (for example *Acrocanthosaurus*: Currie & Carpenter, 2000; *Sinraptor*: Currie & Zhao, 1993) typically possess a raised dorsal margin of the lacrimal, which is elaborated into a pronounced 'hornlet' in *Allosaurus* (Madsen, 1976). A similar hornlet is also seen in *Ceratosaurus* (Madsen & Welles, 2000) and some tyrannosaurids (Currie, 2003), and a much lower eminence is present in some spinosauroids, such as *Eustreptospondylus* (Sadlier, Barrett & Powell, 2008) and *Torvosaurus* (Britt, 1991). *Cryolophosaurus* possesses a unique morphology in which the lacrimals expand dorsally into a transverse, fluted crest (Smith *et al.*, 2007), and *Dilophosaurus* is characterized by an extreme sheet-like dorsal expansion of the lacrimals (Welles, 1984). This latter condition is most similar to that in *Monolophosaurus*. However, the entire dorsal margin of the lacrimal is expanded in *Dilophosaurus*, whereas only the margin immediately above the preorbital bar is expanded in *Monolophosaurus*. Thus, unlike in *Dilophosaurus*, the dorsal expansion of *Monolophosaurus* takes the form of a discrete tab-like projection, and the anterior ramus is unexpanded dorsally and of a more typical theropod morphology.

Postorbital: The postorbital is 'T'-shaped as in most theropods, and comprises anterior, posterior and ventral rami (Figs 1–4). The anterior ramus is shaped like a blunt triangle, and turns strongly medially as it

extends anteriorly. This process is 30 mm long and forms most of the posterodorsal border of the orbit. It contacts the frontal medially via the powerfully inturned anterior margin of the ramus, as in many basal theropods (for example, *Ceratosaurus*: Madsen & Welles, 2000; *Cryolophosaurus*: Smith *et al.*, 2007; *Zupaysaurus*: Ezcurra, 2007; coelophysids: Colbert, 1989). The anterior ramus is also oriented medially in *Allosaurus* (Madsen, 1976) and *Sinraptor* (Currie & Zhao, 1993), but both taxa exhibit a rugose bulge that extends anteriorly and nearly contacts the lacrimal. This rugosity is free-standing and separated from the frontal, prefrontal and remainder of the anterior ramus by a notch, and is clearly absent in *Monolophosaurus*. Carcharodontosaurids (for example, Sereno *et al.*, 1996; Coria & Currie, 2006; Sereno & Brusatte, 2008) and abelisaurids (Sampson & Witmer, 2007) exhibit a more extreme condition in which the postorbital and lacrimal meet above the orbit, and thus the anterior ramus meets both the lacrimal anteriorly and the frontal medially.

The posterior ramus extends for 55 mm posteriorly and contributes to the dorsal margin of the lateral temporal fenestra. It takes the form of a gracile, elongate triangle, which is 22 mm deep dorsoventrally at its base and tapers to a point posteriorly. The ventral margin of this process is strongly concave ventrally and the entire process is deflected slightly ventrally. Medially, this process articulates with a lateral groove on the squamosal. Along this articulation, the posterior ramus is entirely exposed laterally, a condition seen in many (for example, *Afrovenator*, *Acrocanthosaurus*, *Allosaurus*, *Dubreuillosaurus*, *Zupaysaurus*), but not all (for example, *Sinraptor*), basal theropods.

The ventral ramus is 120 mm deep dorsoventrally and slightly inclined anteroventrally. It contacts the jugal ventrally via a slightly laterally facing groove, which trends anteroventrally. This articulation begins at the posteroventral margin of the orbit and, as a result, the postorbital reaches the floor of the orbit (Figs 1, 2). This morphology is also seen in many basal theropods (for example, *Afrovenator*, *Dilophosaurus*, *Dubreuillosaurus*, *Zupaysaurus*), but contrasts with the condition in *Ceratosaurus*, most abelisaurids (Sampson & Witmer, 2007) and allosauroids (Madsen, 1976; Currie & Zhao, 1993; Sereno *et al.*, 1996; Currie & Carpenter, 2000), in which the postorbital–jugal articulation begins well dorsal to the ventral floor of the orbit, thus excluding the postorbital from this margin.

Unremoved matrix remains between the postorbital and the jugal at their articulation. As such, it is not possible to determine whether the cross-section of the ventral process is 'U'-shaped, as in spinosauroids, or triangular, as in other non-coelurosaurian theropods (Sereno *et al.*, 1996; Rauhut, 2003). The posterior margin of the ventral process of the postorbital is slightly convex until reaching the jugal articulation, at which point it becomes concave to meet the jugal. The anterior margin is concave for most of its length, but is marked by a slight suborbital projection approximately 40 mm from the floor of the orbit (Fig. 2D, sop). This projection is similar to that in *Sinraptor* (IVPP 10600; Currie & Zhao, 1993), and differs from the more pronounced and discrete projections of carcharodontosaurids (Sereno *et al.*, 1996; Chure, 2000; Sereno & Brusatte, 2008). Like the corresponding process on the posterior margin of the lacrimal, this projection would have served to delimit the ventral extent of the eyeball. Its ventral position in *Monolophosaurus* indicates that the eyeball was much larger in this taxon than in allosauroids (Currie & Zhao, 1993).

The lateral surface of the postorbital is slightly rugose in the region in which the three rami meet ('postorbital body'). This rugosity continues down the anterior margin of the ventral process, whereas the posterior edge of the ventral process and the entire posterior process are weakly excavated by a smooth fossa surrounding the lateral temporal fenestra (Fig. 2D, por, ltfos). This fossa also extends onto adjacent circumtemporal bones, and is demarcated by a very slight change in bone texture. Although the anterior process and postorbital body are somewhat sculptured, they do not exhibit the pronounced rugose texture characteristic of abelisaurids and allosauroids, which expand into the anterior rugosities of *Allosaurus* and *Sinraptor* described above and reach an extreme state in the bulbous orbital 'brows' of carcharodontosaurids (Sereno *et al.*, 1996; Coria & Currie, 2006; Sereno & Brusatte, 2008). Instead, the postorbital sculpturing of *Monolophosaurus* is similar to that in many other basal theropods (for example, *Afrovenator*, *Ceratosaurus*, *Cryolophosaurus*, *Dubreuillosaurus*, *Torvosaurus*, *Zupaysaurus*, coelophysids).

Dorsally, the anterior process and postorbital body extend into a medial sheet that contacts the frontal and a narrow wing of the parietal (Fig. 4). The posterior region of the dorsal surface of the postorbital body and the anteromedial corner of the posterior ramus are smoothly excavated by the supratemporal fossa (Fig. 4, stfos). This portion of the fossa is continuous with the supratemporal fossa on the frontal and demarcated anteriorly by an arched ridge.

Prefrontal: The prefrontal is a small element in *Monolophosaurus* (Figs 1–4). It is rectangular-shaped in dorsal view, wedged between the lacrimal and the frontal, and articulates with the nasal medially. The prefrontal contacts only the anterior margin of

the frontal and does not appear to make contact with the lateral margin as in most basal theropods (Fig. 4), which is probably correlated with the unique antero-posteriorly shortened frontals that are autapomorphic of *Monolophosaurus*. Anteriorly, the prefrontal contacts the lacrimal in a transversely straight suture. The lateral margins of both the prefrontal and lacrimal are strongly upturned and rugose at this contact. The prefrontal broadly contributes to the dorsal orbit rim, and is more exposed laterally than the prefrontals of *Allosaurus* (Madsen, 1976) and *Sinraptor* (Currie & Zhao, 1993), as well as the heavily modified elements of abelisaurids and carcharodontosaurids, which are hidden laterally by a postorbital–lacrimal articulation and probably fused to the lacrimal (Sereno *et al.*, 1996; Sampson & Witmer, 2007; Sereno & Brusatte, 2008).

Jugal: The jugal is tetraradiate as in most basal theropods (Figs 1, 2). It comprises anterior and posterior rami, as well as separate dorsal rami for articulation with the lacrimal and postorbital (here termed the lacrimal and postorbital rami, respectively). The entire element is 235 mm long anteroposteriorly, and forms the ventral margin of the orbit and much of the ventral margin of the lateral temporal fenestra, and also makes a narrow contribution to the posteroventral corner of the antorbital fenestra.

The anterior ramus is 120 mm long, and extends from the posterior margin of the antorbital fenestra to the ventral margin of the orbit. It meets the maxilla anteriorly via a posteroventrally inclined articulation, which narrowly excludes the lacrimal from contacting the maxilla in this region (Fig. 2D). A similar morphology is seen in many basal theropods (for example, abelisaurids: Sampson & Witmer, 2007; allosauroids: Currie & Zhao, 1993; Sereno *et al.*, 1996; Currie & Carpenter, 2000; *Afrovenator*: Sereno *et al.*, 1994; *Dilophosaurus*: Welles, 1984), whereas other taxa exhibit a broad maxilla–lacrimal contact in this region (*Allosaurus*: Madsen, 1976; *Ceratosaurus*: Madsen & Welles, 2000; *Torvosaurus*: Britt, 1991; *Zupaysaurus*: Ezcurra, 2007; coelophysids: Colbert, 1989). The jugal of *Monolophosaurus* contributes to the posteroventral margin of the antorbital fenestra, as in other taxa without a maxilla–lacrimal contact (Fig. 2D). However, this contribution is slight in *Monolophosaurus*, measuring approximately 20 mm. A similar condition is figured in *Afrovenator* (Sereno *et al.*, 1994: fig. 2), and differs from the much more extensive jugal contributions to the antorbital fenestra seen in most other taxa.

The dorsal margin of the anterior ramus rises slightly dorsally into the plate-like lacrimal ramus, which meets the lacrimal in an approximately horizontal butt joint. This ramus is dorsoventrally short

as in *Acrocanthosaurus* (Currie & Carpenter, 2000), *Afrovenator* (Sereno *et al.*, 1994), *Carcharodontosaurus* (Sereno *et al.*, 1996), *Ceratosaurus* (Madsen & Welles, 2000; Sampson & Witmer, 2007), *Zupaysaurus* (Ezcurra, 2007) and coelophysids (Colbert, 1989), whereas it is more dorsoventrally expanded in *Allosaurus* (Madsen, 1976), *Carnotaurus* (Bonaparte *et al.*, 1990), *Dilophosaurus* (Welles, 1984), *Majungasaurus* (Sampson & Witmer, 2007) and *Sinraptor* (Currie & Zhao, 1993).

The postorbital ramus extends 80 mm dorsally to meet the postorbital via an elongate scarf joint. This articulation is slightly laterally exposed dorsally, but ventrally the postorbital wraps around the jugal to articulate with the medial surface of the ramus, similar to the condition described in *Sinraptor* (Currie & Zhao, 1993). In *Monolophosaurus*, the postorbital ramus is shaped like an elongate triangle that is slightly inclined posteriorly; it is 25 mm long antero-posteriorly at its base, but tapers dorsally to a thickness of 7 mm. This process is only narrowly separated from the lacrimal ramus, thereby resulting in a narrow ventral margin of the orbit, which essentially tapers to a point. As in most theropods, the postorbital ramus is slender, not anteroposteriorly expanded and plate-like as in *Acrocanthosaurus* (Currie & Carpenter, 2000), *Cryolophosaurus* (Smith *et al.*, 2007) and *Torvosaurus* (Britt, 1991). Moreover, the postorbital ramus of *Monolophosaurus* does not contact the squamosal and constrict the lateral temporal fenestra as described in *Cryolophosaurus* (Smith *et al.*, 2007).

The posterior ramus is 75 mm long and bifurcates posteriorly to receive the anterior ramus of the quadratojugal. The dorsal prong forms most of the concave ventral border of the lateral temporal fenestra, and is much shorter than the ventral prong, as it only extends 40 mm posteriorly. The dorsal prong is also shortened in most basal theropods (for example, *Acrocanthosaurus*: Currie & Carpenter, 2000; *Allosaurus*: Madsen, 1976; *Coelophysis*: Ezcurra, 2007; *Sinraptor*: Currie & Zhao, 1993; *Zupaysaurus*: Ezcurra, 2007), whereas the prongs are of approximately equal length in *Ceratosaurus* (Madsen & Welles, 2000) and abelisaurids (Sampson & Witmer, 2007).

Externally, the lateral surface of the jugal is strongly convex ventral to the orbit, a condition seen in other theropods with jugal pneumaticity (for example, *Carcharodontosaurus*: SGM-Din 1; *Sinraptor*: IVPP 10600), but absent in those theropods without pneumatic jugals (for example, *Allosaurus*: Madsen, 1976; *Ceratosaurus*: Madsen & Welles, 2000; *Cryolophosaurus*: FMNH PR1821; *Majungasaurus*: FMNH PR 2100, Sampson & Witmer, 2007; *Zupaysaurus*: Ezcurra, 2007). The lateral surface of this

convex region is generally smooth and is not expanded into a rugose boss. However, a slightly rugose depression is present ventral to the postorbital ramus (Fig. 2D, jrug), and the posterior ramus is marked by numerous fine, anteroposteriorly inclined striations.

