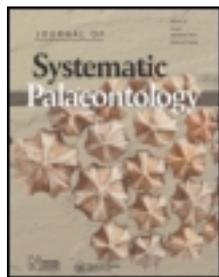


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## A juvenile specimen of a new coelurosaur (Dinosauria: Theropoda) from the Middle–Late Jurassic Shishugou Formation of Xinjiang, People’s Republic of China

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We describe the anatomy of a new coelurosaurian theropod *Aorun zhaoi* gen. et sp. nov., from the Middle–Late Jurassic of Xinjiang, China. Histological analysis of the holotype and only known specimen shows that the new taxon is represented by the skeleton of a juvenile individual aged no more than one year. A phylogenetic analysis of theropod relationships places *Aorun* as a basal member of the Coelurosauria. Although the sole use of a sub-adult ontogenetic exemplar is potentially problematic for phylogenetic reconstruction, we show that the phylogenetic position of *Aorun* as a member of Coelurosauria is robust to the exclusion of characters known to change during theropod ontogeny. *Aorun* is the seventh theropod taxon, and temporally oldest coelurosaur, known from the Shishugou Formation, which has one of the most taxonomically diverse Jurassic coelurosaurian theropod faunas in the world.

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**Keywords:** coelurosaur; juvenile; Middle Jurassic; Late Jurassic; Shishugou Formation; China

### Introduction

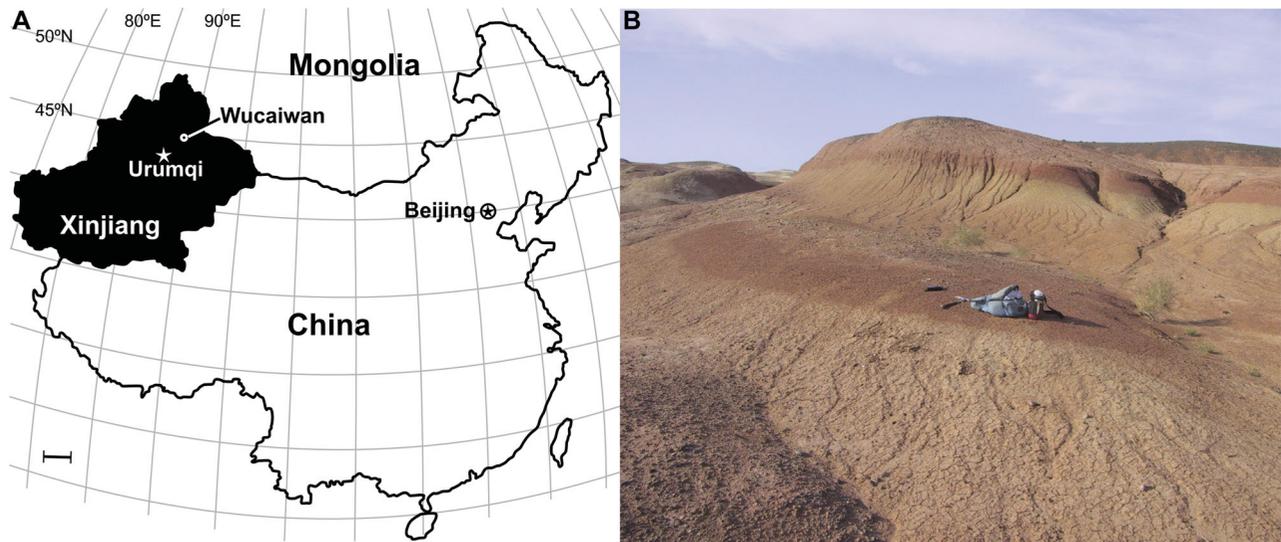
Despite predictions from ghost lineages that early coelurosaurian divergence occurred during the Middle–Late Jurassic (Norell *et al.* 2001b; Rauhut 2003a; Hu *et al.* 2009; Choiniere *et al.* 2010b; Xu *et al.* 2011), coelurosaur fossils dating to the Jurassic are rare, and specimens of coelurosaurs during this time interval are often limited to isolated bones and teeth. A spate of recent discoveries has provided exciting new skeletal evidence of coelurosaurs in the Middle–Late Jurassic. These include members of the derived coelurosaurian clade Scansoriopterygidae from north-eastern China (Czerkas & Yuan 2002; Zhang *et al.* 2002, 2008; Xu & Zhang 2005; Hu *et al.* 2009), paravian fossils from the Daohugou Beds of China (Xu & Zhang 2005; Hu *et al.* 2009; Xu *et al.* 2009b, 2010b), some of which call into question the avian status of *Archaeopteryx* (Xu *et al.* 2011), basal tyrannosauroids from the Jurassic of England (Benson 2008) and Siberia (Averianov *et al.* 2010), and reaffirmation of the coelurosaurian affinities of the Middle

Jurassic taxon *Proceratosaurus* (Rauhut *et al.* 2010). Importantly, a diverse new coelurosaurian fauna has also been discovered from the earliest Late Jurassic Shishugou Formation (Clark *et al.* 2006a, b; Choiniere *et al.* 2010a, b). These new Shishugou taxa have provided a wealth of anatomical information on basal coelurosaurs (Choiniere *et al.* 2008, 2010a), basal tyrannosauroids (Xu *et al.* 2006), and basal alvarezsauroids (Choiniere *et al.* 2010b).

Early ontogenetic stages of dinosaurs are becoming increasingly well known (Xu & Wu 2001; Rauhut & Fechner 2005; Reisz *et al.* 2005; Goodwin *et al.* 2006; Schwarz *et al.* 2007; Balanoff *et al.* 2008; Dal Sasso & Maganuco 2011), but fossils of young non-avian coelurosaur specimens remain rare (Bever & Norell 2009). Most fossils preserving early coelurosaurian ontogenetic stages are either embryos (Norell *et al.* 1994; Balanoff & Rowe 2007; Mateus *et al.* 1997; Kundrat *et al.* 2008) or perinates such as the specimens of the troodontid *Byronosaurus* (Bever & Norell 2009), the approximately 3-week-old compsognathid *Scipionyx* (Dal Sasso & Signore 1998; Dal Sasso & Maganuco 2011), and the

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**Figure 1.** Locality of holotype. **A**, map of China showing Xinjiang and location of Wucaiwan locality; **B**, photograph of holotype locality of IVPP V15709. Scale bar in **A** equals approximately 150 km.

basal coelurosaur *Juravenator* (Göhlich & Chiappe 2006; Göhlich *et al.* 2006; Chiappe & Göhlich 2010). Notable exceptions among coelurosaurs are most *Archaeopteryx* specimens, which are approximately one year old (Erickson *et al.* 2009) and partial developmental sequences for tyrannosaurids (Carr 1999; Carr & Williamson 2004), including the recent description of a specimen of *Tarbosaurus* estimated at 2–3 years old (Tsuihiji *et al.* 2011).

In 2006, the IVPP-GWU Field Expedition recovered the skull and partial postcranial skeleton of a small coelurosaurian theropod in Shishugou Formation (Fm.) at the Wucaiwan locality in Xinjiang, China (Figs 1, 2). Here we describe this material, which represents a new species of coelurosaur. From the stratigraphic position of the holotype, we show that this specimen is the oldest coelurosaur known from the Shishugou Formation, and possibly dates to the latest Middle Jurassic (Callovia). Based on histological analysis of the femur and tibia and skeletal characteristics of the holotype, the specimen is at most one year old but not a perinate. We discuss the morphological and phylogenetic implications of the early ontogenetic stage of the holotype for the new species.

## Methods

### Descriptions and comparisons

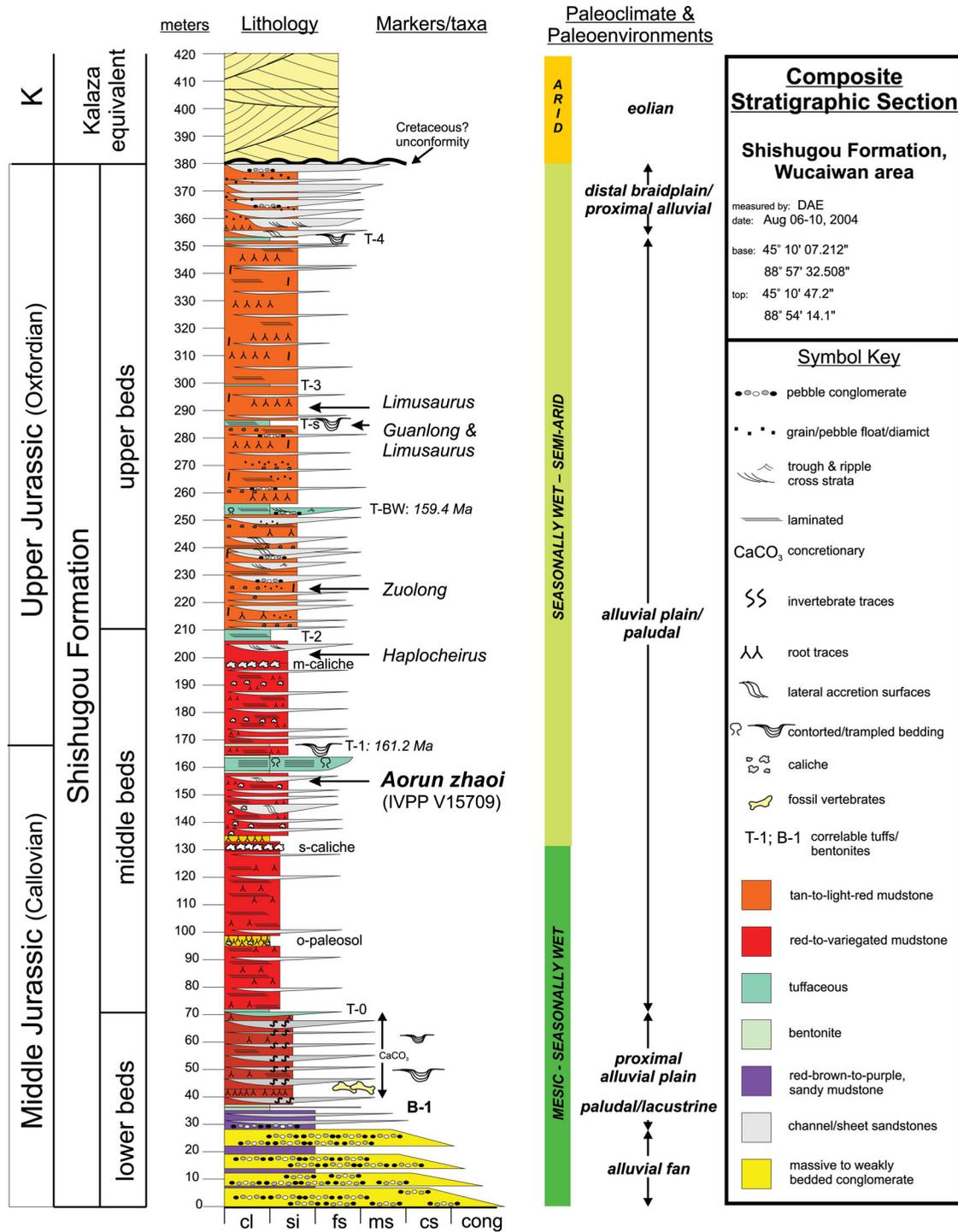
All descriptions of the new taxon are observations made directly from the holotype specimen, IVPP V15709. Comparisons with other taxa were made using direct observations of specimens or with published descriptions, illustrations and photographs. Note that we homologize the three fingers of *Aorun* with digits II, III and IV of the primitive

theropodan manus, and refer to these positions as such in the text, as is currently hypothesized for all tetanurans (Xu *et al.* 2009a); see Wagner & Gauthier (1999) for a contradictory opinion.

Measurements of key dimensions of the skeletal elements of IVPP V15709 were taken with Miyamoto dial callipers to the nearest tenth of a millimetre and are presented in Table 1 of the Online Supplementary Material.

### Phylogenetic analysis

The phylogenetic position of IVPP V15709 was assessed by incorporating it into a broadly sampled, species-level theropod data matrix (Online Supplementary Material Data 1 and 3) composed of characters drawn from recent publications of the Theropod Working Group (e.g. Turner *et al.* 2007; Zanno 2008; Makovicky *et al.* 2009; Choiniere *et al.* 2010b) and recent publications on theropod systematics (e.g. Rauhut 2003a; Senter 2007; Smith *et al.* 2007; Carrano & Sampson 2008; Benson *et al.* 2010b). The dataset was assembled in Mesquite v.2.7 (Maddison & Maddison 2009) and phylogenetic analysis of the dataset was performed using TNT v.1.1 (Goloboff *et al.* 2003). The final dataset comprised 555 characters and 114 taxa. Trees were rooted on *Herrerasaurus*. Multistate characters were ordered only if they contained nested character states. The phylogenetic analysis protocol consisted of a heuristic search using the following ‘New Technology’ settings: driven search; stabilized consensus twice with a factor of 75; using sectorial searches and tree fusing (Goloboff 1999). The resulting most parsimonious trees (MPTs) from this search were then submitted to an additional round of tree bisection and reconnection (TBR) branch swapping to ensure a thorough sampling of tree space. Exploration of character



**Figure 2.** Composite stratigraphic section of the Shishugou Formation at Wucaiwan. Stratigraphic position of *Aorun zhaoi* (IVPP V15709) indicated by arrow. Separate stratigraphic positions of four other theropod taxa (discussed here) are indicated by genera and arrows. The type of *Aorun zhaoi* occurs in the upper portion of the Middle Jurassic part of the formation, and is assessed as Callovian in age. All the other theropod specimens occur in the Upper Jurassic part of the formation and are assessed as Oxfordian in age. Two  $^{40}\text{Ar}/^{39}\text{Ar}$  radiometric ages associated with tuffs T-1 and T-BW are the basis for our calculation of an uncompacted sediment accumulation rate of  $\sim 4.6$  cm/ka for the middle of the formation.

optimization was done using TNT v1.1 and WinClada v. 1.00.18 (Nixon 2002). Bremer Support (Bremer 1994) for nodes was calculated by saving 10 000 suboptimal topologies up to 10 steps longer than the MPTs in TNT v1.1.