The anterior portion of the lacrimal ramus and the anterodorsal region of the anterior ramus are smoothly excavated by the antorbital fossa. The ventral rim of the fossa is sharp and approximately straight horizontally, and floors a small pneumatopore in the posteroventral corner of the fossa (Figs 1, 2D, jfor). This oval-shaped pneumatopore opens anterodorsally into the fossa, and is much larger on the left side. Pneumatopores of a similar morphology and position are known in other basal theropods, and jugal pneumaticity is considered to be a synapomorphy of Tetanurae by some authors (for example, Sereno *et al.*, 1996; Allain, 2002). External evidence of pneumaticity is lacking in *Ceratosaurus* (Madsen & Welles, 2000), *Cryolophosaurus* (Smith *et al.*, 2007), *Dilophosaurus*, *Zupaysaurus* and abelisaurids (Sampson & Witmer, 2007), but is present in most allosauroids and some coelurosaurs (Sereno *et al.*, 1996; Holtz *et al.*, 2004). Allain (2002) describes evidence of jugal pneumaticity in *Dubreuillosaurus*, but the specimen (MNHN 1998-13 RJN 10) is heavily weathered and the more complete right jugal (RJN 11) is not swollen laterally. Similarly, Sereno *et al.* (1994) describe and figure a jugal pneumatopore in *Afrovenator*, but our observation of casts (UC OBA 1) confirms that the jugal is not pneumatic, as no clear pneumatopore is visible and the element is plate-like, not strongly swollen as in all theropods with jugal pneumaticity.

An additional opening, which may be pneumatic in nature, is present on the lacrimal ramus of the right jugal (Figs 2D, 3, jaf). This opening takes the form of a distinct, deep, circular excavation that is bordered ventrally by a narrow fossa. It has a diameter of 9 mm, and is thus much larger than the pneumatopore in the posteroventral corner of the antorbital fossa, which only has a diameter of 3 mm on the right side. This accessory opening is absent on the left jugal, which is penetrated by a much larger single pneumatopore and, to our knowledge, has not been reported in other theropods. However, given the variability of pneumatic features and its presence on only one side of the skull, we hesitate to regard this opening as an autapomorphy of *Monolophosaurus*.

The ventral margin of the jugal is concave for a small length anteriorly before expanding into a convex cornual process underneath the orbit (Fig. 2D, jcp). Although this process is sculptured by dorsoventrally oriented striations, it is not as rugose or distinct as in tyrannosaurids (Carr, 1999). A similar process is present in other basal theropods, and differs from the more expansive and bulbous cornual projection of *Allosaurus* (Madsen, 1976). Posterior to this process, the ventral margin becomes concave again in the region of its contact with the quadratojugal.

Quadratojugal: The quadratojugal is roughly 'L'-shaped as in most theropods, and forms much of the posterior and ventral margins of the lateral temporal fenestra (Figs 1, 2, 5). It comprises two principal processes: a dorsal ramus that contacts the squamosal and quadrate, and an anterior ramus that articulates with the jugal. In addition, the posteroventral corner of the quadratojugal projects slightly posteriorly and almost completely covers the condyles of the quadrate laterally in the region of the jaw articulation. However, this projection does not take the form of a discrete, tab-like process as in *Acrocanthosaurus* (Currie & Carpenter, 2000), *Allosaurus* (Madsen, 1976) and some abelisaurids (*Carnotaurus*: Bonaparte *et al.*, 1990; *Majungasaurus*: Sampson & Witmer, 2007).

The dorsal ramus is broad and slightly expands dorsally, unlike the dorsally tapering condition of *Dubreuillosaurus* (Allain, 2002) and coelophysids (Tykoski & Rowe, 2004). Both anterior and posterior margins are concave, as in most theropods. In contrast, the anterior margin of some abelisaurids is convex (Sampson & Witmer, 2007). The dorsal ramus of *Monolophosaurus* is oriented anterodorsally at an angle of approximately 25° from vertical. As a result, it protrudes anteriorly into the lateral temporal fenestra, thus constricting the fenestra at midheight (Fig. 5, pro). Most of this constriction is formed by the corresponding anteroventrally oriented ventral ramus of the squamosal, which contacts the quadratojugal in this region. This contact takes the form of a 37-mm-long, posterodorsally inclined, rugose suture that is nearly co-ossified (Fig. 5). Broad contact between the squamosal and quadratojugal is seen in most theropods, including *Zupaysaurus* (Ezcurra, 2007), allosauroids (Madsen, 1976; Currie & Zhao, 1993; Currie & Carpenter, 2000) and, apparently, spinosauroids (Allain, 2002; Sues *et al.*, 2002) and *Cryolophosaurus* (Smith *et al.*, 2007). However, many basal theropods exhibit only slight contact or lack such contact altogether (for example, *Ceratosaurus*: Madsen & Welles, 2000; *Dilophosaurus*: Welles, 1984; abelisaurids: Sampson & Witmer, 2007; coelophysids: Tykoski & Rowe, 2004), a morphology also seen in *Eoraptor* (Sereno *et al.*, 1993) and *Herrerasaurus* (Sereno & Novas, 1993).

Posterior to the quadratojugal–squamosal contact, the quadrate cotylus is exposed laterally, and its anterior margin contacts the dorsal ramus of the
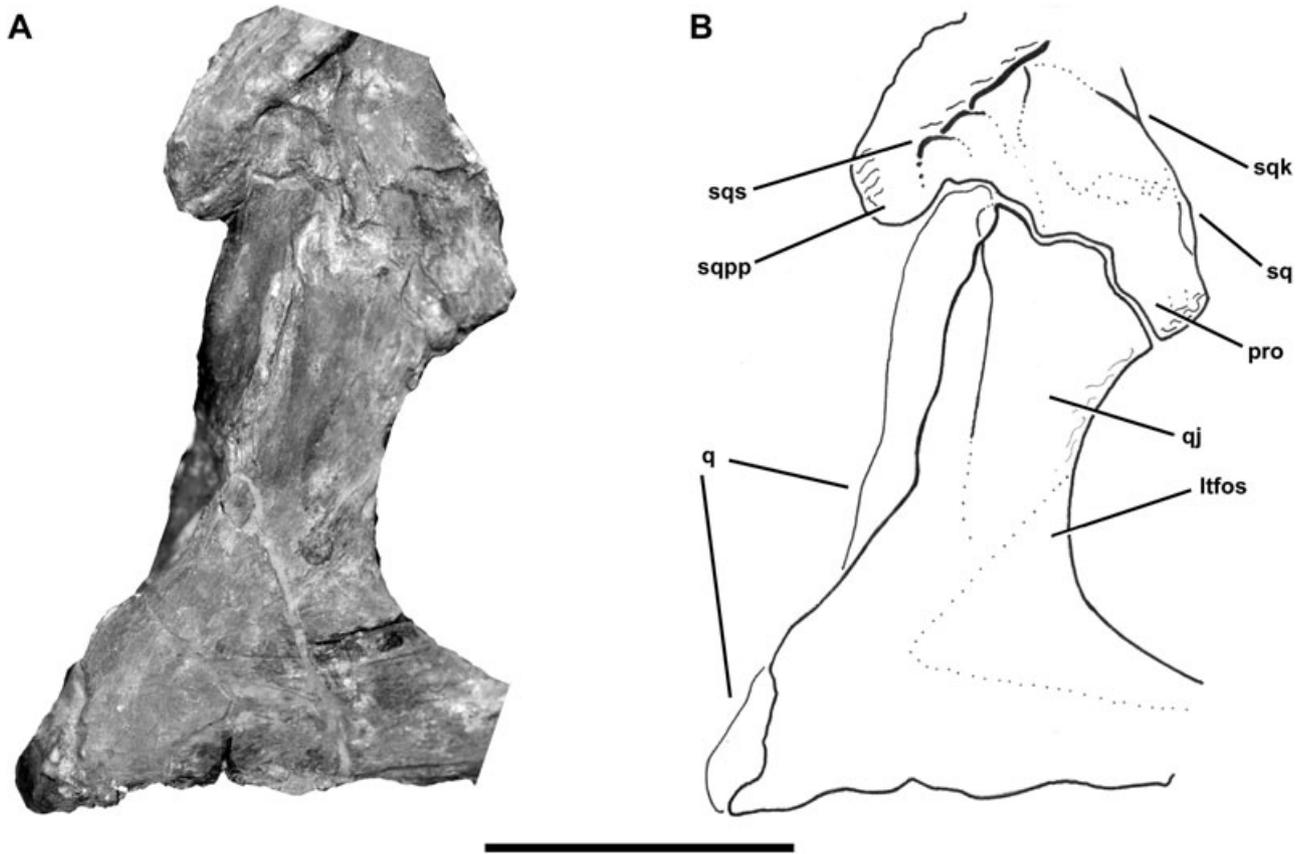
Figure 5. Posterior skull region of *Monolophosaurus jiangi* in right lateral view: A, photograph; B, line drawing. Abbreviations: ltfos, lateral temporal fossa; pro, projection into the lateral temporal fenestra; q, quadrate; qj, quadrato-jugal; sq, squamosal; sqk, kink in the squamosal; sqpp, posterior process of the squamosal; sqs, squamosal shelf. Scale bar represents 50 mm.

quadratojugal (Fig. 5, q). However, ventral to this exposure, the quadrate twists such that its anterolateral margin articulates with the medial surface of the dorsal ramus of the quadratojugal. The quadrate is hidden in lateral view across this contact, but again becomes exposed laterally for a slight 6-mm-long margin at the posteroventral corner of the quadrato-jugal. Thus, contrary to the reconstruction of Zhao & Currie (1993: fig. 1), it is the quadrate that forms the posteroventral corner of the cranium in lateral view (Fig. 5, q). Although the quadratojugal approaches the jaw articulation, it does not contribute to it, similar to the condition in other theropods.

The anterior ramus projects 94 mm anteriorly, to a point level with the midpoint of the ventral ramus of the postorbital (Fig. 2). Therefore, this ramus projects further anteriorly than the anterior margin of the lateral temporal fenestra, as in *Dilophosaurus* (Welles, 1984) and *Zupaysaurus* (Ezcurra, 2007). However, this is unlike the condition in most other basal theropods (for example, *Allosaurus*: Madsen, 1976; *Cryolophosaurus*: Smith *et al.*, 2007; *Dubreuil-*

losaurus: Allain, 2002; *Sinraptor*: Currie & Zhao, 1993; coelophysids: Tykoski & Rowe, 2004), in which the anterior ramus terminates ventral to the lateral temporal fenestra. The anterior rami of *Ceratosaurus* (Madsen & Welles, 2000; Sampson & Witmer, 2007) and *Majungasaurus* (Sampson & Witmer, 2007) are greatly expanded and nearly extend anterior to the lateral temporal fenestra, but fall slightly short. In *Monolophosaurus*, the anterior ramus tapers to a narrow point anteriorly, where it is wedged between the dorsal and ventral prongs of the posterior ramus of the jugal. A similar morphology is seen in *Ceratosaurus* (Sampson & Witmer, 2007), *Dilophosaurus* (Welles, 1984), *Dubreuillosaurus* (Allain, 2002), *Sinraptor* (Currie & Zhao, 1993), *Zupaysaurus* (Ezcurra, 2007) and coelophysids (Tykoski & Rowe, 2004). In contrast, the anterior ramus of *Acrocanthosaurus* (Currie & Carpenter, 2000), *Allosaurus* (Madsen, 1976) and abelisaurids is deeper and does not strongly taper anteriorly (Sampson & Witmer, 2007).

The lateral surface of the quadratojugal is generally smooth and unsculptured. An anterodorsally ori-

ented step, beginning 25 mm ventral to the anterior point of the squamosal contact, demarcates a shallow fossa surrounding the lateral temporal fenestra (Figs 2, 5, ltfos). This fossa continues ventrally on the ventral ramus and excavates the anterodorsal corner of the anterior ramus. Here, it dissipates anteriorly, such that its ventral border becomes confluent with the dorsal margin of the anterior ramus. Thus, the fossa continues anteriorly on the dorsal prong of the posterior ramus of the jugal, but is not present on the anterior process of the quadratojugal for most of its length.

Squamosal: The squamosal (Figs 1, 2, 5) comprises three principal processes visible in lateral view: an anterior ramus that bifurcates to articulate with the postorbital, a ventral ramus that articulates with the quadratojugal and quadrate, and a downturned posterior ramus that also contacts the quadrate. As in many basal theropods, the 'dorsal' surface of the squamosal is oriented posterodorsally. In *Monolophosaurus*, the dorsal surface is angled at approximately 45° posteriorly from the remainder of the skull roof and, as a result, the ventral ramus projects anteriorly into the lateral temporal fenestra (Fig. 5, pro) and the posterior ramus is oriented nearly ventrally, a condition exaggerated by the downturned distal end of this process (Fig. 5, sqpp). However, for ease of comparison with other theropods, we use traditional terms such as 'dorsal surface' and 'ventral ramus'.