Because histological analysis of IVPP V15709 showed that the specimen was less than one year old at time of death (see below), we performed two separate phylogenetic analyses to assess the phylogenetic position of *Aorun* and to determine if its phylogenetic position was influenced by the young ontogenetic stage of the holotype. The first analysis (hereafter ‘full analysis’) was done with all character scorings relevant for *Aorun* included (Online Supplementary Material Data 1). The second analysis (hereafter ‘ontogenetic analysis’) was done with characters that we considered ontogenetically variable (Online Supplementary Material Table 2), coded as missing (i.e. ‘?’; Online Supplementary Material Data 2) for *Aorun*, and also for *Scipionyx* and *Juravenator*, the unique holotypes of which are also suggested to be juveniles (Dal Sasso & Signore 1998; Göhlich & Chiappe 2006; Göhlich *et al.* 2006; Chiappe & Göhlich 2010).

### Histological techniques

The ontogenetic stage of IVPP V15709 was assessed by analysis of histological sections of the right tibia and fibula. Mid-diaphyseal transverse plane sections were extracted using a rotary Dremel-type device fitted with a diamond-tipped blade. The bone sections were embedded in a clear epoxy resin (EpoxySet; Allied High Tech Products, Rancho Dominguez, CA, USA). They were then sectioned transversely using a slow-speed diamond saw (Isomet 1000, Buehler, Lake Bluff, IL, USA) at 1 mm intervals. The sections were affixed to petrographic microscope slides using cyanoacrylate adhesive. The sections were wet-sanded on a rotary grinder/polisher (RotoPol 11; Stuers, Cleveland, OH, USA) to 60–100  $\mu\text{m}$  using descending grades of silicon carbide paper and viewed using polarizing and dissecting microscopy (BX60 and SZX12 respectively; Olympus America, Center Valley, PA, USA). Bone vascularization and the presence/absence of lines of arrested growth (LAGs) were assessed visually in comparison with histological sections from other archosaurs, including ornithischian and saurischian dinosaurs (e.g. Erickson *et al.* 2001).

### Institutional abbreviations

**AMNH FARB:** American Museum of Natural History, New York, NY, USA; **IGM:** Paleontological Institute, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; **GWU:** George Washington University, Washington, DC, USA; **IVPP:** Institute for Vertebrate Paleontology and Paleoanthropology, Beijing, China; **IWCMS:** Dinosaur Isle Museum, Sandown, Isle of Wight, UK; **NHMUK:** Natural History Museum, London, UK; **TPII:** Thanksgiving Point

Institute, Provo, UT, USA; **YPM:** Yale Peabody Museum, New Haven, CT, USA.

## Systematic palaeontology

**Theropoda** Marsh, 1881

**Tetanurae** Gauthier, 1986

**Coelurosauria** *sensu* Gauthier, 1986

*Aorun* gen. nov.

**Type species.** *Aorun zhaoi* sp. nov.

**Derivation of name.** ‘Aorun’, Mandarin Chinese, masculine, elision of ‘Ao Run’, the Dragon King of the West in the epic *Journey to the West*.

**Diagnosis.** As for type and only species.

*Aorun zhaoi* sp. nov.

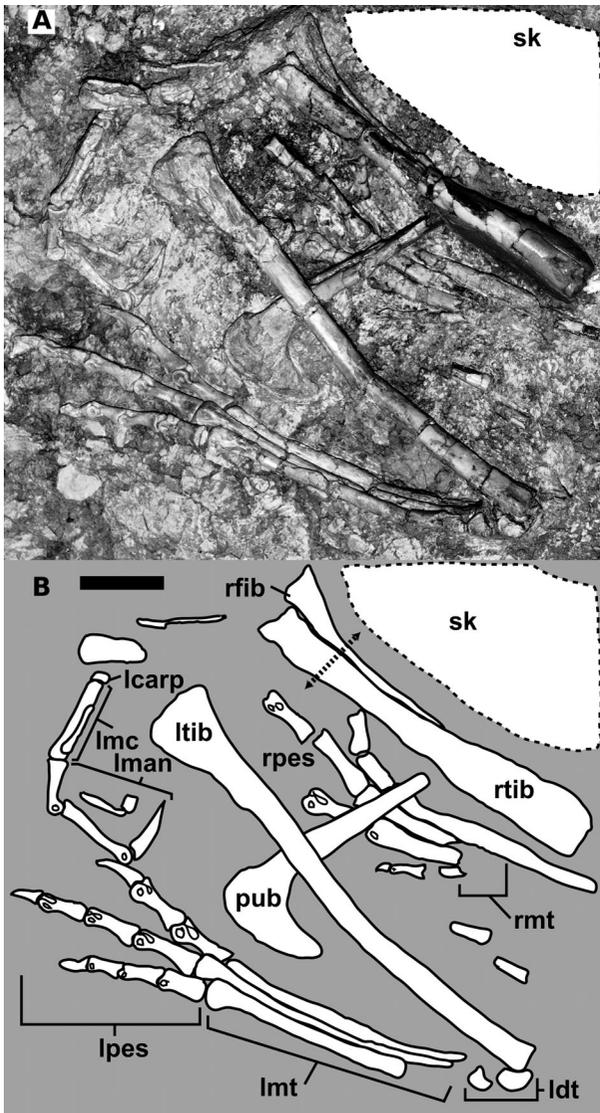
(Figs 3–19, 21, 22)

**Derivation of name.** In honour of Professor Zhao Xi-jin, who led several important vertebrate palaeontological expeditions to the Junggar Basin and introduced XX, CAF and JMC to the field area.

**Holotype.** IVPP V15709, skull and partially articulated skeleton consisting of cervical, dorsal and caudal vertebrae, left ulna, left manus, distal pubes, and articulated left and right tibiotarsi, metatarsi and pedes (Figs 3–19).

**Occurrence and age.** Non-pedogenic, red-brown clayey siltstone bed in the lower half of the Shishugou Formation exposed at the Wucaiwan locality in Xinjiang, People’s Republic of China (Fig. 1). IVPP V15709 occurs 13 m below a tuffaceous mudstone horizon (Fig. 2) that has been assessed a radiometric ( $^{40}\text{Ar}/^{39}\text{Ar}$ ) age of  $161.2 \pm 0.2$  Ma, approximately at the Oxfordian/Callovian boundary (Middle–Late Jurassic; Gradstein *et al.* 2004; Clark *et al.* 2006a, b; Eberth *et al.* 2006, 2010). The Oxfordian/Callovian boundary is poorly constrained (Gradstein *et al.* 2004) and the holotype could be older or younger than it. However, the occurrence of the specimen well below the dated horizon suggests its assignment to the latest Middle Jurassic (Callovian). Based on the ages of two dated tuffs in this section separated by 82 m of section, we estimate the rate of sediment accumulation in this part of the section at  $\sim 4.6$  cm/ka (Eberth *et al.* 2006) and therefore assess the specimen an estimated age of  $\sim 161.5$  Ma.

Other theropods collected from Wucaiwan are mostly Late Jurassic (Oxfordian) in age and include the basal ceratosaur *Limusaurus inextricabilis* (Xu *et al.* 2009a), the basal coelurosaur *Zuolong salleei* (Choiniere *et al.* 2010a), the basal tyrannosauroid *Guanlong wucaii* (Xu *et al.* 2006) and the basal alvarezsauroid *Haplocheirus sollers* (Choiniere *et al.* 2010b). Isolated teeth collected from the upper beds of the Shishugou Fm. at Wucaiwan suggest the



**Figure 3.** Overview of partially prepared block containing *Aorun zhaii* (IVPP V15709). The skull was removed prior to this photograph and its approximate position is indicated by the dashed black line with white fill. The dashed line with arrows indicates the approximate position of the histological section taken for analysis. **A**, photograph of block; **B**, line drawing. Abbreviations: sk, skull; rfib, right fibula; lcarp, left carpus; lmc, left metacarpus; ltib, left tibia; rpes, right pes; rtib, right tibia; lman, left manus; pub, pubis; rmt, right metatarsus; lpes, left pes; lmt, left metatarsus; ldt, left distal tarsals. Scale bar equals 2 cm.

presence of a large-bodied, *Sinraptor*-like theropod (Xu & Clark 2008) and potentially four other theropod taxa as yet unknown from non-dental skeletal material (Han *et al.* 2011). The large-bodied theropods *Monolophosaurus jiangi* (Zhao & Currie 1993; Brusatte *et al.* 2010a; Zhao *et al.* 2010) and *Sinraptor dongi* (Currie & Zhao 1993) are known from the Shishugou Formation at the Jiangjunmiao locality, 100 km to the east. *Sinraptor* is from the upper half of the formation and likely contemporaneous with the other

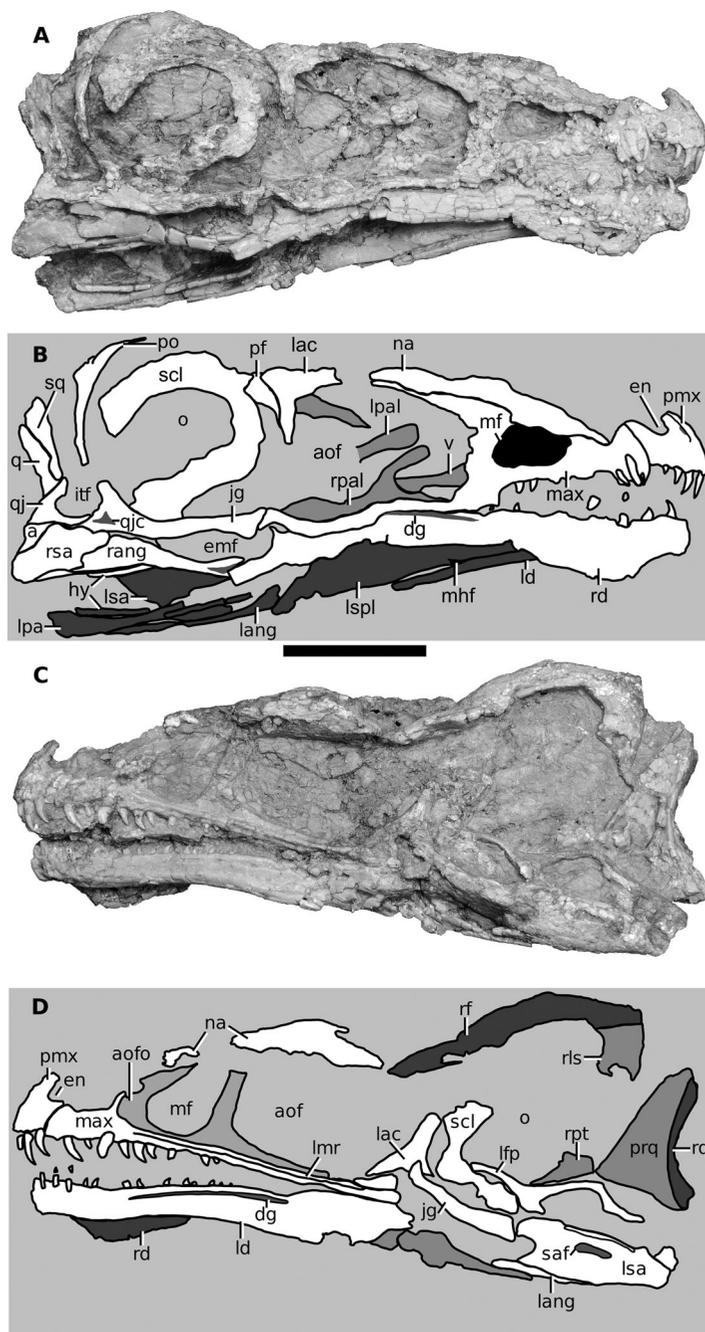
Oxfordian taxa listed here, whereas *Monolophosaurus*, from lower beds that are likely Callovian in age, is probably closer in age to *Aorun*.

**Diagnosis.** Small coelurosaurian theropod diagnosed by the following unique combination of characters: large maxillary fenestra occupying most of antorbital fossa; maxillary teeth with very small, apically directed serrations restricted to the distal carinae; weakly opisthocoelous cervical centra; heterogeneous manual ungual morphology with large, recurved medial ungual and two smaller lateral unguals that have linear, rather than curved, ventral surfaces; tibia with mediolaterally narrow, proximodistally tall articular groove accepting the ascending process of astragalus that is only developed on anterolateral margin; ascending process of astragalus low and restricted to lateral side of tibia.