The anterior process is 57 mm long and bifurcates anteriorly to articulate with the posterior ramus of the postorbital. This bifurcation divides the anterior process into separate dorsal and ventral prongs across its entire length. These prongs extend anteriorly to the same level, and terminate at the anterior margin of the lateral temporal fenestra. Thus, it is the squamosal that forms the entire dorsal margin of the fenestra. The dorsal surface of the ventral prong becomes prominent posteriorly and gives rise to a thin ridge that overhangs the remainder of the squamosal by approximately 4 mm (Fig. 5, sqs). This ridge is laterally facing as in most theropods, not downturned as is autapomorphic for *Eustreptospondylus* (OUMNH J.13558; Sadlier *et al.*, 2008). Ventral to this ridge, the ventral prong is extensively excavated by a deep fossa, which continues ventrally before terminating against an anteroventrally oriented step on the dorsal portion of the ventral process. This fossa is deepest immediately ventral to the ridge, and surrounds much of the squamosal contribution to the lateral temporal fenestra. The dorsal prong is marked by numerous linear striations that generally follow the long axis of the ramus. This prong forms the posterior region of the lateral margin of the supratemporal fenestra.

As described above, the ventral ramus is oriented anteroventrally, and makes contact with the quadratojugal and the quadrate cotylus, which fits in between this ramus and the downturned posterior ramus. The ventral process is anteroposteriorly expanded and plate-like, and makes broad contact with the quadratojugal. Immediately posterior to this contact, the quadrate articulates with the ventral process for approximately 7 mm, following the same trend as the quadratojugal contact.

Together, the inclined ventral ramus of the squamosal and dorsal ramus of the quadratojugal project into the lateral temporal fenestra, constricting this opening to approximately 60% of its maximum anteroposterior length (Fig. 5, pro). Most of this constriction is formed by the ventral ramus of the squamosal, which projects so strongly anteriorly (approximately 40° from vertical) that the quadratojugal articulates with a bone surface that appears to be equivalent to the posterior margin of this ramus in more basal theropods (for example, *Ceratosaurus*: Sampson & Witmer, 2007; abelisaurids: Sampson & Witmer, 2007; coelophysids: Colbert, 1989; Tykoski & Rowe, 2004). A similar condition is present in *Zupaysaurus* (Ezcurra, 2007), but differs from the morphology in other basal theropods with a constricted lateral temporal fenestra. In these taxa (for example, *Acrocanthosaurus*: Currie & Carpenter, 2000; *Allosaurus*: Madsen, 1976), the articulating processes on the squamosal and quadratojugal project into the fenestra to the same degree and the quadratojugal clearly articulates with the ventral margin of the ventral ramus of the squamosal. The ventral ramus of *Monolophosaurus* is marked by a small kink (Figs 2D, 5 sqk), which is not as pronounced as the autapomorphic process of *Zupaysaurus* (Ezcurra, 2007: fig. 3). A similar kink is unknown in other basal theropods.

The posterior ramus projects posteroventrally and turns slightly anteriorly at its distal end (Fig. 5, sqpp). This process is smaller than the ventral ramus, measuring 15 mm in maximum length in lateral view (compared with 20 mm for the ventral ramus), and terminates 15 mm dorsally to the ventral ramus. This contrasts with the condition in *Acrocanthosaurus* (Currie & Carpenter, 2000), *Allosaurus* (Madsen, 1976) and *Ceratosaurus* (Sampson & Witmer, 2007), in which the posterior ramus is expanded and downturned to such a degree that it extends to the same ventral level as the ventral process. *Monolophosaurus* also differs from coelophysids (Tykoski & Rowe, 2004) and abelisaurids (Sampson & Witmer, 2007), in which this ramus generally is rod-like and projects posteriorly, sometimes with a slight downturn. Instead, the morphology of *Monolophosaurus* is broadly similar to that in *Afrovenator* (Sereno *et al.*, 1994), *Dilophosaurus* (Welles, 1984), *Dubreuillosaurus* (Allain, 2002),

Sinraptor (Currie & Zhao, 1993) and *Zupaysaurus* (Ezcurra, 2007), in which the posterior ramus is slightly expanded and moderately downturned.

Unfortunately, the articulated nature of the skull precludes a detailed observation of the articular surfaces for the parietal and paroccipital processes. However, it is clear that the squamosal only makes slight contact with the parietal medially (Zhao & Currie, 1993: fig. 1). In fact, in posterior view, the squamosal and parietal are almost entirely separated by a narrow cleft extending posteroventrally from the supratemporal fenestra. This cleft may represent a remnant of the post-temporal fenestra, an opening between the parietal, squamosal and paroccipital processes in many sauropsids that may have housed the dorsal head vein (Sampson & Witmer, 2007). This opening is reduced in dinosaurs primitively (Benton, 2004) and entirely lost in most dinosaurs, but appears to be present as a small remnant in *Majungasaurus* (Sampson & Witmer, 2007).

Frontal: As with other skull elements, few details of the frontal can currently be observed because of the embedded mount. However, photographs taken before the mounting of the specimen reveal the frontal to be a highly unique and autapomorphic element in *Monolophosaurus* (Zhao & Currie, 1993: fig. 1). Uniquely among theropods, the associated frontals of *Monolophosaurus* are rectangular in dorsal view and much wider than long, with a width to length ratio of 1.67. Associated frontals that are wider than long are sometimes considered a synapomorphy of Neotetanurae (Allosauroidea + Coelurosauria; for example, Smith *et al.*, 2007). However, the condition in *Monolophosaurus* is extreme compared with basal neotetanurans, as taxa such as *Acrocanthosaurus*, *Allosaurus* and *Sinraptor* possess frontals only slightly wider than long (width to length ratios between 1.05 and 1.35). Furthermore, frontals in these taxa are generally triangular, and taper in width somewhat anteriorly. Thus, the wide, rectangular frontals of *Monolophosaurus* are autapomorphic.

In dorsal view, the frontal is relatively flat and unsculptured, unlike the nasals, lacrimals and premaxillae that comprise the cranial crest. The anterior edge of the frontal does rise slightly anteriorly to articulate with the nasals (Figs 3, 4, fcr), but for the most part does not contribute to the crest. The posterolateral corner of the frontal is excavated by the supratemporal fossa, which is widely exposed in dorsal view (Fig. 4, stfos), unlike the condition in derived carcharodontosaurids (Coria & Currie, 2002; Brusatte & Sereno, 2007). Posteriorly, the frontal meets the parietal in a transversely straight suture, and laterally contacts the postorbital via a parasagittally straight articulation. The anterolateral corner

contacts the prefrontal and makes a narrow contribution to the orbital rim (Figs 2D, 3, 4, forb). The interfrontal suture is open and nearly straight sagittally.

Parietal: As with the frontal, only some details of the parietal are visible in the current mount. This element is hourglass-shaped in dorsal view, as a result of supratemporal fenestrae that extend far medially. In lateral view, a low midline crest is visible, which rises to a point dorsal to the level of the postorbital–squamosal articulation. The condition in *Monolophosaurus* appears to be broadly similar to that in *Ceratosaurus* (Madsen & Welles, 2000) and *Zupaysaurus* (Ezcurra, 2007), which possess a distinct but low eminence. In contrast, a more pronounced and mound-like bulge is present in *Acrocanthosaurus* (Currie & Carpenter, 2000), *Allosaurus* (Madsen, 1976), *Sinraptor* (Currie & Zhao, 1993), carcharodontosaurids (*Carcharodontosaurus*: SGM-Din 1; *Giganotosaurus*: Coria & Currie, 2002) and abelisaurids (Bonaparte *et al.*, 1990; Sampson & Witmer, 2007), in which it forms a knob-like projection. However, although small, the midline crest of *Monolophosaurus* clearly differs from the condition in some basal theropods (for example, *Dubreuillosaurus*: Allain, 2002), in which the dorsal surface of the parietal is flat and completely lacks a crest. In posterior view, the parietal is exposed broadly on the occiput, rises above the supraoccipital and seems to give rise to a tongue-like process that overlaps the supraoccipital posterodorsally. Openings along the parietal–supraoccipital suture on both sides of the midline probably represent passage for the dorsal head vein (Larsson, 2001).

Braincase: The articulated nature of the skull only allows limited observation of the braincase (Fig. 6). Although not visible in the present mount, the occipital region (posterior view) was photographed by PJC and illustrated (Zhao & Currie, 1993: fig. 1) before mounting. Parts of the lateral wall of the braincase are also visible inside the lateral temporal fenestra, although obstructed ventrally by the quadrate, pterygoid and epipterygoid (Fig. 6).

The supraoccipital is broadly exposed on the occiput, and rises dorsally into a triangular wedge that nearly reaches the top of the nuchal crest of the parietal. Sutural contacts with the parietal and exoccipital–opisthotic are visible, and the supraoccipital makes a narrow contribution to the dorsal rim of the foramen magnum. The supraoccipital also reaches the foramen magnum in many basal theropods (for example, *Acrocanthosaurus*: OMNH 10146; *Allosaurus*: UMNH VP 16606; *Baryonyx*: Charig & Milner, 1997; *Dubreuillosaurus*: Allain, 2002; *Giganotosau-*
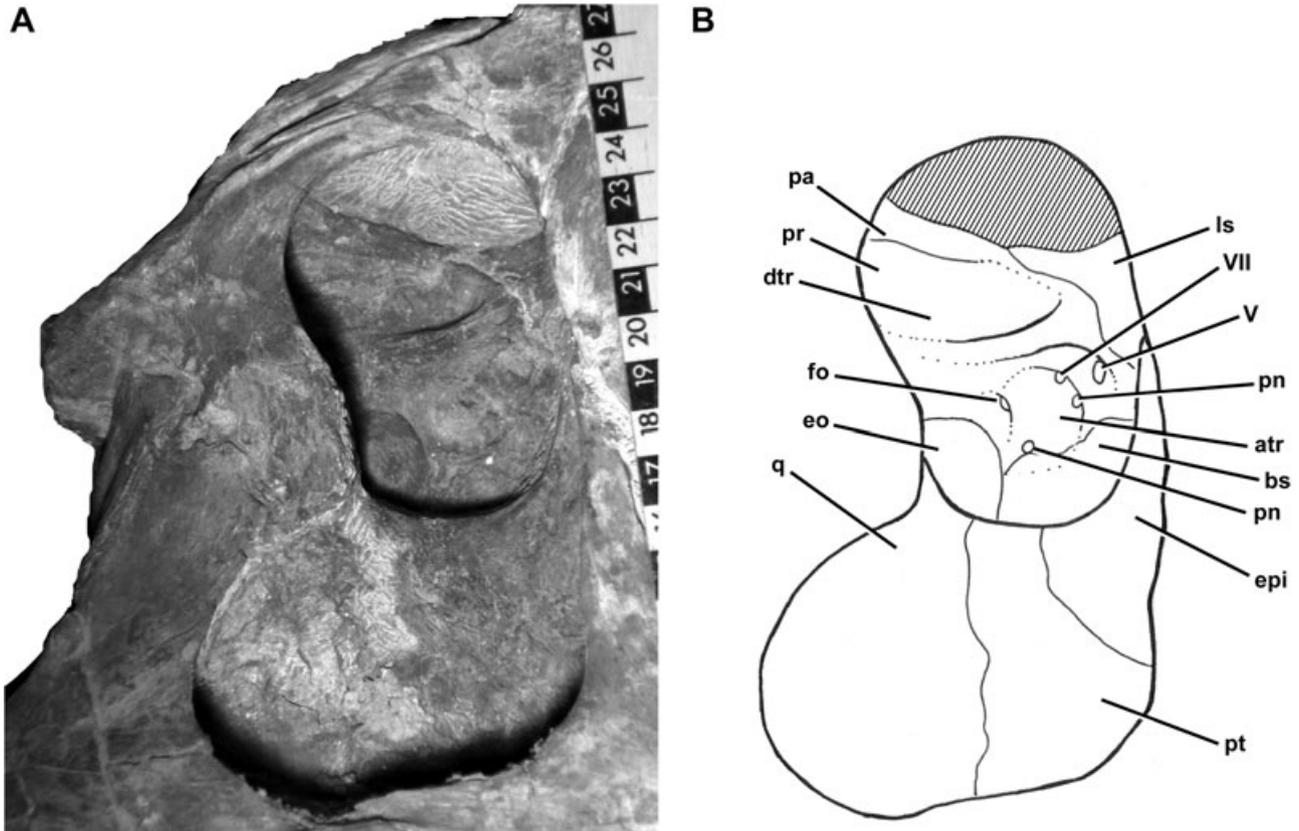
Figure 6. Braincase of *Monolophosaurus jiangi* in right lateral view (looking within the lateral temporal fenestra): A, photograph; B, line drawing. Abbreviations: atr, anterior tympanic recess; bs, basisphenoid; dtr, dorsal tympanic recess; eo, exoccipital–opisthotic; epi, epipterygoid; fo, fenestra ovalis; ls, laterosphenoid; pa, parietal; pn, pneumatopore; pr, prootic; pt, pterygoid; q, quadrate; V, foramen for cranial nerve V; VII, foramen for cranial nerve VII.

rus: Coria & Currie, 2002; *Majungasaurus*: Sampson & Witmer, 2007; *Piatznitzkysaurus*: Rauhut, 2004; *Piveteausaurus*: Taquet & Welles, 1977; *Sinraptor*: Currie & Zhao, 1993), but is excluded from the rim in *Cryolophosaurus* (Smith *et al.*, 2007), *Dilophosaurus* (Welles, 1984), and coelophysids (Raath, 1977; Colbert, 1989).

The occipital condyle is kidney-shaped. Based on the condition in other basal tetanuran theropods (for example, Madsen, 1976; Rauhut, 2004; Brusatte & Sereno, 2007), the basioccipital probably contributed to the condyle, but sutures with the exoccipital–opisthotic are obliterated by fusion. Ventrally, the basal tubera descend from the neck of the occipital condyle as a narrow sheet. Unfortunately, sutural relationships between the basioccipital and basisphenoid in this region are not clear. The tubera are deeper dorsoventrally than the occipital condyle, as in some theropods, including *Baryonyx* (BMNH R9951), *Ceratosaurus* (Madsen & Welles, 2000) and *Majungasaurus* (Sampson & Witmer, 2007). In contrast, the tubera are subequal and often much shorter than the occipital condyle in a wide array of basal theropods, including *Acrocanthosaurus* (OMNH 10146), *Allosaurus* (Madsen, 1976), *Cryolophosaurus* (Smith *et al.*, 2007), *Dilophosaurus* (Welles, 1984), *Dubreuillosaurus* (Allain, 2002), *Piveteausaurus* (Taquet & Welles, 1977), *Sinraptor* (IVPP 10600) and 'S*yntarsus' kayentakatae* (Tykoski, 1998). Distally, the tubera are slightly separated by a broad concave notch, as in most basal theropods. *Ceratosaurus* and, especially, *Cryolophosaurus* exhibit a more extreme condition in which the tubera are more completely separated by a wider, 'V'-shaped notch. The conjoined basal tubera of *Monolophosaurus* are approximately as wide transversely as the occipital condyle, as in *Allosaurus*, *Acrocanthosaurus*, *Baryonyx* and *Sinraptor*, not substantially wider as in other basal theropods. Posteriorly, they are excavated by a shallow median groove, as in many other theropods, but the presence of a subcondylar recess (Rauhut, 2004) cannot be determined.

The fused exoccipital and opisthotic comprise nearly the entire border of the foramen magnum and

expand laterally into large paroccipital processes. These processes are massive and downturned distally, with the distal end located slightly ventral to the occipital condyle. The base of the paroccipital process, where it emerges from the metotic strut, is level with the midpoint of the condyle. The systematic utility of these characters is reviewed below.

The prootic is the best exposed of the elements of the lateral wall of the braincase, with the preotic pendant and surrounding areas visible inside the lateral temporal fenestra (Fig. 6). A large, circular opening for the trigeminal (V) nerve is located immediately posterior to the prootic–laterosphenoid suture, and thus is enclosed entirely within the prootic (Fig. 6, V). Only a single opening is apparent, not separate openings for the ophthalmic branch (CN V[1]) and maxillary and mandibular branches (CN V[2,3]), as in some basal theropods (*Allosaurus*: Madsen, 1976; *Piveteausaurus*: Taquet & Welles, 1977) and several coelurosaurs (Currie, 1985; Sues, 1997; Brochu, 2002; see a review of this character in Brusatte & Sereno, 2007, 2008). Posteroventral to the trigeminal foramen is a much smaller opening for the facial (VII) nerve, which is infilled with matrix (Fig. 6, VII). These two openings are separated by a narrow but raised strut of bone that is only 4 mm thick at its widest point.

Two additional openings penetrate the prootic, both of which are approximately equal in size to the facial foramen (Fig. 6, pn). The first is located slightly anteroventral to the facial foramen, in a similar location to a pneumatopore described in *Piatznitzkysaurus* by Rauhut (2004). The second is approximately 10 mm ventral to the facial foramen and immediately dorsal to the articulation with the basisphenoid. Although this foramen may be for the internal carotid, it is located much further dorsally than this opening in other basal theropods with well-described braincases (*Acrocanthosaurus*: Franzosa & Rowe, 2005, OMNH 10146; *Piatznitzkysaurus*: Rauhut, 2004). Instead, it is more likely a pneumatopore associated with the heavily pneumatic anterior tympanic recess (Fig. 6, atr). This recess shallowly excavates much of the prootic in this region, and houses the facial foramen and both pneumatopores. It is demarcated anteriorly by a concave ridge, which also forms the anterior margin of the facial foramen and the first pneumatopore. The recess appears to be much shallower than in *Piatznitzkysaurus* (Rauhut, 2004), a condition almost certainly exaggerated by postmortem crushing. However, some basal theropods (for example, *Cryolophosaurus*: Smith *et al.*, 2007) genuinely appear to possess only a shallow anterior tympanic recess.

Dorsally, the prootic meets the parietal in a nearly horizontal, heavily rugose suture (Fig. 6, pa). Few details of the parietal are observable, but the prootic is clearly excavated by a deep, anteroposteriorly elongate dorsal tympanic recess immediately ventral to this contact (Fig. 6, dtr). This recess is delimited ventrally by a thick and prominent ridge of bone that trends slightly posteroventrally, and is similar in morphology to the corresponding recess in *Piatnitzkysaurus* (Rauhut, 2004). Anterior to the parietal suture, the prootic contacts the laterosphenoid via an elongate, curving suture that is oriented strongly anteroventrally. Only a narrow portion of the posterodorsal region of the laterosphenoid is exposed, immediately posterior to where the capitate process begins to expand laterally to meet the frontal (Fig. 6, ls). Three small depressions penetrate the laterosphenoid in this region, including a small opening that may have housed the middle cerebral vein. Ventrally, the prootic contacts the basisphenoid, but only a very narrow and heavily abraded region of the latter bone is exposed (Fig. 6, bs). Anteroventrally, the prootic meets the lateral wing of the exoccipital–opisthotic (Fig. 6, eo). A deep, semilunate depression between the two elements in the anterodorsal corner of this contact may represent the fenestra ovalis (Fig. 6, fo), as this opening is located in a similar position in other basal theropods (for example, *Acrocanthosaurus*; *Cryolophosaurus*; *Dubreuillosaurus*; *Giganotosaurus*: Coria & Currie, 2002; *Piveteausaurus*; *Sinraptor*). However, in *Monolophosaurus*, this opening is obscured by matrix, precluding further observation.

Quadrate: Only parts of the lateral and posterior surfaces of the quadrate are visible in the current mount (Figs 1, 2, 5). The quadrate cotylus is visible laterally as it articulates between the ventral and posterior rami of the squamosal. Ventrally, the quadrate twists posteriorly, such that it is not visible laterally until a small margin is exposed at the posteroventral corner of the cranium (Fig. 5, q). The quadrate is not fused to the quadratojugal, as in *Ceratosaurus* (Madsen & Welles, 2000) and some abelisaurids (Bonaparte *et al.*, 1990), or partially co-ossified, as in *Cryolophosaurus* (Smith *et al.*, 2007).

In posterior view, the entire quadrate is 135 mm tall dorsoventrally and excavated by a deep groove trending dorsoventrally. A similar groove is present in other basal theropods (for example, *Ceratosaurus*: Madsen & Welles, 2000; *Giganotosaurus*: MUCPv-CH-1; *Majungasaurus*: Sampson & Witmer, 2007; *Mapusaurus*: Coria & Currie, 2006; *Torvosaurus*: Britt, 1991). This groove appears to lead into the quadrate foramen, which is a large, dorsoventrally elongate oval (17 mm × 10 mm) formed almost equally by the quadrate and quadratojugal, similar to the condition in *Baryonyx* (Charig & Milner, 1997). In contrast, this foramen is absent in *Ceratosaurus* and abelisaurids (Sampson & Witmer, 2007) and formed
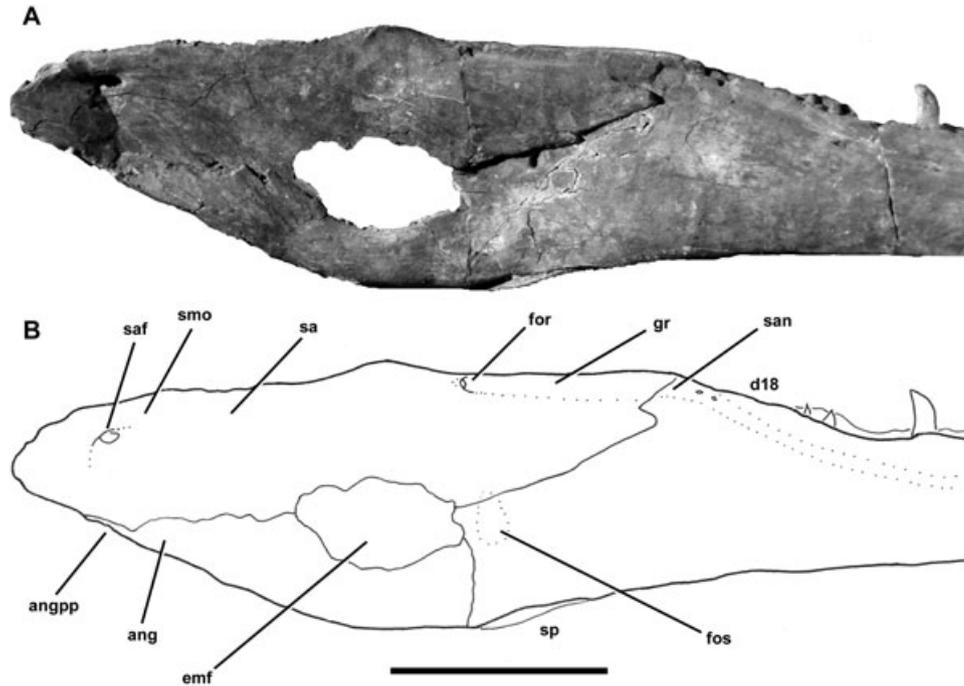
Figure 7. Posterior region of the lower jaw of *Monolophosaurus jiangi* in right lateral view: A, photograph; B, line drawing. Abbreviations: ang, angular; angpp, posterior projection of the angular; emf, external mandibular fenestra; d18, dentary alveolus 18; for, foramen; fos, fossa; gr, groove; sa, surangular; saf, surangular foramen; san, surangular notch; smo, smooth region dorsal to the surangular foramen; sp, splenial. Scale bar represents 100 mm.

almost entirely by the quadrate in *Dilophosaurus* (Welles, 1984), most allosauroids (Currie & Zhao, 1993; Currie & Carpenter, 2000) and, apparently, *Cryolophosaurus* (Smith *et al.*, 2007). The foramina of *Mapusaurus* (Coria & Currie, 2006) and, apparently, *Torvosaurus* (Britt, 1991) are formed by a wide contribution from the quadratojugal, but these openings are much smaller than the foramen in *Monolophosaurus*. The condition in *Allosaurus* is variable (R. B. J. Benson, pers. observ.), and the foramen is not uniformly formed almost entirely from the quadrate as is often stated in the literature (for example, Madsen, 1976).

Contact with the articular is made via two articular condyles, with the lateral condyle slightly wider transversely (34 mm) than the medial (29 mm). However, the medial condyle is more massive than the lateral element, and projects further ventrally. These condyles are separated by a deep cleft, and their posterior surface is heavily rugose for approximately 35 mm dorsal to the lower jaw articulation. Anteriorly, the quadrate expands into a broad flange for articulation with the pterygoid, which is visible inside the lateral temporal fenestra. Unfortunately, the articulated nature of the skull precludes observation of the quadratojugal contact, which is developed as a flange in some basal theropods (see below).

Palate: Other elements of the palate are visible within the antorbital fenestra (vomer, palatine) and lateral temporal fenestra (pterygoid, epipterygoid), but little can be said of their morphology. However, a pneumatopore visible between the exposed jugal and vomeropterygoid processes of the palatine clearly indicates that this element was pneumatic, as in many other theropods (Currie & Zhao, 1993).

LOWER JAW

As with the cranium, the lower jaw as currently mounted is visible in lateral view, permitting detailed observation of the lateral surfaces of the dentary, surangular and angular (Figs 1, 7). However, the medial surface of the dentary, as well as the splenial, prearticular, articular, coronoid and supradentary, are obscured. An illustration of the lower jaw in medial view is provided by Zhao & Currie (1993: fig. 2), and some important features gleaned from this illustration and photographs taken before the specimen was mounted will be discussed.