**Differential diagnosis.** Here we present differentiation of *Aorun zhaii* to show that this taxon is not a juvenile specimen of other named Shishugou Fm. theropod taxa. Known ontogenetic changes in some of these characters are described in the discussion.

*Aorun zhaii* differs from the coeval lower Shishugou basal tetanuran *Monolophosaurus jiangi* (IVPP V84019; Brusatte *et al.* 2010a; Zhao *et al.* 2010) in: lacking a medial crest on the premaxilla, nasals and frontals; lacking a horizontally oriented, relatively large external naris; lacking an anterior, step-like maxillary process; having a shorter premaxillary body; having a larger maxillary fenestra; bearing a horizontally oriented ridge along the lateral surface of the jugal process of the maxilla; having a rod-like jugal; having a ventrally tapering quadratojugal process of the squamosal; having closely spaced fine serrations on the distal tooth carinae of the maxilla and dentary; having elongate cervical vertebral centra; having two pneumatic foramina in the lateral surfaces of the cervical centra; having anteroposteriorly elongate neural spines in the dorsal vertebrae; and having a posterodistally curved pubic shaft.

It differs from the stratigraphically younger upper Shishugou allosauroid *Sinraptor dongi* (IVPP V10600; Currie & Zhao 1993) in: lacking extensive pneumatization of the nasal ramus of the maxilla; having a larger and more posteriorly placed maxillary fenestra; bearing a pronounced horizontal ridge on the lateral surface of the maxilla; having a dorsoventrally low, rod-like jugal; lacking a pneumatic recess in the lateral surface of the anterior end of the jugal; having premaxillary teeth of approximately the same size as the maxillary teeth; lacking a lacrimal foramen; lacking a rugosity on the lateral surface of the postorbital; having a relatively short infratemporal fenestra with a pronounced constriction at mid-height; having elongate cervical centra; having shorter cervical neural spines that are directed strictly dorsally; lacking pneumatization of the infrazygapophyseal laminae; lacking a medially and laterally expanded proximal end of metacarpal III;

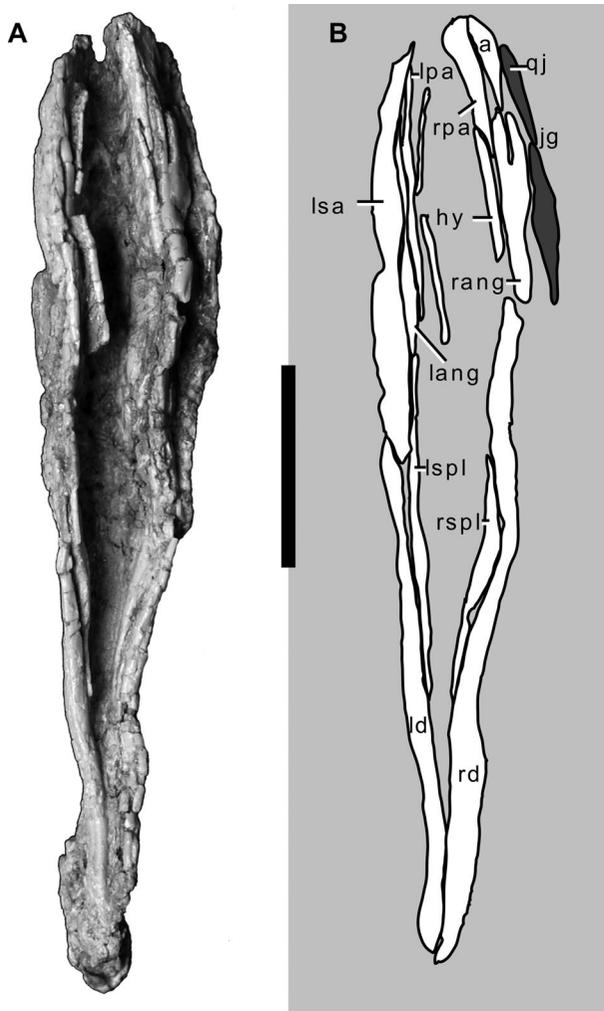


**Figure 4.** Skull and mandible of *Aorun zhaoi* (IVPP V15709). **A**, right lateral view; **B**, line drawing of right lateral view; **C**, left lateral view; **D**, line drawing of left lateral view. Abbreviations: a, articular; aof, antorbital fenestra; aof, antorbital fossa; dg, dentary groove; emf, external mandibular fenestra; en, external naris; hy, hyoid; itf, infratemporal fenestra; jg, jugal; lac, lacrimal; lang, left angular; ld, left dentary; lfp, left frontal and parietal; lmr, lateral maxillary ridge; lpa, left prearticular; lpal, left palatine; lspl, left splenial; max, maxilla; mf, maxillary fenestra; mhf, mylohyoid foramen; na, nasal; o, orbit; pf, prefrontal; pmx, premaxilla; po, postorbital; prq, pterygoid ramus of the quadrate; q, quadrate; qj, quadratojugal; qjc, quadratojugal contact; rang, right angular; rd, right dentary; rls, right laterosphenoid; rpal, right palatine; rpt, right pterygoid; rq, right quadrate; rsa, right surangular; saf, surangular foramen; scl, sclerotic ring; sq, squamosal; v, vomer. Scale bar equals 1 cm.

lacking deep extensor pits on the distal ends of the dorsal surface of the metacarpals; having a weakly curved manual unguis IV-4; having a posterodorsally curved pubic shaft; having a more gracile tibia; and having more gracile and

elongate pedal phalanges, particularly of pedal digits II and III.

*Aorun zhaoi* differs from the younger upper Shishugou tyrannosauroid *Guanlong wucaii* (IVPP V14531, V14532;



**Figure 5.** Skull and mandible of *Aorun zhaoi* (IVPP V15709). **A**, ventral view; **B**, line drawing of ventral view. Abbreviations as in Fig. 4, and: rpa, right prearticular; rspl, right splenial. Scale bar equals 2 cm.

Xu *et al.* 2006) in: lacking a D-shaped cross section of the premaxillary tooth crowns; bearing fine serrations on only the distal carinae of the dentary and maxillary teeth; lacking a median crest along the dorsal surface of the premaxilla, nasals and frontals; having opisthocoelous rather than platycoelous cervical vertebrae; having a short, laterally restricted ascending process of the astragalus; having a shorter, more dorsally oriented external naris; lacking an anteriorly expanded pubic boot; lacking four metacarpals; and having flat unguals on the lateral two digits of the manus.

It differs from the younger upper Shishugou coelurosaur *Zuolong salleei* (IVPP V15912; Choiniere *et al.* 2010a) in: having a larger maxillary foramen; having a sharper, more pronounced lateral ridge on the jugal process of the maxilla; having a small quadrate foramen without a deep pocket extending dorsally; having opisthocoelous cervical

vertebrae; lacking a flange on the anteromedial surface of the distal end of metatarsal III; and having a more medio-laterally compressed distal end of metatarsal IV.

*Aorun zhaoi* differs from the younger upper Shishugou alvarezsaurid *Haplocheirus sollers* (IVPP V15988; Choiniere *et al.* 2010b) in: lacking a dorsally expanded orbital region; having a larger maxillary fenestra; having a fourth metacarpal that is subequal in length to the third metacarpal; lacking a prominent medial tab on the proximal end of the semilunate distal carpal; lacking a ventral axial furrow on the first phalanx of digit II; having flat unguals on the lateral manual digits; having opisthocoelous cervical vertebrae; and having a relatively larger pubic boot.

Finally, it differs from the younger upper Shishugou ceratosaur *Limusaurus inextricabilis* (IVPP V15923; Xu *et al.* 2009a) in: having a relatively longer skull, particularly in the rostrum; having teeth; having an unreduced manus with only three metacarpals; having a smaller external mandibular fenestra; first phalanx of pedal digit II approximately the same length as the first phalanx of pedal digit III; distal phalanges of pedal digit IV longer; and many other differences consistent with ceratosaurian affinities of *Limusaurus*.

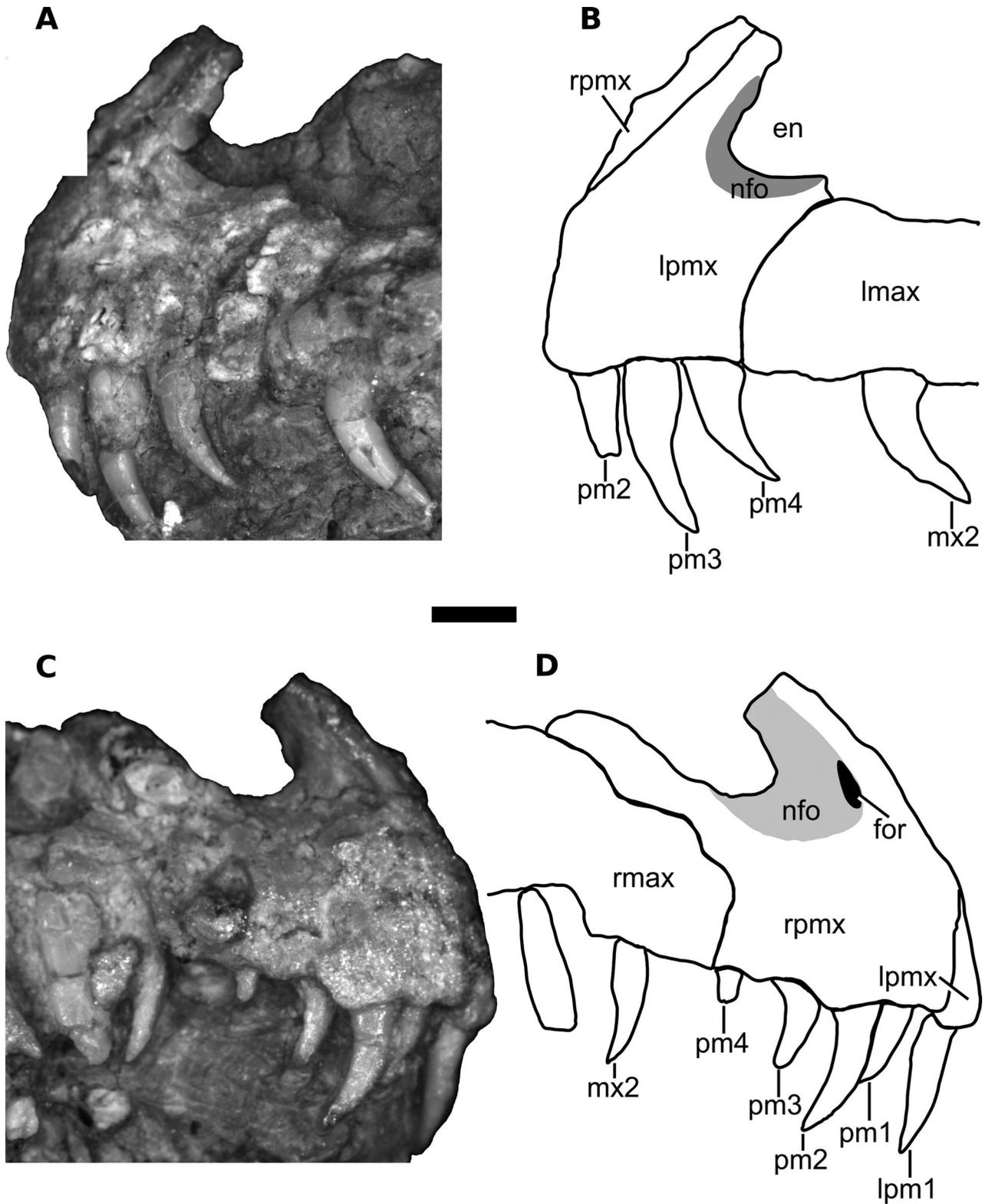
## Description

### Skull overview

The skull (Figs 5–10) is long and low. The bones of the skull and mandibles have been mediolaterally compressed during preservation, so the true shape of the skull in the mediolateral direction cannot be ascertained. Although most cranial and mandibular bones are preserved in articulation, the lateral surface of the right side of the skull has been abraded and most of the anterior end of the right maxilla consists of broken fragments.

### Skull openings

The size of the external naris cannot be determined because the nasal and maxillary processes of the premaxillae are broken distally. However, unlike the horizontally oriented and rectangular narial opening of the co-occurring tyrannosauroid *Guanlong wucaii* (Xu *et al.* 2006), the long axis of the anteroventral portion of the naris is angled approximately 45° from horizontal and its anterior end is semicircular in outline, rather than square. The antorbital fossa is large and extends ventrally onto the jugal ramus of the maxilla to occupy more than half the height of the bone. The antorbital fenestra is subovoid and longer than it is tall, unlike the subtriangular, anteroposteriorly short antorbital fenestra of *Scipionyx* (Dal Sasso & Maganuco 2011). It is positioned posteriorly within the antorbital fossa and occupies approximately 63% of the entire length of the antorbital fossa. The maxillary fenestra is large, as in both adult and juvenile troodontids (Makovicky & Norell 2004; Bever & Norell



**Figure 6.** Premaxillae of *Aorun zhaoui* (IVPP V15709). **A**, left lateral view; **B**, line drawing of left lateral view; **C**, right lateral view; **D**, line drawing of right lateral view. Abbreviations as in Fig. 4, and: for, foramen; rpmx, right premaxilla; lmax, left maxilla; lpmx, left premaxilla; mx2, maxillary tooth 2; nfo, nasal fossa; pm1–4, premaxillary teeth 1–4; rmax, right maxilla. Scale bar equals 5 mm.