The entire lower jaw is 750 mm long anteroposteriorly. The dentary, surangular and angular contribute to the external mandibular fenestra, which is 67 mm long and 25 mm deep dorsoventrally on the left side. The right opening appears slightly larger as

a result of breakage. The maximum dimension of the external mandibular fenestra is approximately one-tenth the length of the lower jaw, approximately the same ratio as in *Acrocanthosaurus* (0.12, Currie & Carpenter, 2000), *Ceratosaurus* (0.12, Madsen & Welles, 2000) and *Zupaysaurus* (0.13, Ezcurra, 2007), but reduced compared with *Sinraptor* (0.17, Currie & Zhao, 1993), coelophysids (*Coelophysis*: 0.19, Colbert, 1989) and abelisaurids (*Carnotaurus*: 0.22, Tykoski & Rowe, 2004; *Majungasaurus*: 0.24, Sampson & Witmer, 2007). However, this fenestra is not reduced to the extreme extent seen in *Allosaurus* (0.08, Madsen, 1976) and *Dilophosaurus* (0.09, Welles, 1984).

Dentary: The dentary is gracile, extending 438 mm from the anterior margin to its posterior termination at the external mandibular fenestra (Fig. 1). It is deepest at the anterior edge of the surangular contact, at which point it is 86 mm deep dorsoventrally. It narrows anteriorly to a depth of 52 mm at the level of the tenth alveolus, expands again to 62 mm at the fifth alveolus and narrows slightly to a depth of 55 mm at its anterior margin. Although the dentary expands somewhat anteriorly, this expansion is not as extreme as in carcharodontosaurids (Calvo & Coria, 2000; Brusatte & Sereno, 2007) or *Spinosaurus* (Smith *et al.*, 2006), in which the anterior dentary is squared off and much deeper than the remainder of the alveolar ramus. Furthermore, there is no ventral process protruding from the anteroventral corner of the dentary, as in *Piatznitzkysaurus* (Bonaparte, 1986) and derived carcharodontosaurids (Brusatte & Sereno, 2007, 2008).

Contacts with the surangular, angular and splenial are visible in lateral view. Details of the medial contacts with the coronoid, prearticular and splenial are obscured in the present mount, but illustrated by Zhao & Currie (1993: fig. 2) and will not be discussed further. The dentary contacts the surangular via a 125-mm-long contact that appears to have been quite loose in life. This articulation begins anteriorly immediately posterior to the tooth row, trends posteroventrally and terminates at the anterodorsal margin of the external mandibular fenestra. Slightly ventral to this region, the dentary meets the angular at a 40-mm-tall, nearly vertical suture at the anteroventral corner of the fenestra. Finally, a narrow portion of the splenial (65 mm long by 55 mm deep) is exposed laterally as it wraps around the ventral margin of the dentary immediately anterior to the external mandibular fenestra (Figs 1, 7, sp). Such lateral exposure is also seen in *Herrerasaurus* (Sereno & Novas, 1993), *Ceratosaurus* (Currie & Zhao, 1993) and dromaeosaurids (Currie, 1995), but is absent in allosauroids (*Acrocanthosaurus*: Currie & Carpenter,

2000; *Allosaurus*: Madsen, 1976; *Sinraptor*: Currie & Zhao, 1993). The splenial is also exposed laterally in *Majungasaurus*, but this taxon exhibits a hypertrophied process for articulation with the angular that is widely visible in lateral view, unlike the condition in *Monolophosaurus* (Sampson & Witmer, 2007).

The surangular and angular of *Monolophosaurus* do not contact each other anterior to the fenestra, allowing the dentary to make a minor contribution (~25 mm) to its anterior margin (Fig. 7, emf). A similar condition characterizes *Acrocanthosaurus* (Currie & Carpenter, 2000) and *Sinraptor* (Currie & Zhao, 1993), but differs from the morphology in *Ceratosaurus*, *Dilophosaurus*, *Zupaysaurus*, coelophysids (Tykoski & Rowe, 2004) and abelisaurids (Sampson & Witmer, 2007), in which the dentary contributes more broadly to the fenestra and often comprises part of the dorsal and ventral margins. *Allosaurus* exhibits an autapomorphic condition in which the dentary is completely excluded from the strongly reduced external mandibular fenestra (Madsen, 1976). In *Monolophosaurus*, the dentary is excavated by a deep, triangular fossa immediately anterior to the fenestra. This fossa does not appear to communicate with the fenestra externally.

The lateral surface of the dentary is slightly rugose anteriorly and is penetrated by numerous foramina, which are especially common along the tooth row and the ventral margin (Fig. 1). Near the tooth row, four very prominent, oval-shaped foramina, up to 10 mm in maximum dimension, open dorsally immediately below the first four alveoli. However, at the level of the fifth alveolus, this primary row curves ventrally, and the foramina become less distinct, smaller and circular, with a maximum diameter of 2–3 mm. At the level of the ninth alveolus, distinct foramina disappear and are replaced by a sharp groove, which arches dorsally, becomes less prominent posteriorly and reaches the alveolar margin where the dentary contacts the surangular. The ventral curvature of the primary row is pronounced, as it is only 8 mm ventral to the tooth row anteriorly and drops to 22 mm at the level of the eighth alveolus. A similar condition is seen in *Baryonyx* (Charig & Milner, 1997), *Dubreuillosaurus* (Allain, 2002) and carcharodontosaurids (*Carcharodontosaurus*: Brusatte & Sereno, 2007; *Giganotosaurus*: Calvo & Coria, 2000; *Neovenator*: Brusatte *et al.*, 2008). However, the principal row of *Allosaurus* (Madsen, 1976) and *Sinraptor* (Currie & Zhao, 1993) runs parallel and immediately ventral to the tooth row for its entire length, whereas that of *Ceratosaurus* (Madsen & Welles, 2000) and abelisaurids (Sampson & Witmer, 2007) runs far ventral to the tooth row for its entire length.

In addition to the primary row of neurovascular foramina dorsally, the dentary of *Monolophosaurus* is

also marked by a row of ventral foramina (Fig. 1). These foramina are smaller than their dorsal counterparts, measuring 2–4 mm in diameter, and extend in a nearly horizontal series approximately 8 mm above the ventral margin. Most basal theropods do not possess a discrete row of foramina ventrally, but rather a more random array of openings that vary drastically in size (for example, *Baryonyx*: Charig & Milner, 1997; *Ceratosaurus*: Madsen & Welles, 2000; *Majungasaurus*: Sampson & Witmer, 2007; *Piatznitzkysaurus*: Bonaparte, 1986). Other theropods (for example, *Dubreuillosaurus*: MNHN 1998-13 RJN 22; *Sinraptor*: IVPP 10600) do possess a similar row, but this does not extend as far posteriorly as the series in *Monolophosaurus*, which terminates at the level of the 13th alveolus.

Few details of the medial surface of the dentary are visible in the current mount, but such a view is figured by Zhao & Currie (1993: fig. 2). The interdental plates are unfused, and the Meckelian groove terminates anteriorly at the level of the third alveolus, grading into two elongate foramina which are staggered one on top of the other. The dentary symphysis is poorly defined, and the articulated dentaries form a narrow 'V' shape in dorsal view. This is similar to the condition in many basal theropods, but unlike the more expanded and 'U'-shaped articulation in *Allosaurus*, carcharodontosaurids (Brusatte & Sereno, 2007) and abelisaurids (Sampson & Witmer, 2007). There are 18 alveoli on the right dentary and 17 on the left. The third alveolus is slightly enlarged relative to the second (Table 2). However, the dentary is not swollen laterally to accommodate a greatly enlarged third dentary tooth as in coelophysoids and spinosauroids (Rauhut, 2003; Benson *et al.*, 2008; Sadlier *et al.*, 2008).

Surangular: The elongate surangular extends 317 mm anteroposteriorly from its anterior contact with the dentary to a posterior flange that covers the articular laterally (Figs 1, 7). It achieves a maximum dorsoventral depth of 55 mm above the midpoint of the external mandibular fenestra, which is completely roofed by the surangular dorsally.

Articulation with the dentary is achieved via an elongate contact described above. The anterodorsal region of this contact is complex, with a finger-like process on the dentary fitting into a notch on the surangular (Fig. 7, san). This notch is demarcated ventrally by a smaller finger-like process on the surangular, which fits into a corresponding notch on the dentary, as described for *Sinraptor* (Currie & Zhao, 1993) and present in many theropods. Posteriorly, a groove leads away from this contact and follows the dorsal margin of the surangular for approximately 100 mm, before terminating in a small foramen (Fig. 7, gr, for). Often referred to as the anterior surangular foramen, this opening probably transmitted branches of the inferior alveolar nerve (Currie & Zhao, 1993). The groove, which is present in many other theropods (for example, *Allosaurus*: Madsen, 1976; *Majungasaurus*: Sampson & Witmer, 2007; *Sinraptor*: Currie & Zhao, 1993) is essentially continuous with the principal neurovascular groove on the dentary, and is only separated from it briefly by the double-notched dentary–surangular contact.

The surangular and angular meet at a nearly horizontal suture, which begins at the midpoint of the posterior margin of the external mandibular fenestra. It continues posteriorly to the level of the posterior surangular foramen, at which point there is a marked ventral step. Posterior to the step, a thin process of the angular continues posteriorly past the posterior surangular foramen and nearly reaches the mandibular articulation (Fig. 7, angpp). A similar condition has been described in *Cryolophosaurus* (Smith *et al.*, 2007) and 'S*yntarsus*' *kayentakatae* (Tykoski, 1998), and may also be present in *Dilophosaurus* (Smith *et al.*, 2007). However, the step in *Cryolophosaurus* is much larger, and better described as a deep notch (Smith *et al.*, 2007: figs 4, 5). The posterior process of the angular does not reach the mandibular articulation in *Monolophosaurus*, thus allowing the surangular to contribute to the posteroventral margin of the lower jaw. This contrasts with the case in the aforementioned taxa, as well as some theropods without a stepped contact (*Allosaurus*: Madsen, 1976; *Zupaysaurus*: Ezcurra, 2007; apparently *Dracovenator*: Yates, 2005: fig. 6), in which the angular forms the entire posteroventral margin of the jaw. The surangular reaches the posteroventral margin in most other basal theropods (for example, *Acrocanthosaurus*, *Dubreuillosaurus*, *Sinraptor*, abelisaurids), but, unlike *Monolophosaurus*, these taxa do not possess a stepped surangular–angular contact and a discrete posterior process of the angular.

Externally, the surangular is penetrated by an oval-shaped posterior surangular foramen, which measures 11 mm in anteroposterior length and 5 mm in dorsoventral depth (Fig. 7, saf). This opening is small as in most basal theropods, and opens anteriorly into a very low fossa which fans out and reaches the posterodorsal margin of the external mandibular fenestra. Posteriorly, the foramen is bordered by a rugose ridge that runs vertically down the surangular and terminates at the posteroventral margin of the lower jaw. However, dorsally the foramen is bordered by a smooth and unexpanded surface that is at the same level as the lateral surface of the surangular ventrally (Fig. 7, smo). This is a rare feature among theropods, as most other taxa are characterized by a thickened and robust shelf of bone that overhangs the

posterior surangular foramen dorsally. This shelf is massive and elongated in some taxa (for example, *Acrocanthosaurus*: Currie & Carpenter, 2000; *Cryolophosaurus*: Smith *et al.*, 2007; abelisaurids: Sampson & Witmer, 2007) and shorter and pendant anteriorly in others (for example, *Allosaurus*: Madsen, 1976; *Sinraptor*: Currie & Zhao, 1993), but some sort of ridge that overhangs the remainder of the surangular is invariably present in most other basal theropods. The lack of a surangular ridge is also seen in a specimen from the Taynton Limestone Formation (Bathonian, Middle Jurassic) of England (OUMNH J.29813) that may be referable to *Megalosaurus*.

Angular: The angular is 179 mm long anteroposteriorly and reaches a maximum depth of 38 mm immediately posterior to the external mandibular fenestra (Figs 1, 7, ang). The angular comprises the entire ventral border and most of the posterior border of the fenestra. The anterior region of the dorsal surface of the angular is strongly concave where it forms the floor of the fenestra, which is much more rounded than the dorsal margin formed by the surangular. Posteriorly, a small posterior process is separated from the remainder of the angular by a step, as described above (Fig. 7, angpp). The ventral margin of the angular is convex across most of its length, but is concave for a small region immediately anterior to the base of the posterior process.