2009), but unlike the small maxillary fenestrae of most coelurosaurs (e.g. dromaeosaurids: Norell & Makovicky 2004; ornithomimosaurids: Makovicky *et al.* 2004) including *Scipionyx* (Dal Sasso & Maganuco 2011). It occupies almost the entirety of the antorbital fossa anterior to the maxillary pila. The maxillary pila is anteroposteriorly short and does not appear to bear an anteroposteriorly oriented foramen along its ventral contact with the jugal ramus of the maxilla, although both sides of the skull are damaged in this region. A small, ovoid promaxillary foramen is located ventrally on the anterior end of the antorbital fossa. The circular orbit is approximately the same length as the antorbital fenestra, as in many coelurosaurs but unlike *Scipionyx*, where the orbit is considerably larger than the antorbital fenestra (Dal Sasso & Maganuco 2011). The infratemporal fenestra is anteroposteriorly much shorter than the orbit and is constricted mesially by the squamosal and quadratojugal as they approach the posterior edge of the postorbital, although this constriction is not pronounced as it is in tyrannosauroids (Holtz 2004). The dimensions of the supratemporal fossa cannot be determined because of mediolateral diagenetic crushing. The external mandibular fenestra is large (~33% of the length of the dentary), but not hypertrophied, like in oviraptorosaurs (Osmólska *et al.* 2004), *Limusaurus* (IVPP V15923), and scansoriopterygids (Czerkas & Yuan 2002; Zhang *et al.* 2008), where it is approximately 50% the length of the dentary.

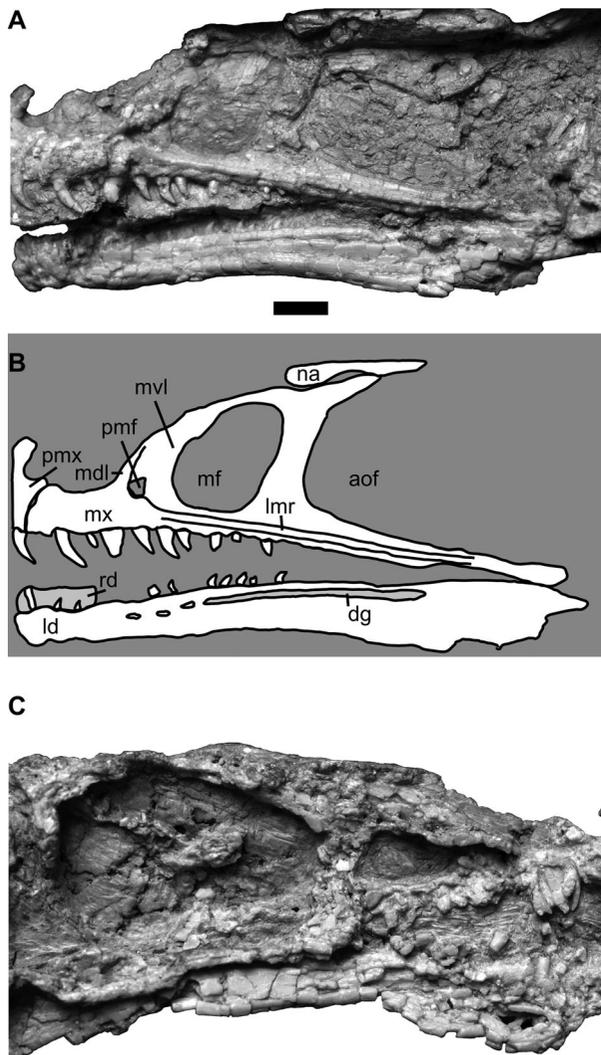
### Skull bones

**Premaxilla.** The two premaxillae (Figs 4, 6) are preserved in articulation with each other and with the anterior ends of their respective maxillae. The external surfaces of both premaxillae are mildly abraded. The nasal and maxillary processes are broken close to the premaxillary bodies. The right side is more complete, preserving these processes above and below the anterior quarter of the external naris. The premaxillae are not co-ossified to each other, and in ventral view the anterior ends of the premaxillae form a mediolaterally narrow, U-shaped symphysis (Fig. 5). The premaxillary body is as long as it is tall, and the portion ventral to the external naris is subequal in length to the prenasal portion, unlike in *Scipionyx* where the prenasal portion is longer than the subnasal portion (Dal Sasso & Maganuco 2011). The anterior margin of the premaxilla is angled posterodorsally approximately 15° from vertical. The posterodorsally oriented contact of the premaxilla with the maxilla is a shallow, posteriorly concave arc in lateral view. The left side of the skull preserves what appears to be a small subnasal foramen between the premaxilla and the maxilla at approximately the mid-height of the premaxillary body, although this interpretation is tentative because the right side of the skull does not preserve this region and the left side is slightly abraded. There is no gap at the ventral margin between the premaxilla and the maxilla, unlike many basal theropods (e.g.

coelophysoids and baryonychids: Welles 1984; Gauthier 1986; Colbert 1989; Rauhut 2003a). Although the lateral surfaces of the premaxillae are abraded, there is no evidence of a sulcus extending from the anteroventral corner of the external naris as in *Guanlong* (Xu *et al.* 2006), *Haplocheirus* (IVPP V15988) and *Eotyrannus* (IWCMS 1997.550). The narial fossa shallowly excavates the dorsal portion of the premaxillary body, unlike in *Haplocheirus* (IVPP V15988), ornithomimosaurids (e.g. *Pelecanimimus* (LH 7777), *Limusaurus* (IVPP V15923) and *Shuvuuia* (IGM 100/99), where the narial fossa extends ventrally to excavate at least the dorsal half of the premaxillary body. A small, round foramen is present on the posterior edge of the base of the nasal process of the premaxilla, at the anteroventral edge of the narial fossa, like in many theropods. The condition differs from that of *Haplocheirus* (IVPP V15988), where this foramen is associated with a tall ovoid fossa that extends along the posterior edge of the nasal process. The bases of the nasal processes of the premaxillae are dorsoventrally flat, strongly suggesting that the entire internarial bar was dorsoventrally flat, as in many troodontids (e.g. *Sinovenator* (IVPP V 12615)), alvarezsaurids (e.g. *Haplocheirus* (IVPP V15988)), and some ornithomimosaurids (e.g. *Gallimimus* (IGM 100/1133), *Pelecanimimus* (LH 777)). The premaxilla contains four alveoli of subequal size that are evenly spaced along the alveolar margin, as is typical of many maniraptorans.

**Maxilla.** The right maxilla (Figs 4A, B, 7C) is nearly complete, missing only portions of the anteriormost end, but it is very poorly preserved due to abrasion and breakage of the cortical surface. The left maxilla (Figs 4C, D, 7A, B) is missing the nasal ramus and the anterior end of the maxillary body, but the left jugal ramus is complete and well preserved. The maxillary/jugal contact is poorly preserved on both sides of the skull. The maxilla is long and low. Because of the breakage of the anterior ends of both maxillae, the architecture of the junction between the nasal ramus and jugal ramus cannot be fully determined. The shape of the anterior end of the left maxilla suggests that the nasal ramus is offset posteriorly from the anterior end of the maxilla and that a short anterior process was present. At best, evidence for this process, which is present in compsognathids (Peyer 2006) and well developed in some non-coelurosaurian tetanurans (e.g. *Monolophosaurus*: Zhao & Currie 1993) and the basal tyrannosauroid *Guanlong* (IVPP V14532, V14531), is equivocal. Unlike in most theropods, there is no evidence for small, superficial foramina on the anterior end of the lateral surface of the maxilla, which may be due to the early ontogenetic stage of the specimen or due to poor preservation.

The nasal ramus of the maxilla is composed of a vertically oriented lamina, located ventrally, and a horizontally oriented lamina, located dorsally and mostly developed lateral to the vertical lamina. The dorsal lamina is



**Figure 7.** Anterior skull and mandible of *Aorun zhaoi* (IVPP V15709). **A**, left lateral view; **B**, line drawing of left lateral view; **C**, right lateral view. Abbreviations as in Fig. 4, and: mdl, dorsal lamina of maxilla; mvl, ventral lamina of maxilla; pmf, promaxillary foramen. Scale bar equals 1 cm.

dorsoventrally low and only developed at the anterior end of the maxillary antorbital fossa. It projects laterally and extends posteriorly only to the level of the posterior end of the maxillary fenestra. The ventral lamina is best-developed posterior to the interfenestral pila, but a small portion is preserved above the maxillary fenestra on the left side of the skull and has been partially obscured by downward displacement of the dorsal lamina on that side during preservation. This preserved portion is dorsoventrally low and bears a single small foramen on its lateral surface. In contrast, *Haplocheirus* shows a well-developed ventral lamina above the maxillary fenestra with several small foramina perforating its lateral surface (Choiniere *et al.* 2010b). In *Aorun*, the dorsal lamina of the nasal ramus of the maxilla forms the roof of the anterior end of the

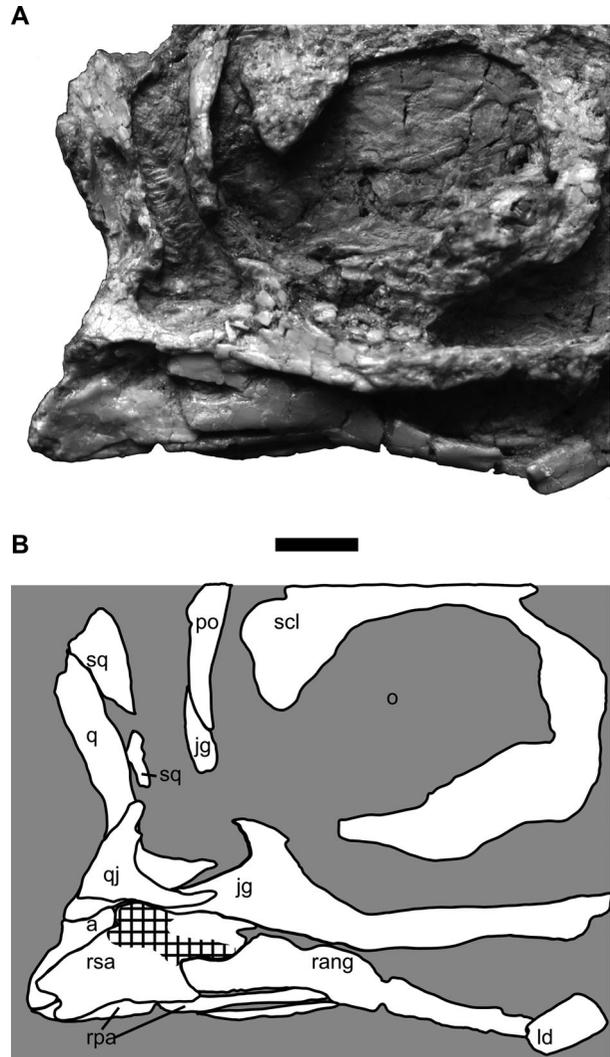
antorbital fossa. The dorsal lamina is reduced posterior to the interfenestral pila, indicating that the nasals (which are poorly preserved) formed the majority of the dorsal roof of the antorbital fossa. Posterior to the interfenestral pila, the lateral surface of the ventral lamina bears at least five small, ovoid foramina located immediately ventral to the nasomaxillary contact and oriented with their long axes parallel to the nasal ramus. Foramina at this position are present in a wide range of theropod taxa, including maniraptorans (e.g. *Haplocheirus*: Choiniere *et al.* 2010b) and non-coelurosaurian tetanurans (e.g. *Sinraptor*: Currie & Zhao 1993).

The ventral edge of the jugal ramus is straight in lateral view, rather than curved. The lateral surface bears a well-developed, laterally projecting ridge that extends posteriorly from its origin on the anteroventral corner of the antorbital fossa along the entire length of the ramus. This ridge is located ventral to the horizontal midline of the jugal ramus and marks the ventral extent of the emargination of the antorbital fossa. This feature is developed in a variety of theropods (Rauhut 2003a), and although its change during ontogeny is poorly known, at least in the basal tyrannosaur *Guanlong* it is better developed in juveniles (IVPP V14532) than in adults (IVPP V14531). A row of shallow, evenly spaced foramina associated with and parallel to the tooth row is present along the lateral surface of the maxilla ventral to the ridge on the jugal ramus. There is one foramen per alveolus. The medial surfaces of the maxillae are not visible. The palatal process of the posteriormost end of the left maxilla is visible in ventral view, suggesting that the maxillary shelves made a contribution to the palate. The extent of this contribution is uncertain because most of the medial surface is obscured by matrix. Posteriorly, the palatal processes of the maxillae do not contact the vomer along the midline of the skull. The maxillary tooth row is completely antorbital, ending at the level of the maxillary pila. The left maxilla preserves 12 tooth positions, a number similar to that of most theropods but fewer than the numerous small teeth present in the co-occurring taxon *Haplocheirus* (Choiniere *et al.* 2010b) and many other coelurosaur taxa (e.g. *Pelecanimimus* LH777; troodontids: Makovicky & Norell 2004) and nearly double the seven maxillary teeth present in *Scipionyx* (Dal Sasso & Maganuco 2011). The right maxilla is too badly damaged to corroborate this tooth count. Interdental septa are present between the alveoli, but most interdental plates are covered by matrix. The few exposed interdental plates are unfused and pentagonal.

**Jugal.** The posterior two-thirds of the right jugal is well preserved (Fig. 4A, B), although the surface of the anterior end is abraded. Most of the left jugal (Fig. 4C, D) is missing, but portions of the anterior end are preserved in contact with the jugal ramus of the left maxilla and the ventral process of the left lacrimal. As in most maniraptorans (e.g. the basal Alvarezsaurid *Haplocheirus*: Choiniere *et al.*

2010b; *Archaeopteryx*: Mayr *et al.* 2005; oviraptorosaurs: Osmólska *et al.* 2004; and ornithomimosaur, e.g. *Pelecyanimus* (LH 7777)), the jugal is dorsoventrally thin and rod-like. The ventral margin of the jugal is ventrally convex in lateral view, but it is unclear whether this is due to deformation during preservation. The anterior end of the jugal is only slightly expanded dorsoventrally at the maxillary contact. A short anterior spur meets the jugal ramus of the maxilla at the posteroventral margin of the antorbital fossa, and this fossa forms a small, crescentic emargination on the dorsal half of this spur. Unlike the jugals of ornithomimosaur (Makovicky *et al.* 2004), *Scipionyx* (Dal Sasso & Maganuco 2011) and the therizinosaurid *Erlikosaurus* (Clark *et al.* 1994), the anterior spur of the jugal does not extend anteriorly under the antorbital fenestra. The lateral surface of the jugal body is smooth and bears no foramina, but the superficial texture shows many fine, horizontal striations. There is a faintly developed rugosity on the ventral edge of the right jugal at the level of the posterior end of the orbit. This cannot be confirmed on the left side. This rugosity is not as well developed as in tyrannosauroids (e.g. the basal tyrannosauroid *Proceratosaurus*: Rauhut *et al.* 2010), and in some dromaeosaurids (e.g. *Tsaagan*: Norell *et al.* 2006; *Linheraptor*: Xu *et al.* 2010a). The postorbital process of the jugal is anteroposteriorly short. The dorsal end is broken, but pieces of the process adhere to the posterior margin of the postorbital, indicating that the postorbital bar was anteroposteriorly short and formed equally by the postorbital and the ascending process of the jugal. The posterior end of the jugal is broken at the contact with the quadratojugal, but it is clear from the sutural marks on the preserved portions of both of these bones that it was forked for the reception of the anterior end of the quadratojugal. The ventral process of this fork extended farther posteriorly than the dorsal process, and terminated at a level posterior to the midpoint of the infratemporal fenestra.

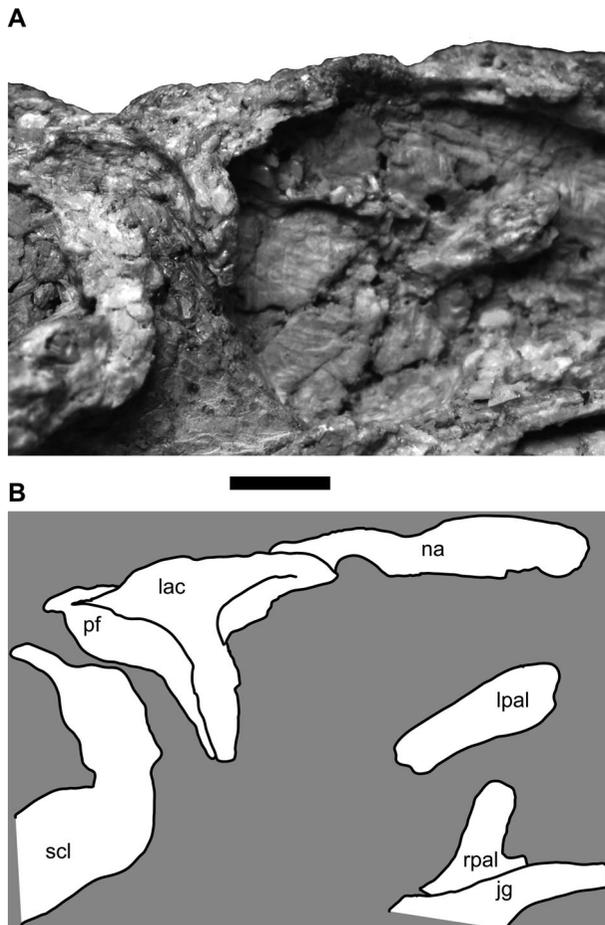
**Quadratojugal.** Only the right quadratojugal (Figs 4A, B, 8) is preserved, and it is complete. The quadratojugal is L-shaped in lateral view, unlike the inverted T-shaped quadratojugals (Norell *et al.* 2001b) of most maniraptorans (e.g. oviraptorosaurs: Osmólska *et al.* 2004; the therizinosaurid *Erlikosaurus*: Clark *et al.* 1994; and dromaeosaurids: Norell & Makovicky 2004). It has a mediolaterally thin and dorsoventrally tall posteromedial process that contacts the lateral surface of the quadrate. This process extends to approximately mid-height of the quadrate shaft. The anterior process of the quadratojugal is dorsoventrally low and tapers anteriorly, extending distally almost to the level of the anterior end of the infratemporal fenestra. Unlike the condition of some non-coelurosaurian theropods (e.g., *Majungasaurus*: Sampson & Witmer 2007; *Monolophosaurus*: Zhao & Currie 1993), derived ornithomimosaur (Makovicky *et al.* 2004), *Scipionyx* (Dal Sasso & Maganuco 2011), and many manirap-



**Figure 8.** Posterior skull and mandible bones of *Aorun zhaoi* (IVPP V15709). **A**, right lateral view; **B**, line drawing of right lateral view. Hatched area shows damage to surangular. Abbreviations as in Figs 4, 5 and: rpa, right prearticular. Scale bar equals 1 cm.

torans (e.g. *Erlikosaurus*: Clark *et al.* 1994; *Linheraptor*: Xu *et al.* 2010a), the anterior end of the quadratojugal does not extend anterior to the posterior corner of the infratemporal fenestra.

**Lacrimal.** Both lacrimals (Figs 4, 9) are incomplete. The right lacrimal preserves the lacrimal angle, posterior process, and proximal portions of the nasal and jugal rami. The only preserved portion of the left lacrimal is the distal tip of the jugal ramus. As in most theropods which have a prefrontal, the lacrimal in *Aorun* contacts the prefrontal posteriorly, the jugal and maxilla ventrally, the nasal dorsally, and the maxilla anteriorly. The lacrimal angle shows no evidence of a foramen or fossa for the nasolacrimal duct, although its lateral surface is abraded. Most theropods have at least a small foramen on the lacrimal



**Figure 9.** Close-up of anterior orbital region of *Aorun zhaoi* (IVPP V15709). **A**, right anterolateral view; **B**, line drawing of right anterolateral view. Abbreviations as in Figs 4–6. Scale bar equals 1 cm.

angle, but this foramen is absent in some basal theropods (e.g., *Eoraptor*: Sereno *et al.* 1993), ornithomimosaurs (Makovicky *et al.* 2004), compsognathids (Peyer 2006), and alvarezsauroids (Choiniere *et al.* 2010b). The nasal ramus of the lacrimal is much longer than the posterior process. Although the anterior tip is not preserved, sutural marks on the nasal ramus of the maxilla show that it clearly contacted the nasal ramus of the maxilla within the antorbital fossa and contributed to the posterior half of the dorsal margin of the antorbital fenestra. There are no foramina on the lateral surface of the nasal ramus. The posteriorly tapering posterior process of the lacrimal is short and projects posterodorsally, as in ornithomimosaurs and *Zuolong* (Choiniere *et al.* 2010a). It forms a lap joint with the lateral surface of the prefrontal. The jugal ramus of the lacrimal is anteroposteriorly short. It extends to the level of the ventral margin of the orbit, where it expands anteriorly and posteriorly to contact the jugal ramus of the maxilla and the anterior end of the jugal, respectively, but the nature of these contacts cannot be determined because of breakage. Unlike

the strongly anteroposteriorly expanded ventral ends of the jugal rami of tyrannosaurines (Holtz 2004) and many non-coelurosaurian theropods (Holtz *et al.* 2004), the expansion in *Aorun* is only moderate.

**Nasal.** The right nasal (Figs 2A, B, 4A) is incomplete; parts of it are preserved in articulation with the nasal ramus of the maxilla dorsal to the anterior end of the antorbital fenestra and the maxillary fenestra. Only a small portion of the left nasal (Figs 4A, B, 7A, B) is preserved, lying above the antorbital fenestra. The separation of the nasals along the midline suggests that they were unfused, but this cannot be confirmed. The dorsal surfaces of the nasals are flat and show no foramina or crenulations. The shape and sutural contacts of the nasals are uncertain, although based on the morphology of the nasal process of the maxilla, the nasals formed the majority of the dorsal roof of the antorbital fossa.

**Postorbital.** The left postorbital is not preserved. The right postorbital (Fig. 4A, B) is badly abraded laterally and is missing its squamosal process. The frontal process of the postorbital arches dorsally, unlike the straight frontal processes of tyrannosauroids (e.g., *Alioramus*: Brusatte *et al.* 2009) and *Scipionyx* (Dal Sasso & Maganuco 2011), and it forms the posterior border of the large, circular orbit. Although the squamosal process is not preserved, its base is positioned ventral to the dorsal level of the frontal process, so that the postorbital was not T-shaped, as it is in many non-coelurosaurian theropods (e.g. *Eustreptospondylus*: Sadleir *et al.* 2008) and in tyrannosauroids (Holtz 2004). The squamosal process must have been anteroposteriorly short, because the infratemporal fossa is much shorter than the orbit.

**Sclerotic ring.** The right orbit contains a nearly complete sclerotic ring (Fig. 4A, B), composed of overlapping ossicles. The sclerotic ring is incomplete posteriorly, due to several missing ossicles, and the lateral surfaces of the ossicles are badly abraded, precluding an exact count. The sclerotic ring occupies almost the entire orbit, leaving a circular region open in the centre with a diameter that is approximately 50% of the orbital diameter.

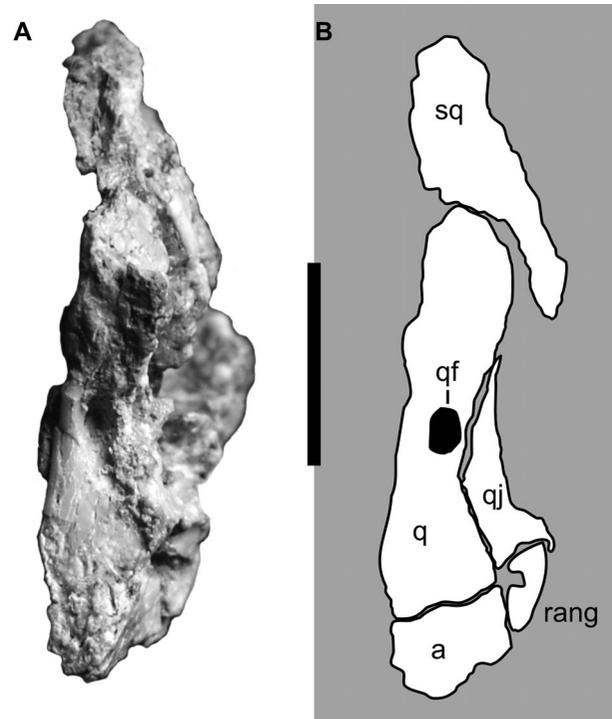
**Prefrontal.** A small portion of the prefrontal (Fig. 9) lies in articulation with the posterior process of the lacrimal along the medial wall of the anterodorsal orbit on the right side of the skull. A slender lacrimal process extends ventrally from the preserved portion of the prefrontal along the medial edge of the lacrimal. A long, slender lacrimal process of the prefrontal is also present in a variety of theropod taxa, including *Zuolong* (IVPP V15912). Although the preserved portion of the skull roof is only fragmentary and the relative contributions of the individual elements cannot be fully determined, it is unlikely that the prefrontal formed a large portion of the dorsal margin of the orbit because the preserved portion of the frontal shows no notch or sutural

mark for the prefrontal. In ornithomimosaurids and derived alvarezsauroids, the prefrontal is hypertrophied (Sereno 2001) and forms a large portion of the skull roof (see Suzuki *et al.* 2002 and Chiappe *et al.* 1998 for a differing opinion on the homology of the alvarezsauroid prefrontal). Similar to the condition in basal maniraptorans such as *Haplocheirus* (IVPP V15988), in *Aorun* the prefrontal probably separated the posterior process of the lacrimal from contacting the frontal medially and the dorsal surface of the prefrontal was likely mediolaterally narrow.

**Frontal.** The frontals (Fig. 4C, D) have been extensively damaged and displaced during preservation. A thin portion of the right frontal is preserved in partial articulation with the right postorbital. The preserved portion of the left frontal is composed of the postorbital process and possibly the parietal articular region. It is visible on the left side of the skull, displaced ventrally and medially from the skull roof, and lying immediately dorsal to the surangular. Poor preservation of the frontal precludes much description, but the dorsal surface of the frontal is smooth, and the postorbital process was laterally tapering and well demarcated from the more anterior orbital rim.