DISCUSSION

PHYLOGENETIC POSITION OF *MONOLOPHOSAURUS*

Monolophosaurus was originally described as a 'megalosaur grade' theropod with a curious mixture of primitive theropod characters and more derived features seen in *Allosaurus* and kin (Zhao & Currie, 1993). Subsequent cladistic analyses frequently recovered *Monolophosaurus* as a member of Allosauroidea (sometimes referred to as Carnosauria), a basal tetanuran clade that includes *Allosaurus*, the Middle Jurassic Asian Sinraptoridae and the primarily large-bodied and Gondwanan Carcharodontosauridae (for example, Sereno *et al.*, 1994, 1996; Currie & Carpenter, 2000; Holtz, 2000; Rauhut, 2003; Holtz *et al.*, 2004; Novas *et al.*, 2005; Coria & Currie, 2006). However, Smith *et al.* (2007) placed *Monolophosaurus* in a slightly more basal position, as the sister taxon to a clade of Allosauroidea + Coelurosauria (Neotetanurae). They found a wider distribution for five cranial characters previously used to place *Monolophosaurus* within Allosauroidea, and identified four features that may unite *Monolophosaurus* with more basal clades. Our redescription of the postcranial skeleton of *Monolophosaurus* (X.-J. Zhao *et al.*,

unpubl. data) also highlighted a number of primitive features unknown in other tetanurans, suggesting a more basal position of *Monolophosaurus* than is commonly advocated. This appraisal is supported by the reassessment of the skull.

Cladistic analysis: We do not include a new cladistic analysis here, as it is outside the scope of this paper. However, information from this study will be incorporated into a larger cladistic analysis of basal theropods to be published elsewhere (M. T. Carrano, R. B. J. Benson & S. D. Sampson, unpubl. data). In the meantime, we present a slightly modified version of Smith *et al.*'s (2007) analysis, currently the largest and most informative dataset yet applied to basal theropods. We have rescored *Monolophosaurus* based on our redescription of the skull and postcranium (X.-J. Zhao *et al.*, unpubl. data), and have also slightly altered the scores for one character (Appendix 1). The revised analysis recovers 108 most parsimonious trees [MPTs; consistency index (CI), 0.482; retention index (RI), 0.768], the same number as found by Smith *et al.* (2007), but of length 843, 10 steps longer than the MPTs in the original analysis. The strict consensus of these trees is identical to the strict consensus reported by Smith *et al.* (2007), which places *Monolophosaurus* as a basal tetanuran immediately outside of the clade Allosauroidea + Coelurosauria (Neotetanurae). Characters supporting the placement of *Monolophosaurus* within Tetanurae and a monophyletic Allosauroidea exclusive of *Monolophosaurus* are essentially the same as those found and reviewed by Smith *et al.* (2007).

Allosauroid cranial characters: Smith *et al.* (2007) pointed out that some cranial characters previously used to place *Monolophosaurus* within Allosauroidea have a wider distribution, and are sometimes even present in non-tetanuran theropods. They listed five characters in particular: pneumatic openings in the nasal, extension of the antorbital fossa onto the nasal, broad contact between the squamosal and quadratojugal, pneumatism associated with the internal carotid canal, and a pendant medial process on the articular. However, these characters were only listed, and other cranial features used to link *Monolophosaurus* to allosauroids were not reviewed. We provide a discussion of several cranial characters once thought to diagnose Allosauroidea, which should clarify their usage for future phylogenetic analyses.

1. Nasal antorbital fossa: Several authors (for example, Sereno *et al.*, 1994, 1996; Holtz, 2000; Rauhut, 2003; Holtz *et al.*, 2004) have scored *Monolophosaurus* and allosauroids as possessing an antorbital fossa that continues dorsally onto the

lateral surface of the nasal (Fig. 3, nantfos). In contrast, the fossa of most other theropods is restricted to the maxilla, lacrimal and jugal. However, a nasal antorbital fossa is also present in the basal theropods *Cryolophosaurus* (Smith *et al.*, 2007), *Dilophosaurus* (Smith *et al.*, 2007) and *Majungasaurus* (Sampson & Witmer, 2007). The presence of this feature in an abelisaurid (*Majungasaurus*), basal neotheropods (*Cryolophosaurus*, *Dilophosaurus*) and allosauroids suggests that it is a particularly homoplastic character.

2. Nasal pneumatopores: Holtz (2000), Rauhut (2003) and Holtz *et al.* (2004) found pneumatic openings in the lateral surface of the nasal as an allosauroid synapomorphy, and an important character linking *Monolophosaurus* to this clade. Indeed, most basal theropods lack nasal pneumatopores, as has been confirmed by recent redescriptions of several taxa (for example, *Ceratosaurus*: Madsen & Welles, 2000, *contra* Rauhut, 2003; *Cryolophosaurus*: Smith *et al.*, 2007; *Zupaysaurus*: Ezcurra, 2007). On the other hand, *Monolophosaurus* (Figs 1, 3, nfor) and many allosauroid taxa (for example, *Allosaurus*, *Giganotosaurus*, *Mapusaurus*, *Neovenator*) do possess pneumatic openings, which vary in size and number, as reviewed above. However, at least one abelisaurid (*Majungasaurus*: Sampson & Witmer, 2007) also possesses a pneumatopore, and the missing nasals of many basal theropods preclude a broader survey of this character. Thus, its utility as an allosauroid synapomorphy is currently limited by homoplasy and missing data.

3. Short quadrate: Sereno *et al.* (1994, 1996) listed a short quadrate, in which the head articulates with the squamosal nearly level with the midpoint of the orbit, as a synapomorphy of Allosauroidea, and a character uniting *Monolophosaurus* with this clade. A short quadrate is clearly present in *Monolophosaurus* (Figs 1, 2, 5) and several allosauroids (for example, *Acrocanthosaurus*: Currie & Carpenter, 2000; *Allosaurus*: Madsen, 1976; *Giganotosaurus*: Coria & Salgado, 1995; *Sinraptor*: Currie & Zhao, 1993). However, reinterpretation of material and discovery of new specimens show this character to be more widely distributed. If measured with the skull roof held horizontal, this character is also present in spinosaurids (*Irritator*: Sues *et al.*, 2002: fig. 6) and basal coelurosaurs (*Compsognathus*: Peyer, 2006: fig. 4; *Guanlong*: Xu *et al.*, 2006; possibly Ornitholestes: Carpenter *et al.*, 2005). Furthermore, a short quadrate is figured for *Torvosaurus* (Britt, 1991) and *Afrovenator* (Sereno *et al.*, 1994: fig. 2), although this latter reconstruction is based on *Allosaurus*.

4. Jugal pneumatopore: Rauhut (2003) optimized a pneumatic opening in the posteroventral corner of the jugal antorbital fossa as a synapomorphy of Allosauroidea (including *Monolophosaurus*), and convergently acquired in tyrannosauroids. Jugal pneumaticity is present in many allosauroids and absent in most basal theropods (see above) and derived coelurosaurs (see review in Weishampel, Dodson & Osmolska, 2004). However, it is absent in the allosauroid *Allosaurus* and present in basal coelurosaurs (tyrannosauroids: Holtz, 2004; Xu *et al.*, 2004, 2006; potentially *Ornitholestes*: Sereno *et al.*, 1996). In addition, Sereno *et al.* (1994) described a jugal pneumatopore in the basal spinosauroid *Afrovenator*, but we were unable to verify this score based on our observation of casts (UC OBA 1) and consider it absent. Thus, this character appears to be present at the base of several large clades (Allosauroidea, Coelurosauria, possibly Spinosauroidea), rendering it unlikely as an allosauroid synapomorphy. Indeed, a more basal optimization, probably at the base of Tetanurae or the clade Allosauroidea + Coelurosauria (Neotetanurae), has been recovered in other cladistic analyses (for example, Holtz, 2000; Holtz *et al.*, 2004; Smith *et al.*, 2007).

5. Quadrate with broad articular flange for quadratojugal: Sereno *et al.* (1996) listed this character as diagnostic of Allosauroidea, although it could not be scored in several taxa, including *Monolophosaurus*. Narrow flanges are present in many basal theropods (for example, *Eustreptospondylus*: Sadlier *et al.*, 2008; *Majungasaurus*: Sampson & Witmer, 2007; *Torvosaurus*: Britt, 1991). In contrast, a broad flange is clearly present in *Allosaurus* (Madsen, 1976: pl 3F) and *Sinraptor* (Currie & Zhao, 1993: fig. 8G), but one of similar size is also present in *Dilophosaurus* (Welles, 1984: fig. 5B) and spinosaurids (*Baryonyx*: Charig & Milner, 1997: fig. 11A). The quadrate and quadratojugal are co-ossified in *Ceratosaurus* (Madsen & Welles, 2000), precluding comparison.

6. Downturned paroccipital processes: Ventrally directed paroccipital processes with a distal end located ventral to the foramen magnum have been considered as a synapomorphy of Allosauroidea, including *Monolophosaurus* (Rauhut, 2003; Holtz *et al.*, 2004). However, two aspects of the paroccipital processes deserve further comment. First, allosauroids (for example, *Acrocanthosaurus*: OMNH 10146; *Allosaurus*: Madsen, 1976; *Carcharodontosaurus*: Brusatte & Sereno, 2007; *Sinraptor*: Currie & Zhao, 1993) are characterized by a unique condition in which the ventral base of the paroccipital process, where it emerges from the metotic strut, is located entirely below the occipital condyle. In *Monolophosaurus*, the base is level with the midpoint of the condyle, as is also the

case in an array of basal theropods (*Baryonyx*: Charig & Milner, 1997; *Cryolophosaurus*: Smith *et al.*, 2007; *Majungasaurus*: Sampson & Witmer, 2007; *Piatznitzkysaurus*: Rauhut, 2004). Other basal theropods have paroccipital process bases located entirely dorsal to the occipital condyle (*Ceratosaurus*: Madsen & Welles, 2000; *Dilophosaurus*: Welles, 1984; *Dubreuillosaurus*: Allain, 2002; *Piveteausaurus*: Taquet & Welles, 1977; *Zupaysaurus*: Ezcurra, 2007). Second, the aforementioned allosauroid taxa possess paroccipital processes with distal ends located ventral to the occipital condyle, which Rauhut (2003: character 54) specifically used to link *Monolophosaurus* and allosauroids. Although *Monolophosaurus* does possess this character state, so do some other basal theropods, including *Ceratosaurus* and *Cryolophosaurus*. Furthermore, the distal end extends only slightly below the condyle in *Monolophosaurus*, whereas it is located far ventrally in *Acrocanthosaurus*, *Allosaurus* and *Ceratosaurus*.

7. Basal tubera width: Holtz (2000) recovered narrow basal tubera, with a transverse width less than that of the occipital condyle, as diagnostic of Allosauroidea, including *Monolophosaurus*. However, narrow basal tubera are not uniformly present in allosauroids, as they are found in some taxa (*Acrocanthosaurus*, *Allosaurus*, *Sinraptor*: Brusatte & Sereno, 2008), but not in *Carcharodontosaurus* (Brusatte & Sereno, 2007, 2008). Unfortunately, missing data in other allosauroids precludes comparison. In addition, narrow basal tubera are also seen in the spinosaurid *Baryonyx* (Charig & Milner, 1997).

8. Small external mandibular fenestra: Sereno *et al.* (1994, 1996) considered a small external mandibular fenestra, which they equated to a deep anterior ramus of the surangular, as diagnostic of Allosauroidea. As discussed above, the maximum dimension of the fenestra of *Monolophosaurus* is approximately one-tenth the length of the lower jaw, which is approximately the same ratio as in some allosauroids and basal tetanurans. However, allosauroids are not characterized by a uniform condition, as originally noted by Sereno *et al.* (1996). *Sinraptor*, for instance, has a large fenestra, whereas *Allosaurus* has an autapomorphically reduced opening. Thus, this character is highly variable across basal theropods, and is unlikely to support a grouping of *Monolophosaurus* and Allosauroidea to the exclusion of other taxa.

9. Pendant medial process of the articular: Several authors (Sereno *et al.*, 1994, 1996; Holtz *et al.*, 2004) have recovered a pendant medial process of the articular as diagnostic of Allosauroidea, although unscorable in *Monolophosaurus*. This

process is clearly present in allosauroids (*Allosaurus*: Madsen, 1976: pl 7B; *Giganotosaurus*: MUCPv-CH-1; *Sinraptor*: Currie & Zhao, 1993: fig. 10D), but new discoveries and reinterpretations have revealed its presence in a range of basal theropods, including *Cryolophosaurus* (Smith *et al.*, 2007), *Dilophosaurus* (Yates, 2005) and *Dracovenator* (Yates, 2005). It is likely that increased taxon sampling will confirm its presence in other basal theropods (Yates, 2005).

Additional characters, once used to unite *Monolophosaurus* with Allosauroidea, have been reviewed elsewhere, and include shortened basipterygoid processes (Rauhut, 2003), pneumaticity associated with the internal carotid canal (Brusatte & Sereno, 2008) and a basioccipital excluded from the basal tubera (Rauhut, 2003; Brusatte & Sereno, 2008).