**Squamosal.** The left squamosal is missing, and only the quadratojugal process of the right squamosal (Figs 4A, B) is preserved. It is vertically oriented and parallels the quadrate along its anterior face. The proximal portion is anteroposteriorly long, but it tapers as it extends ventrally to contact the squamosal process of the quadratojugal, excluding the quadrate from participation in the border of the posterior margin of the infratemporal fenestra.

**Quadrate.** The right quadrate (Figs 4A, B, 10) is missing the dorsal quadrate head and is preserved in articulation with the articular, the quadratojugal and the squamosal. The quadrate is oriented vertically, so that the mandibular condyles are directly ventral to the quadrate head. The shaft of the quadrate is posteriorly concave in lateral view. The quadrate foramen is a tall ovoid in posterior view, occupying the majority of the middle of the quadrate shaft. There is no fossa associated with the quadrate foramen, unlike the deep fossa of *Haplocheirus* (Choiniere *et al.* 2010b) and ornithomimosaurids (Makovicky *et al.* 2004), and it is developed without an associated quadrate fossa as in *Zuolong* (Choiniere *et al.* 2010a), carcharodontosaurids (Eddy & Clarke 2011) and *Allosaurus* (Madsen 1976). Although the lateral side of the posterior surface of the quadrate shaft is poorly preserved, small pieces of broken quadrate are present on the lateral edge of the quadrate shaft, suggesting that the quadrate foramen was entirely developed within the quadrate. This differs from the condition in tyrannosauroids (Holtz 2004) and most maniraptorans (e.g. dromaeosaurids: Norell *et al.* 2006), where the quadrate foramen is developed as a distinct opening between the quadratojugal and the lateral edge of the quadrate. Because



**Figure 10.** Quadrate of *Aorun zhaoui* (IVPP V15709). **A**, posterior view; **B**, line drawing of posterior view. Abbreviations as in Figs 4–6, and: qf, quadrate foramen. Scale bar equals 2 cm.

of the close articulation between the articular and the quadrate, the morphology of the quadrate condyles cannot be determined, but the lateral surface of the lateral condyle is entirely covered by a flat facet for the medial surface of the quadratojugal.

The pterygoid ramus of the quadrate is tall, triangular, anteroposteriorly longest at the ventral end of the quadrate nearest the condyles, and tapers into the quadrate shaft immediately ventral to the level of the dorsal quadrate head. The medial surface of the pterygoid ramus is concave. The medial surface bears no pneumatic fossae as are present in some tyrannosauroids (e.g. *Tyrannosaurus*: Brochu 2003) and carcharodontosaurids (Eddy & Clarke 2011). A thin, vertically oriented sliver of bone adheres to the medial surface of the pterygoid ramus, extending posteroventrally along the posterior edge of the bone. This bone sliver does not appear to be a portion of the broken quadrate, and its identity cannot be determined.

**Palate.** The left palatine (Figs 4C, D) only preserves the vomerine process, and this is badly abraded. The right palatine (Figs 4A, B, 9) only preserves the proximal base of the vomerine process and the maxillary process. The vomerine process projects anterodorsally to the mid-height of the antorbital fenestra. The posterior ends of both vomers are preserved in contact with the right palatine, but nothing can be said of their morphology due to breakage.

## Mandibular bones

**Dentary.** The left and right dentaries (Figs 4, 7) are nearly complete and preserved in articulation with the surangular and the angular. The left dentary is badly weathered at the anterior end of the external mandibular fenestra, where it consists of little more than quadrangular pieces of shattered bone. The anterior end of the right dentary is broken and deformed so that its ventral surface projects ventrally beyond the extent of the contralateral dentary.

The dentary is anteroposteriorly long and dorsoventrally thin, with parallel dorsal and ventral edges. Although damaged, the anterior end of the left dentary has a slightly upturned dorsal edge, as in *Haplocheirus* (Choiniere *et al.* 2010b), many megalosauroids (Benson 2010), *Ornitholestes* (AMNH FARB 619) and some ornithomimosaur (e.g. *Garudimimus*: Kobayashi & Barsbold 2005b). Several small foramina are present on the lateral surface of the anterior tip of the dentary, as in most theropods. The dentary symphysis is unfused. The articulated anterior ends of the dentaries are V-shaped in ventral view. The symphyseal surface is flat and parallel to the lateral surface of the dentary. There is no medial curvature of the anterior end of the dentaries as in ornithomimosaur (Makovicky *et al.* 2004), therizinosauroids (Clark *et al.* 2004), advanced troodontids (Makovicky *et al.* 2004) and oviraptorosaurs (Osmólska *et al.* 2004). The labial surface of the dentary is flat. Alveolar foramina are present in a subhorizontal row on the labial surface of the dentary, beginning posterior to the fourth dentary tooth position. They begin anteriorly as a series of independent foramina at approximately the mid-height of the dentary, then move dorsally in a shallow arc as they extend posteriorly. Beginning at the midpoint of the dentary, the alveolar foramina are more deeply incised and are connected by a continuous, dorsoventrally low fossa that extends posteriorly to the level of the midpoint of the antorbital fenestra. Beginning at the level of the posterior end of the alveolar foramina, the dentary expands slightly dorsoventrally. The dorsal portion of the posterior end of the dentary is partially obscured by the overlying junction of the lacrimal, jugal and maxilla. It is short and does not extend dorsal to the external mandibular fenestra. The ventral portion of the posterior dentary is long and low, extending farther posteriorly to contact the angular at the level of the midpoint of the external mandibular fenestra and fully covering the splenial in lateral view.

The dentary is fully toothed, and the dentary tooth row extends posteriorly beyond the posterior extent of the maxillary tooth row by at least three tooth positions, ending ventral to the midpoint of the antorbital fenestra. There are at least 20 teeth with preserved crowns in the dentary, but several tooth positions lack preserved crowns, so the estimate for the number of teeth in the dentary is 25–30. This number is similar to many hyperdentate coelurosaurs, including therizinosauroids (Clark *et al.* 2004), troodontids (Makovicky & Norell 2004), *Pelecanimimus* (Perez-

Moreno *et al.* 1994), and alvarezsauroids (Choiniere *et al.* 2010b), but is considerably greater than in coelurosaurs generally, especially taxa such as *Ornitholestes* which have only 12 teeth in the dentary (Osborn 1903).

**Surangular.** The left surangular (Fig. 4C, D) is poorly preserved, with an abraded lateral surface. It is missing the dorsal portion of the posterior half, and the sutural connection between the left surangular and the left angular is either fused or has been obliterated by damage. The posterior end of the right surangular (Fig. 4A, B, 8) is well preserved at the mandibular articulation, but anterior to this it is missing large portions of its lateral surface. The dorsal half of the right surangular is obscured by the jugal and quadratojugal, and little can be said of the morphology of this region. From the size of the external mandibular fenestra, it is clear that the surangular was less than half the height of the mandible above the external mandibular fenestra and it shared a long, anterodorsally inclined articulation with the angular, unlike the flat or anteroventrally inclined surangular–angular contact in non-coelurosaurian tetanurans (e.g. *Sinraptor*) and tyrannosauroids (e.g. *Tyrannosaurus rex*: Brochu 2003; and *Guanlong*: IVPP V14531). A broken area on the lateral surface of the left surangular anterior to the mandibular articulation is probably a surangular foramen, but the actual size and shape of the foramen is impossible to determine. The posterior end of the surangular forms the lateral portion of a small, posteriorly convex retroarticular process.

**Angular.** Because the left angular cannot be distinguished from the surangular (it is either fused or this contact is damaged and not visible in lateral view), only the right angular (Fig. 4A, B) is well enough preserved to warrant description. The right angular is a triangular bone, with a long, tapering dentary (anterior) process, a tall body and a short, tapering posterior process that is missing portions of its lateral surface. The anterior tip of the dentary process is marked by a shallow groove on its dorsal surface where the angular process of the dentary would have overlapped it. The body of the angular is laterally smooth. The posterior process is broken distally, but the ventral surface of the posterior end of the right surangular shows that the surangular/angular suture extended posteriorly to the level of the mandibular/quadratojugal articulation. In ornithomimosaur, the angular extends posterior to the mandibular/quadratojugal region, forming a portion of the retroarticular process (Makovicky *et al.* 2004). Medially, the angular of *Aorun* forms an extensive, flat contact with the prearticular.

**Splenial.** The left and right splenials (Fig. 4A, B, 5) are preserved in articulation with their respective mandibular bones, but the dorsal portions are obscured by matrix near the palate and the posterior ends are missing. The splenial is triangular in medial view and extends anteriorly to the level of the midpoint of the maxillary fenestra. A small,

ovoid mylohyoid foramen is present on the splenial, opening anteroventrally at the level of the posterior margin of the maxillary fenestra.

**Prearticular.** Both prearticulars (Fig. 5) are preserved in articulation, but the anterior ends are broken. Unlike the U-shaped prearticulars of deeper-jawed theropods (e.g. *Tyrannosaurus*: Holtz 2004), the prearticular is long and relatively straight. The middle portion of the bone is dorsoventrally thin and subcylindrical, with a shallow concave dorsal surface that indicates the internal mandibular fenestra was long and ovoid. The posterior end is mediolaterally thin, expands dorsoventrally from the middle portion, and forms a laminar contact with the medial surface of the surangular. The prearticular extends posteriorly to the end of the preserved retroarticular process, but due to breakage it is unclear whether it formed a medial contact with the articular. The right articular is obscured in posterior view by the quadrate, which has been ventrally displaced, and the left articular is not preserved.

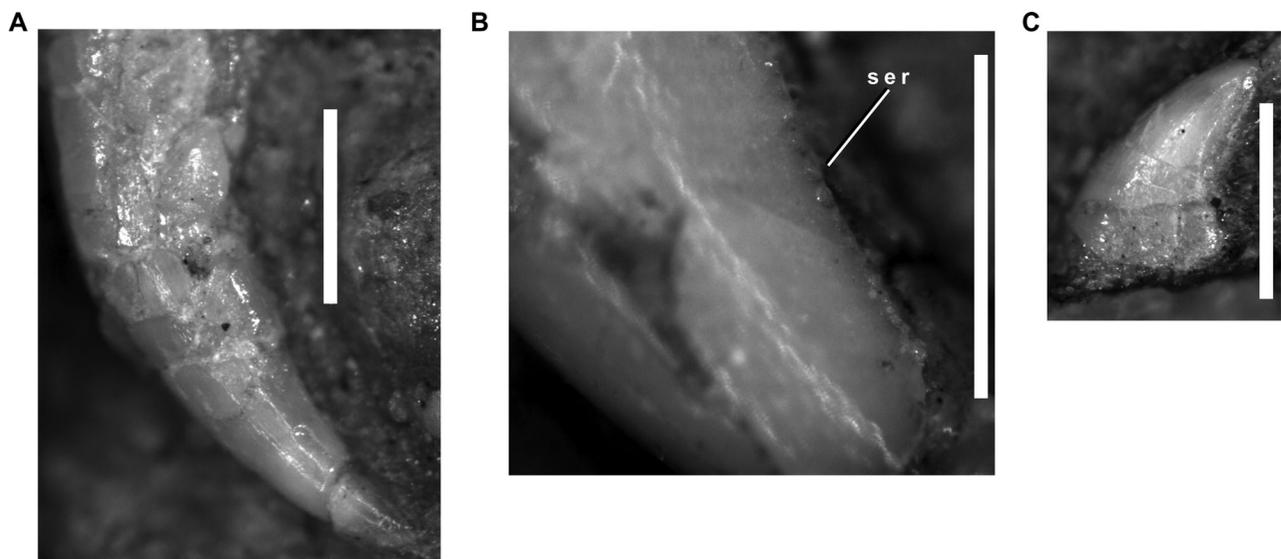
**Hyoids.** Broken pieces of the thin, cylindrical ceratohyals are preserved along the medial surface of the prearticular (Fig. 4A, B, 5). As preserved, they reach anteriorly to at least the level of the postorbital bar, where they terminate in broken ends, and posteriorly to the posterior ends of the retroarticular processes. Ceratohyals are preserved in many theropods, including the co-occurring *Haplocheirus* (IVPP V15988).

### Dentition

**Premaxillary teeth.** The four premaxillary teeth (Figs 4, 6, 11A) are subequal in size. As preserved, right premax-

illary tooth one is very small, but it likely is the tip of a replacement tooth because the corresponding tooth of the left premaxilla is large and approximately the same size as the other premaxillary teeth. The crowns are apicobasally tall, mesiodistally short, and only slightly mediolaterally compressed: in cross section they are ovoidal, unlike the D-shape cross sections of the premaxillary teeth of basal coelurosaurs (e.g. tyrannosauroids: Xu *et al.* 2006; Zuolong: IVPP V15912). There are no serrations on any of the premaxillary teeth, as in *Scipionyx* (Dal Sasso & Maganuco 2011), nor any evidence of carinae. All of the premaxillary teeth are moderately recurved and project posteroventrally.

**Maxillary teeth.** The size of the maxillary tooth crowns (Figs 4, 7, 11B) varies continuously along the maxillary tooth row, from apicobasally tall, mildly recurved anterior teeth to low, moderately recurved posterior teeth. The teeth are small relative to the size of the skull, as in basal ornithomimosaurids (Makovicky *et al.* 2004), therizinosauroids (Clark *et al.* 2004; Kirkland *et al.* 2005), troodontids (Makovicky & Norell 2004), and alvarezsauroids (Chiappe *et al.* 1998; Choiniere *et al.* 2010b). There is separation between all of the maxillary tooth positions, unlike the crowded maxillary tooth rows of some troodontids (e.g. *Zanabazar*: Norell *et al.* 2009; and *Pelecanimimus*: LH 7777). The anterior maxillary tooth crowns are subcircular in cross section, resembling the premaxillary teeth, but the more posterior tooth crowns are mediolaterally compressed. No maxillary teeth show development of a mesial carina, but some have a weakly developed distal carina that bears very small (~10 per mm), poorly separated apically angled serrations. Only



**Figure 11.** Teeth of *Aorun zhaoi* (IVPP V15709). **A**, left premaxillary tooth 3 lateral view; **B**, left anterior maxillary tooth lateral view; **C**, left mid-dentary tooth lateral view. Abbreviation: ser, serrations. Scale bars equal 2 mm.

some troodontids (Makovicky & Norell 2004) and therizinosauroids (Kirkland *et al.* 2005) among theropods have serrations angled apically, but in these taxa the serrations are large and well separated. The maxillary teeth do not resemble any of the tooth morphotypes previously reported from Wucaiwan (Han *et al.* 2011).

**Dentary teeth.** Several crowns of the anterior dentary teeth (Figs 4, 7, 11C) are preserved, and the roots are circular in cross section. The dentary teeth vary in size and shape, from subcylindrical, mildly recurved anterior dentary tooth crowns, to apicobasally low, mediolaterally compressed, moderately recurved posterior crowns. The shift in morphology begins abruptly posterior to dentary tooth position seven. Although the anterior dentary teeth are subequal in size to the premaxillary teeth, the more posterior dentary teeth are shorter than the corresponding maxillary teeth. No dentary tooth crowns have a mesial carina, but one well-preserved crown bears a weakly developed distal carina that lacks serrations. The alveoli of the dentary teeth are separated by osseous septae, unlike the teeth of *Shuvuuia* (IGM 100/977) and *Pelecanimimus* (LH 7777).

### Axial skeleton

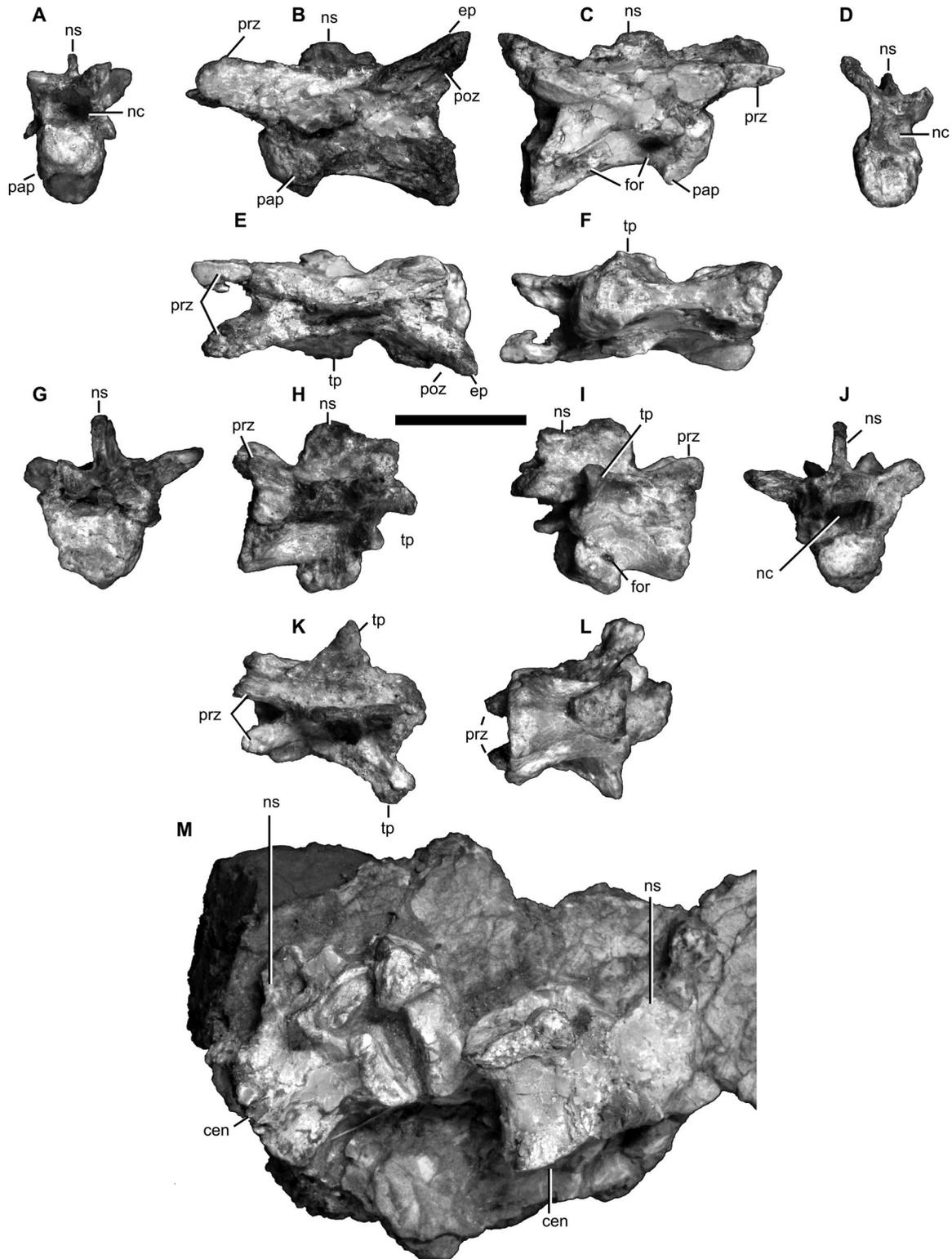
**Cervical vertebra.** Only one cervical vertebra (Fig. 12A–F) is preserved. It is likely an anterior cervical because it is anteroposteriorly long and has well-developed epiphyses. The sutural line between the neural arch and the centrum is visible in lateral view. In lateral view, the ventral surface of the centrum is angled posterovertrally, a common feature of the anterior cervical centra in theropods (e.g. *Guanlong*: IVPP V14531; ornithomimosaur: Makovicky *et al.* 2004). The lateral surface of the centrum bears two foramina on its cortical surface, as in coelophysoids (e.g. *Megapnosaurus*: Raath 1977), ceratosaurs (Carrano *et al.* 2002), and some maniraptorans (e.g., *Falcarius*: UMNH VP 14657; *Nomingia*: IGM 100/119). The more anterior foramen is located directly dorsal to the parapophysis. The posterior foramen is located far posteriorly, close to the posterior vertebral margin at mid-height on the centrum, as in *Falcarius* (UMNH VP14657) but differing from the oviraptorosaur condition (e.g. *Nomingia*: IGM 100/119) and the condition of abelisaurids (Carrano & Sampson 2008) where the posterior foramen is more anteriorly located. Carpenter *et al.* (2005, p. 55, fig. E) also illustrated a cervical vertebra of *Coelurus* with two lateral foramina, but in this case the posterior foramen is located far anterior to the position in *Aorun*. As in *Megapnosaurus* (Raath 1977), the posterior foramen is taller and longer than the anterior foramen. The lateral surface of the centrum bears a horizontally oriented fossa enclosing the foramina. This fossa leaves only small unemarginated surfaces on the lateral surface of the centrum dorsal and ventral to it. The condition of *Aorun* is differ-

ent from that of *Falcarius* (UMNH VP14657), where the posterior foramen is small and the lateral surfaces of the cervical centra bear two well-developed lateral crests that bracket the foramina dorsally and ventrally.

The ventral surface of the cervical centrum is transversely flat. The mesial portion is considerably narrower mediolaterally than either the anterior or posterior ends. A deep recess is developed on the ventral surface between the parapophyses, which are developed on short pedicels. The anterior and posterior articular surfaces of the centrum are inclined anterodorsally. The cervical centrum is opisthocelous, which is a common condition in larger non-coelurosaurian theropods (e.g. *Majungasaurus*: O'Connor 2007; *Sinraptor*: Currie & Zhao 1993; *Allosaurus*: Madsen 1976; *Baryonyx*: Charig & Milner 1997), and in coelurosaurs only within parvicursorine alvarezsauroids (Chiappe *et al.* 2002), where it is pronounced, and in *Compsognathus* (Ostrom 1978; Peyer 2006), where it more closely resembles the condition in *Aorun*. Although slightly wider than high, the anterior articular surface does not show the dorsally depressed, kidney-shaped morphology of many coelurosaurs (Gauthier 1986).

The neural arch is long and narrow and nearly the same length as the vertebral centrum. The prezygapophyses are long and narrow, with flat, anteromedially oriented prezygapophyseal articular facets, unlike the dorsally convex ('flexed') facets of most coelurosaurs (Gauthier 1986; Rauhut 2003a). They project almost entirely anteriorly. The postzygapophyseal facets are directed ventrolaterally. Medially, the postzygapophyses are connected by a dorsoventrally thin intrazygapophyseal lamina (*sensu* Wilson 1999) that is emarginated dorsally by the interspinous ligament fossa. This lamina extends posteriorly almost to the level of the posterior termini of the postzygapophyses, as in many coelurosaurs, including alvarezsauroids (e.g., *Haplocheirus*: IVPP V15988), *Nqwebasaurus* (de Klerk *et al.* 2000), *Guanlong* (IVPP V14531), most ornithomimosaurids (e.g. *Pelecanimimus*: LH 7777), and some dromaeosaurids (e.g. *Linheraptor*: Xu *et al.* 2010a). The postzygapophyses bear well-developed epiphyses dorsal to the postzygapophyseal articular facets. The right epiphysis is broken at the level of the posterior end of the postzygapophysis, but it clearly would have projected posteriorly beyond the level of the articular facet. The neural spine is anteroposteriorly short relative to the centrum length, differing from the long neural spines of most theropods, and more similar to the anteroposteriorly reduced neural spines of the basal therizinosauroid *Falcarius* and other maniraptorans (Gauthier 1986; Clark *et al.* 2002). Although partially broken dorsally, the neural spine is low. The neural canal is large, almost the same diameter as the anterior face of the centrum.

**Dorsal vertebra.** A single dorsal vertebra (Fig. 12G–L) is preserved. It is likely to be a posterior dorsal because

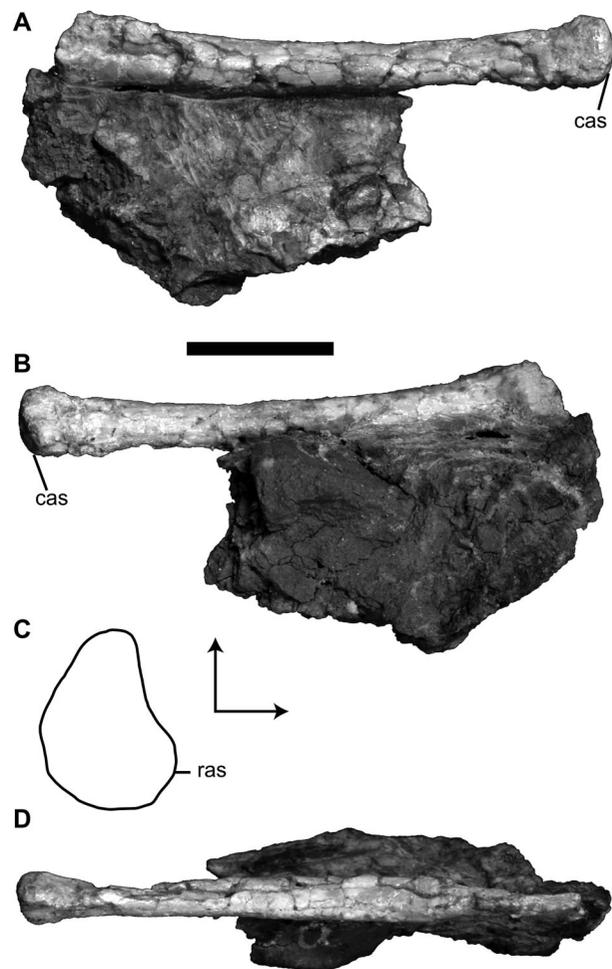


**Figure 12.** Vertebrae of *Aorun zhaoi* (IVPP V15709). **A–F**, cervical vertebra in: **A**, anterior; **B**, left lateral; **C**, right lateral; **D**, posterior; **E**, dorsal; **F**, ventral views. **G–L**, dorsal vertebra in: **G**, anterior; **H**, left lateral; **I**, right lateral; **J**, posterior; **K**, dorsal; **L**, ventral views. **M**, caudal vertebrae in lateral view. Abbreviations: cen, centrum; ep, epipophysis; for, foramen; nc, neural canal; ns, neural spine; pap, parapophysis; poz, postzygapophysis; prz, prezygapophysis; tp, transverse process. Scale bar equals 1 cm.

the neural spine is anteroposteriorly long, and the parapophyses are located dorsally on the neural arch rather than on the centrum. It is anteroposteriorly much shorter than the cervical vertebra, only about two-thirds its anteroposterior length. The posterior end of the lateral surface of the centrum bears a single foramen. The ventral surface of the centrum is mediolaterally convex. The anterior articular surface is flat and approximately circular. The posterior surface is broken and a portion has disarticulated and adheres to the middle of the ventral surface. The posterior end of the centrum is pathologically deformed, with the ventral portion of the posterior articular surface being deflected anteroventrally and displaced anteriorly.