This review indicates that several characters previously used to support a link between Allosauroidea and *Monolophosaurus* are widely distributed among basal theropods, in agreement with Smith *et al.* (2007). In fact, no unequivocal characters uniting these taxa remain. Although it is possible that some phylogenetic signal linking these taxa may override this homoplasy, recent cladistic analyses (Smith *et al.*, 2007 and the modifications herein) strongly indicate that *Monolophosaurus* is not nested within Allosauroidea, and in fact is a more basal tetanuran taxon. On a larger scale, this begs the question of what characters are diagnostic of Allosauroidea (*Allosaurus*, Sinraptoridae, Carcharodontosauridae), a clade whose internal relationships are well studied (Brusatte & Sereno, 2008), but whose monophyly is poorly supported. Smith *et al.* (2007) recovered a monophyletic Allosauroidea united by only two unequivocal synapomorphies and four equivocal synapomorphies, very weak character support relative to that of other major clades in their analysis. Continuing revision of basal tetanuran phylogeny raises the possibility that Allosauroidea may not be monophyletic, a question outside of the scope of this paper that will be addressed in a future publication by one of us (M. T. Carrano, R. B. J. Benson & S. D. Sampson, unpubl. data).

Primitive characters of Monolophosaurus: In our redescription of the postcranium of *Monolophosaurus*, we identified several features of the pelvis that are present in non-tetanuran theropods, but absent in all other tetanurans (X.-J. Zhao *et al.*, unpubl. data). Similarly, Smith *et al.* (2007) identified three features of the skull of *Monolophosaurus* that are also common in more basal theropods: a postorbital that reaches the floor of the orbit, a nasolacrimal crest that includes a contribution from the premaxillae and a

laterally exposed quadrate–quadratojugal suture. Together with the results of recent cladistic analyses (Smith *et al.*, 2007 and modifications herein), these features support a basal tetanuran position for *Monolophosaurus*.

Our redescription of the skull has revealed several retained plesiomorphies often absent in tetanurans. *Monolophosaurus* appears to lack any external signs of lacrimal pneumaticity, a condition shared with some basal theropods (coelophysids and abelisaurids: Ezcurra & Novas, 2007; Sampson & Witmer, 2007; *Dilophosaurus*: Welles, 1984, UCMP 77270), but contrasting with the laterally exposed pneumatopores of most theropods, including basal forms, such as *Cryolophosaurus* (Smith *et al.*, 2007) and *Zupaysaurus* (Ezcurra & Novas, 2007). Second, the maxilla of *Monolophosaurus* is excavated by a single accessory opening (sometimes expressed as a depression), as in some coelophysids (Tykoski, 1998; Tykoski & Rowe, 2004), abelisaurids (Sampson & Witmer, 2007) and *Dilophosaurus* (Welles, 1984), and contrasting with the multiple openings (promaxillary and maxillary fenestrae) of most tetanurans (Witmer, 1997). However, this character is homoplastic, as some tetanurans only have a single opening or depression (for example, *Carcharodontosaurus*: Sereno *et al.*, 1996; Brusatte & Sereno, 2007; *Torvosaurus*: Britt, 1991; spinosaurids: Sereno *et al.*, 1998). Third, the length to depth ratio of the cranium of *Monolophosaurus* approaches 3.0, a threshold often held to be a coelophysoid synapomorphy (Sereno, 1999; Ezcurra, 2007). In contrast, the skulls of many other basal theropods (for example, *Eoraptor*: Sereno *et al.*, 1993; *Ceratosaurus*: Madsen & Welles, 2000; Tykoski & Rowe, 2004; abelisaurids: Sampson & Witmer, 2007) and tetanurans (for example, *Acrocanthosaurus*: Currie & Carpenter, 2000; *Allosaurus*: Madsen, 1976; *Sinraptor*: Currie & Zhao, 1993) are deeper compared with their lengths, with a ratio between 1.5 and 2.5. However, this character is also probably homoplastic, as a range of other basal theropods (*Afrovenator*: Sereno *et al.*, 1994; *Dilophosaurus*: Welles, 1984; *Dubreuillosaurus*: Allain, 2002; *Herrerasaurus*: Sereno & Novas, 1993; *Suchomimus*: Sereno *et al.*, 1998; *Torvosaurus*: Britt, 1991; *Zupaysaurus*: Ezcurra, 2007) and basal coelurosaurs (*Compsognathus*: Peyer, 2006; *Dilong*: Xu *et al.*, 2004; *Guanlong*: Xu *et al.*, 2006; *Juravenator*: Göhlich & Chiappe, 2006; *Ornitholestes*: Carpenter *et al.*, 2005) also possess long and low skulls with a ratio between 2.5 and 3.8. Regardless, the long and low skull of *Monolophosaurus* contrasts with the deeper skulls of Allosauroidea.

The skull of *Monolophosaurus* also possesses several features seen in basal theropods. The main body of the maxilla retains a nearly constant depth across its length, as a result of nearly parallel dorsal and ventral margins. This morphology is also seen in *Zupaysaurus* (Ezcurra, 2007) and abelisaurids (Sampson & Witmer, 2007), but contrasts with the tapering maxillae of most other theropods. The anterior ramus of the quadratojugal projects beyond the anterior margin of the lateral temporal fenestra, also seen in *Dilophosaurus* (Welles, 1984) and *Zupaysaurus* (Ezcurra, 2007), but contrasting with the shortened rami of most theropods (for example, *Allosaurus*: Madsen, 1976; *Ceratosaurus*: Madsen & Welles, 2000; Sampson & Witmer, 2007; *Cryolophosaurus*: Smith *et al.*, 2007; *Compsognathus*: Peyer, 2006; *Dilong*: Xu *et al.*, 2004; *Dubreuillosaurus*: Allain, 2002; *Guanlong*: Xu *et al.*, 2006; *Majungasaurus*: Sampson & Witmer, 2007; *Sinraptor*: Currie & Zhao, 1993; '*Syntarsus*' *kayentakatae*: Rowe, 1989). In addition, the articulation between the squamosal and quadratojugal is similar in *Monolophosaurus* and *Zupaysaurus*. In these taxa, both elements strongly project into the lateral temporal fenestra, with the dorsal ramus of the quadratojugal articulating with the posterior margin of the ventral ramus of the squamosal (compared with other theropods above). Similarly, both taxa have a kinked squamosal ventral process, which is more distinct in *Zupaysaurus*. Finally, the surangular and angular meet at a stepped contact, as in *Cryolophosaurus* (Smith *et al.*, 2007), '*Syntarsus*' *kayentakatae* (Rowe, 1989) and, possibly, *Dilophosaurus* (Smith *et al.*, 2007).

CRANIAL CRESTS IN BASAL THEROPODS

Cranial crests, horns, bosses and other ornamentation are common in theropod dinosaurs, and probably served primarily as display devices (Xu *et al.*, 2006; Smith *et al.*, 2007). A brief review of ornamentation morphology across theropods has been presented elsewhere (Smith *et al.*, 2007) and will not be repeated here. However, we highlight the use of display features, especially parasagittal crests like those of *Monolophosaurus*, as phylogenetic characters. Homologizing the features of the crest among taxa is not trivial, as all theropod crests differ in detail. In the face of this difficulty, it is unsurprising that some authors do not employ characters relating to the cranial crest in their phylogenetic data matrices (for example, Harris, 1998; Rauhut, 2003).

Other authors, however, have attempted to extract phylogenetically informative data from the crests of basal theropods. However, different authors have utilized different coding strategies. Holtz (2000) utilized two characters: a presence/absence character for paired crescentric nasolacrimal crests linking *Dilophosaurus* and some coelophysids (character 27), and an unordered five-state character for various

ornaments of the nasal, with different states for median dorsal horns, lateral ridges and various rugosities (character 26). The underlying assumption of this coding strategy is that these nasal ornaments represent variations of the same character, which is almost certainly not the case, as the features are vastly different in shape and occur on different surfaces (dorsal versus lateral). In an updated version of this dataset, Holtz et al. (2004) retained the character of the paired crescentric crests (character 59), but limited the more general nasal ornament character to a binary character denoting the presence or absence of a 'narial median horn or crest' (character 57). *Ceratosaurus* (horn), *Irritator* (short, solid crest) and *Monolophosaurus* (large, fenestrated crest) are scored for the derived state, whereas *Dilophosaurus* and coelophysids (paired crests) are scored for the primitive condition. Between the two characters emerge a signal of primary homology linking *Dilophosaurus* and coelophysids as basal theropods, whereas no crest data support a linkage between *Dilophosaurus* and *Monolophosaurus*, despite the similar composition of their crests comprising nasals and lacrimals.

In their redescription of the crested basal theropod *Cryolophosaurus*, Smith et al. (2007) atomized features of the crest into five distinct characters. Four relate to the elements comprising the crest, including the participation of the premaxillae (character 15), nasals (character 42), lacrimals (character 44) and frontals (character 64). One character differentiates midline and parasagittal crests for those taxa that possess ornamentation (character 43). As opposed to the characters of Holtz (2000) and Holtz et al. (2004), this cocktail of characters gives an overall signal of primary homology linking *Monolophosaurus* with other basal theropods, such as *Cryolophosaurus*, *Dilophosaurus*, *Dracovenator* and 'S*yntarsus*' *kayentakatae*, as well as *Zupaysaurus*, whose supposed nasal crests had not been reinterpreted (Ezcurra, 2007) by the time Smith et al.'s paper went to press. In particular, all of these taxa are scored for a nasal crest, whereas many of them (including *Monolophosaurus*) have crests that include contributions from the premaxillae and lacrimals. However, even this degree of atomization is problematic with respect to primary homology. For instance, *Monolophosaurus*, *Dilophosaurus* and *Dracovenator* are all scored for premaxillary contributions to the crest, but the contribution in the last two taxa is minimal compared with the greatly expanded and rugose premaxillary nasal process that is smoothly confluent with the nasal crest in *Monolophosaurus*. Furthermore, *Cryolophosaurus*, *Dilophosaurus* and *Monolophosaurus* are all scored for lacrimal contributions, even though the lacrimal is transversely expanded in *Cryolophosaurus*

and there is a parasagittal, sheet-like expansion in the last two taxa.

The detailed character of theropod cranial crests is highly variable (cf. Welles, 1984; Xu et al., 2006; Smith et al., 2007). In light of the fact that no two such crests are alike, it is difficult to render a system for coding characters of the cranial crests that takes into account the variation that may be phylogenetically informative whilst remaining free of the problems of overweighting as a result of excessive atomization. An analogous situation can be seen in phylogenetic studies of ceratopsians and hadrosaurs, in which it is difficult to extract the essential features of a complex and highly variable cranial ornamentation (Dodson, Forster & Sampson, 2004; Horner, Weishampel & Forster, 2004). In most cases, such extravagant complexity belies very little in terms of underlying similarity. However, the crests of some theropods are clearly much more similar than others. For instance, the paired, parasagittal, sheet-like crests of basal theropods, such as *Dilophosaurus* (Welles, 1984) and 'S*yntarsus*' *kayentakatae* (Rowe, 1989), are topologically alike and should be considered as directly homologous (primary homology) to the exclusion of topologically dissimilar crests. Although the crests of *Dilophosaurus* are much larger and incorporate contributions from the premaxillae and lacrimals, the overall size of crests and the number of bones they subtend are clearly correlated. It is unlikely that the size of crests is phylogenetically informative, as such elaborate structures, which may be under sexually driven selection pressures or relate to species recognition (Geist, 1966; Ryan, 1990; Sampson, 1999), probably evolve rapidly relative to the characters that support major divisions within Theropoda. Therefore, participation in the crest of various skull bones probably should not be coded and, in particular, we strongly discourage the use of excessive numbers of characters regarding these contributions. Problems arise when considering bizarre and highly autapomorphic cranial crests, such as that of *Cryolophosaurus* (Smith et al., 2007), and it is possible that, in such cases, the best coding strategy may be one of resignation in the face of autapomorphic, and therefore phylogenetically uninformative, variation.

For the present paper, it is interesting to consider which derived character states of the cranial crest may link *Monolophosaurus* to other taxa. Although this crest is geometrically similar to that of *Guanlong* (Xu et al., 2006) in certain respects (see below), the two are dissimilar in that the crest of *Guanlong* is transversely narrow, whereas that of *Monolophosaurus*, at its base, is as wide as the nasal bones. The crests of *Guanlong*, *Monolophosaurus* and oviraptorosaurs (Osmolska et al., 2004) are similar in their

pneumatic construction, whereby the bones constituting the crest have been inflated and hollowed by pneumatic diverticulae, most probably arising from the paranasal air sac (Witmer, 1997). Such pneumatic structure is absent in other crested theropods and may support a statement of primary homology between the taxa that possess it. However, cranial pneumaticity is widespread in theropods (Witmer, 1997) and the distribution of pneumatic structures of bones surrounding the antorbital fenestra, such as the jugal and nasal pneumatopores, is homoplastic (see above). Particular evidence of this variability is the presence of an open maxillary accessory fenestra and a large jugal pneumatopore on the left side of the skull of *Monolophosaurus* versus an enclosed maxillary depression and small jugal pneumatopore on the right side. Therefore, it seems more likely that the pneumatic crests of *Guanlong*, *Monolophosaurus* and oviraptorosaurs have arisen independently, and that pneumatization is simply a readily co-opted developmental mechanism by which such structures can be produced in theropods. However, this mechanism supports a monophyletic clade within Oviraptorosauria (Osmolska *et al.*, 2004), and so is phylogenetically informative in at least that regard. Thus, we recommend that the presence of a pneumatic cranial crest be treated as a putative statement of primary homology to be included in phylogenetic datasets and tested by parsimony analysis.

Other characters of cranial ornamentation that are present in multiple taxa and bear detailed similarity should also be employed in phylogenetic analysis. Examples are the presence of a nasal horn in *Ceratosaurus* and some spinosaurids (Charig & Milner, 1997; Sues *et al.*, 2002; Dal Sasso *et al.*, 2005), and the presence of raised nasal rims in *Allosaurus* (Madsen, 1976), *Cryolophosaurus* (Smith *et al.*, 2007), and *Neovenator* (Brusatte *et al.*, 2008). Our overall recommendation is that, in the formulation of such characters, undue atomization and pseudosimilarity should be avoided in favour of detailed and topographic similarity.

In this vein, we provide an alternative scoring strategy to that utilized by Smith *et al.* (2007). As reviewed above, Smith *et al.* (2007) atomized the cranial crests of theropods into five characters, which largely concern the participation of various bones in the crest. We favour three characters (Appendix 2), which concern the presence, shape and pneumaticity of specific types of cranial crest. When we substitute our three characters for the five original characters in our modified version of the dataset of Smith *et al.* (2007) (Appendix 1), we recover 972 MPTs of 839 steps (CI, 0.484; RI, 0.769), compared with 108 trees of 843 steps in the original analysis (CI, 0.482; RI, 0.768). The strict consensus of the new trees is iden-

tical to that in the original analysis, with one major exception: Smith *et al.*'s (2007) clade of basal crested 'dilophosaurid' theropods is collapsed. The individual genera in this clade (*Cryolophosaurus*, *Dilophosaurus sinensis*, *Dilophosaurus wetherilli*, *Dracovenator*) fall into a polytomy with *Zupaysaurus* and the large clade Neoceratosauria + Tetanurae. Thus, the reality of a basal theropod clade centred on *Cryolophosaurus* and *Dilophosaurus*, as well as the resolution of basal theropod phylogeny in general, depends heavily on how one chooses to code characters relating to cranial crests. We urge future authors to think carefully about their character coding strategies, and suggest further testing of a 'dilophosaurid' clade, which, if real, has interesting implications for theropod evolution, Mesozoic palaeobiogeography and body size evolution.

GUANLONG WUCAII: BASAL TYRANNOSAUROID, JUVENILE *MONOLOPHOSAURUS* OR NEITHER?

Xu *et al.* (2006) described a mid-sized theropod taxon, *Guanlong wucaii*, from a level of the Shishugou Formation (Oxfordian: Eberth *et al.*, 2001) slightly higher than the type locality of *Monolophosaurus*. *Guanlong* was interpreted as the oldest known tyrannosauroid, and a member of a 'specialized lineage in the early evolution of tyrannosauroids' that possesses a mosaic of primitive tetanuran features and derived coelurosaurian characters (Xu *et al.*, 2006: 717). The most notable feature of this taxon is an enlarged, thin, fenestrated midline crest that resembles the crest of *Monolophosaurus*. Noting this similarity, Carr (2006) suggested that the smaller *Guanlong* may represent a subadult *Monolophosaurus*, or that the two theropods are sister taxa. Histological analysis of the holotype of *Guanlong*, outlined in the supplementary appendix of Xu *et al.* (2006), clearly demonstrates that the specimen pertains to an adult, ruling out the first hypothesis of Carr (2006). The presence of a number of autapomorphies in each taxon (reviewed above and in Xu *et al.*, 2006) also argues against this suggestion. However, the second hypothesis deserves further consideration.

The crests of *Monolophosaurus* and *Guanlong* are strikingly similar, especially in lateral view. Both are single midline crests, comprising primarily the nasals and excavated by large fenestrae, features unknown among other basal theropods. Homologizing features of the crest is difficult, as these structures differ in detail. Most notably, that of *Guanlong* is larger, thinner, excavated by four fenestrae (as opposed to two) and reinforced by several thin laminae (Xu *et al.*, 2006). However, it is possible that a single, fenestrated crest is a synapomorphy uniting a clade of *Monolophosaurus* and *Guanlong*. Less equivocal are

two synapomorphies unrelated to the crest. First, both taxa share a large, ovoid external naris that is 25% or more longer than the length of the skull (Table 1). This derived state is unknown in other basal theropods, and contrasts with the much smaller nares of tyrannosauroids (Brochu, 2002; Currie, 2003; Xu *et al.*, 2004), basal tetanurans (Table 1) and basal coelurosaurs (*Compsognathus*: Ostrom, 1978; Peyer, 2006; *Ornitholestes*: Carpenter *et al.*, 2005; *Pelecanimimus*: Perez-Moreno *et al.*, 1994; *Scipionyx*: Dal Sasso & Signore, 1998; *Sinosauropteryx*: Currie & Chen, 2001). Second, both taxa share a weak to nonexistent lateral shelf on the surangular, a feature otherwise only known in an isolated surangular from the Middle Jurassic of England (OUMNH J.29813). In contrast, tyrannosauroids (Carr, 1999; Currie, 2003; Holtz, 2004; Xu *et al.*, 2004) and basal coelurosaurs (*Compsognathus*: Peyer, 2006; *Sinocalliopteryx*: Ji *et al.*, 2007) have a robust shelf that strongly overhangs the surangular foramen dorsally, a condition that characterizes theropods in general (see theropod chapters in Weishampel *et al.*, 2004).

In addition, several features of *Guanlong*, cited as tyrannosauroid apomorphies by Xu *et al.* (2006), are more widely distributed. Many of these are also present in *Monolophosaurus*, and include: fused nasals (also in *Ceratosaurus*, spinosaurids and some abelisaurids, and which may be related to the development of nasal ornamentation in these taxa); a large frontal contribution to the supratemporal fossa; a pneumatic foramen in the antorbital fossa on the jugal (also in allosauroids); a short retroarticular process; and a median vertical crest on the ilium. Similarly, the elongate anterior ramus of the maxilla and ischial foramen of *Guanlong* are unknown in other tyrannosauroids, but are present in *Monolophosaurus*.

At the same time, however, *Guanlong* possesses several characters diagnostic of Coelurosauria and Tyrannosauroidea, which prompted testing by cladistic methods to resolve this homoplasy. Xu *et al.* (2006) inserted *Guanlong* into the basal theropod cladistic analysis of Rauhut (2003), which found both strong tree support and character support for placing *Guanlong* as a basal coelurosaur (a tyrannosauroid) and distant from the more basal tetanuran taxon *Monolophosaurus*. In particular, 22 unambiguous synapomorphies place *Guanlong* within Coelurosauria, and seven place it within Tyrannosauroidea. Coelurosaurian characters include clear synapomorphies, such as an elongate antorbita fossa (character 14), medially inclined iliac blades (character 171), an anteroposteriorly elongate and narrow pubic peduncle of the ilium (character 175) and a concave anterior margin of the pubic peduncle (character 179). Clear tyrannosauroid characters include the sharp and narrow vertical crest on the ilium (character 172) and a concave anterodorsal region of the preacetabular process of the ilium (character 173). Constraining *Guanlong* and *Monolophosaurus* as sister taxa in Benson's (2008) updated version of the dataset of Xu *et al.* (2006) requires an additional 19 steps, or 3% of tree length (693 versus 674 steps). Thus, there is a strong phylogenetic signal linking *Guanlong* and tyrannosauroids, despite the homoplasy identified above.

We consider the coelurosaurian and basal tyrannosauroid position of *Guanlong* as a well-supported hypothesis based on current datasets. Our suggestion that *Monolophosaurus* is a much more basal tetanuran (see above) strengthens this hypothesis, as it increases the phylogenetic distance between the two taxa (as opposed to their separation by only two nodes in the Rauhut/Xu/Benson dataset), and would invoke additional homoplasy if the two formed a clade of crested basal tetanurans. However, a close affinity between *Guanlong* and *Monolophosaurus*, as suggested by Carr (2006), should be tested further. Most importantly, the two taxa have never been included in an analysis that recovers *Monolophosaurus* as a more basal tetanuran, and thus it is unclear what cost would be invoked by pulling *Guanlong* into this part of the tree. In addition, the two putative synapomorphies of *Guanlong* and *Monolophosaurus* identified above, as well as some of the homoplastic tyrannosauroid 'apomorphies' identified by Xu *et al.* (2006), have yet to be included in an analysis. Ultimately, a large phylogenetic analysis of basal tetanurans and basal coelurosaurs is needed, but this is outside the scope of this paper.

As a final note, the fragmentary basal coelurosaur *Proceratosaurus* from the Bathonian of England (BMNH R 4860) possesses several unique characters of *Monolophosaurus* and *Guanlong*. Most notably, the external naris is enlarged (greater than 20% of the skull length) and some form of thin cranial crest was present (although only the anterior region is preserved), features seen in both *Monolophosaurus* and *Guanlong*. In addition, the form of the squamosal and quadratojugal is similar in *Monolophosaurus* and *Proceratosaurus*, as both taxa have a squamosal ventral ramus that is kinked and projects strongly forward into the lateral temporal fenestra. A close relationship between *Monolophosaurus* and *Proceratosaurus* is unlikely for the same reason as discussed above for *Guanlong*: *Proceratosaurus* possesses a number of coelurosaurian characters that place it in a more derived position among theropods than *Monolophosaurus* (for example, Holtz *et al.*, 2004). However, it appears as if Middle Jurassic basal coelurosaurs (*Guanlong*, *Proceratosaurus*) retained a number of more primitive tetanuran characters, and may have generally resembled basal tetanurans more so than

closer coelurosaurian relatives. As *Proceratosaurus* is currently under study by O. Rauhut and A. Milner, it will not be discussed further here.

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APPENDIX 1

Phylogenetic analysis: We have checked all characters for *Monolophosaurus* in the analysis of Smith *et al.* (2007) and provide the following rescored block of data:

1?20000102??001100?0001210000??1000001111101021
?10010000000110110000000100001000121001000100
0?110?0??1?1011000?0???????10100100011110?010????
???1?1110?10?010020?0000000110?1?100011020????0?
0?0???0??
??????010?001001?0{01}011111000?0000???00?00000??
??

We have also slightly rescored character 315, which is now scored for absent (0) in *Afrovenator*, *Dubreuillosaurus*, *Eustreptospondylus* and *Torvosaurus*.

APPENDIX 2

Cranial crests as phylogenetic characters: We favour the following three characters to encapsulate phylogenetically informative variation among the cranial crests of theropod dinosaurs:

1. Nasals, profile of dorsal surface: convex or flat (0); transversely concave caused by offset lateral ridges (1); rises into sheet-like parasagittal crests (2).
2. Nasals, anteroposteriorly short midline horn: absent (0); present (1).
3. Nasals, inflated and hollowed by series of pneumatic chambers: no (0); yes (1). Note: when considering a wider range of theropods, the derived state can be divided into: slightly inflated (1) and highly inflated (2), with the latter condition characterizing *Guanlong*, *Monolophosaurus* and some oviraptorosaurs.

These characters are scored as follows in the taxa utilized by Smith *et al.* (2007):

Marasuchus ???
Silesaurus 000
Herrerasaurus 000
Eoraptor 000
Saturnalia ???
Plateosaurus 000
Coelophysis bauri 200
Coelophysis rhodesiensis 200
'*Syntarsus*' *kayentakatae* 200
Segisaurus ???
Liliensternus ???
Zupaysaurus 000
Dilophosaurus sinensis 200
Dracovenator ???
Dilophosaurus wetherilli 200
Cryolophosaurus 100
Elaphrosaurus ???
Ceratosaurus 010
Ilokelesia ???
Abelisaurus 00?
Carnotaurus 000
Majungasaurus 001
Masiakasaurus ???
Noasaurus ???
Piatnitzkysaurus ???
Condorraptor ???
Dubreuillosaurus ???
Afrovenator ???
Torvosaurus ???
Eustreptospondylus ???
Streptospondylus ???
Baryonyx 010
Suchomimus ???
Irritator 010
Monolophosaurus 001
Sinraptor 000
Tyrannotitan ???
Megaraptor ???
Carcharodontosaurus 000
Giganotosaurus 000
Acrocanthosaurus 000

Allosaurus 100
Neovenator 100
Tugulusaurus ???
Dilong 000
Tyrannosaurus 001
Coelurus ???
Compsognathus 000
Sinosauropteryx 000

Shenzhousaurus 000
Sinornithosaurus 000
Ornitholestes 000
Deinonychus 000
Velociraptor 000
Archaeopteryx 000
Confuciusornis 000