A faint suture is present at the contact of the centrum and the neural arch which is visible in lateral view. The prezygapophyses are short, extending anteriorly to only about 10% of the centrum length anterior to the anterior articular face of the centrum. They are set at the lateral margins of the neural canal and dorsally inclined. The articular facets of the prezygapophyses face dorsomedially and are ovoid in ventral view. The postzygapophyses are broken. The transverse processes lie posteriorly on the neural arch, just dorsal to the posterior central margin, and are mediolaterally short, anteroposteriorly wide and only slightly inclined above horizontal. The neural spine is also posteriorly placed, with its anterior margin at the level of the anteroposterior midpoint of the centrum and its posterior margin located posterior to the posterior margin of the centrum. The neural spine is rectangular in lateral view and is longer anteroposteriorly than it is dorsoventrally tall. As preserved, the centriadiapophyseal laminae are asymmetrically developed on the left and right sides. On the left side, the transverse process is supported by paired centriadiapophyseal laminae. The anterior lamina extends far anteriorly to the posterior edge of the parapophysis and the posterior one is directed almost completely ventrally and extends to the posterodorsal corner of the lateral surface of the centrum. On the right side, the transverse process is supported by a single lamina that matches the posterior lamina of the left side. It is likely that the anterior lamina of the right side is broken. The fossa created by these paired laminae is deep and lacks accessory laminae. Comparison with the dorsals of other theropods (e.g. *Guanlong*: IVPP V15431) indicates that this vertebra is probably from a posterior position in the dorsal series, perhaps D8–10.

**Caudal vertebrae.** Two other nearly complete vertebrae and a few fragments of a third vertebra (Fig. 12M) are probably caudal vertebrae based on the shape of their articular surfaces, the lack of foramina in the centra and the lack of para- and diapophyses. The ventral surfaces of these vertebrae are almost flat. The anterior articular surfaces of the caudals are square in anterior view, a morphology consistent with the shape of the caudal vertebrae of many theropods. Both of the preserved neural spines are angled



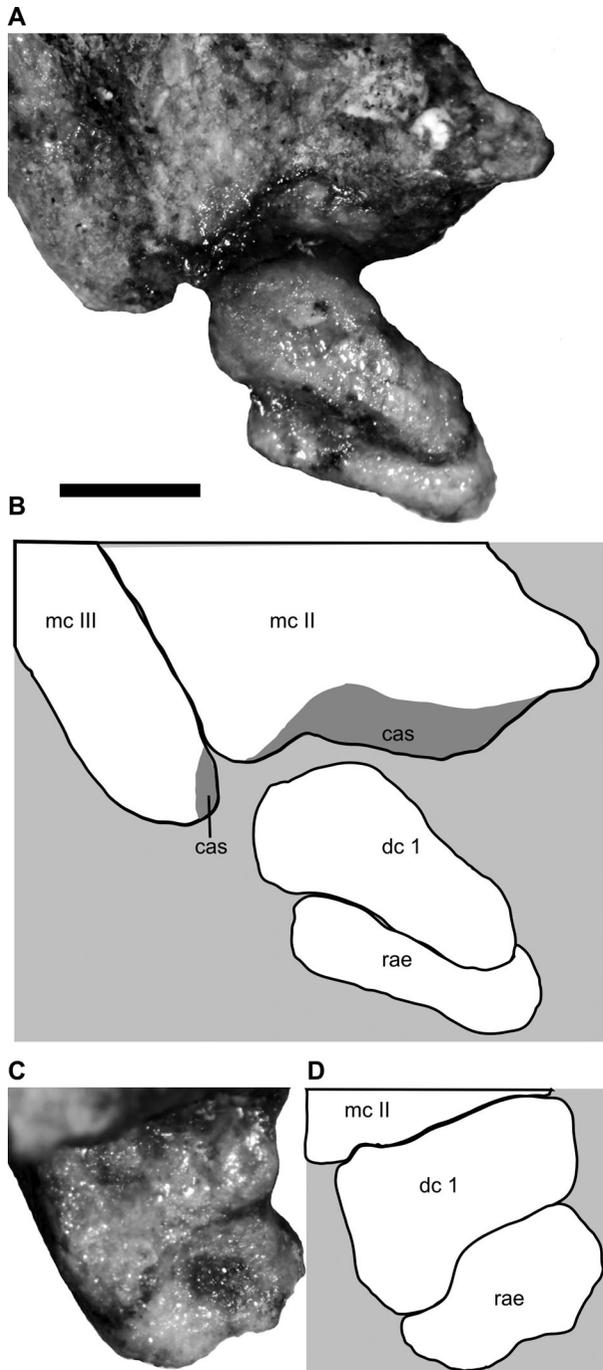
**Figure 13.** Left ulna of *Aorun zhaoui* (IVPP V15709). **A**, lateral view; **B**, medial view; **C**, distal line drawing; **D**, anterior view. Vertical arrow points anteriorly, horizontal arrow points laterally. Abbreviations: cas, carpal articular surface; ras, radial articular surface. Scale bar equals 1 cm; C is not to scale.

strongly posterodorsally, but neither is complete enough to warrant meaningful description.

### Appendicular skeleton

**Ulna.** The left ulna (Fig. 13) is missing its proximal end, including the olecranon process and humeral cotyle. The proximal end of the ulna is mediolaterally narrow and dorsoventrally tall. This shape supports identification of the bone as the ulna because the radius of theropods is generally of similar width and height throughout its length. The shaft of the ulna is nearly straight, unlike the bowed condition of more derived coelurosaurs (Gauthier 1986). The distal end is generally teardrop shaped, with the apex pointing towards the flexor surface. A small radial tubercle projects medially from the medial surface of the distal end.

**Carpals.** In the following descriptions of the manus, we homologize the three fingers of *Aorun* with digits



**Figure 14.** Left carpus and proximal metacarpus of *Aorun zhaoi* (IVPP V15709). **A**, dorsal view; **B**, line drawing of dorsal view; **C**, medial view; **D**, line drawing of medial view. Abbreviations as in Fig. 13, and: dc1, distal carpal 1; mcII–III, metacarpals two and three; rae, radiale. Scale bar equals 5 mm.

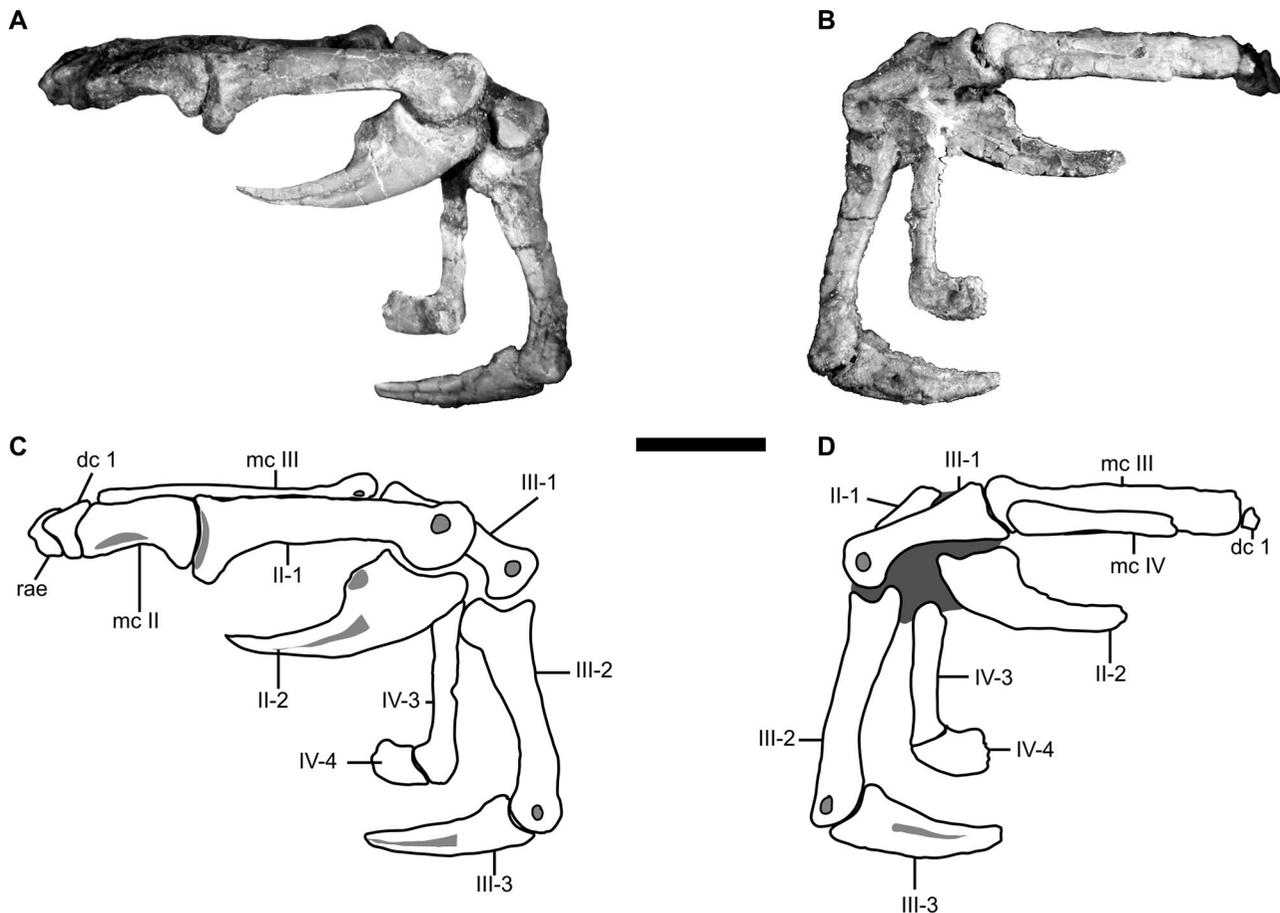
II, III and IV of the primitive theropodan manus, as is currently hypothesized for all tetanurans (Xu *et al.* 2009a); however, see Wagner & Gauthier (1999) for a contradictory opinion.

Left distal carpal 1 and the radiale (Fig. 14) are articulated. Distal carpal 1 contacts the proximolateral surface of metacarpal II and the proximomedial articular surface of metacarpal III. In the preserved orientation, the mediolateral surface of the distal carpal does not closely articulate with the proximal articular surface of metacarpal II, but the carpals seem to have been slightly offset during preservation, displacing the mediolateral surface of distal carpal 1 from the metacarpals.

The radiale is subcircular in proximal view, a morphology that is consistent with the radiale of many theropods, including *Guanlong* (IVPP V14531) and *Haplocheirus* (IVPP V15988). Almost the entire proximal surface of the radiale is occupied by a shallow ovoid fossa that articulates with the distal end of the radius. The dorsal surface of the radiale is proximodistally very short and mediolaterally wide. It is only visible as a thin ridge of bone in dorsal view. The ventral surface of the radiale is obscured by matrix. The medial surface is shallowly concave and ovoid in outline. It is unlikely that the medial concavity formed an articular surface. The distal articular surface is convex and is closely appressed to the shallowly concave proximal surface of distal carpal 1. In *Guanlong* (Xu *et al.* 2006), *Falcarius* (Zanno 2006), and *Haplocheirus* (IVPP V15988), the distal end of the radiale is more strongly convex and articulates within a more well-developed proximal trochlea on distal carpal 1.

Distal carpal 1 is comma-shaped in dorsal view, with the tail pointing proximolaterally, unlike the pentagonal first distal carpals of *Haplocheirus* (Choiniere *et al.* 2010b) and *Guanlong* (IVPP V14531). The proximodorsal margin of the distal carpal is flat, unlike the proximally convex curvature seen in many coelurosaurs, but similar to the flat proximodorsal margin of distal carpal 1 in *Scipionyx* Dal Sasso & Maganuco 2011, *Falcarius* (UMNH VP 12292/12293), *Haplocheirus* (IVPP V15988) and *Guanlong* (IVPP V14531). Although a shallow concavity is present on the proximal surface of the distal carpal, it does not appear to bear a well-developed transverse trochlea, although the shape of the proximal articular surface is only exposed in medial view. The majority of the distal surface appears to have articulated closely with the proximal surface of metacarpal II, but a small ventrolateral tab contacts the proximoventromedial surface of metacarpal III, as in *Haplocheirus* (IVPP V15988), *Falcarius* (Zanno 2006), and *Guanlong* (IVPP V14531). The dorsal surface of distal carpal 1 is flat. The proximal edge is straight, and the distal edge is angular, fitting into a corresponding notch on the proximal surface of metacarpal II. The ventral surface of distal carpal 1 is crescent-shaped. The proximal margin of the ventral surface is convex in outline.

**Metacarpals.** Metacarpal II (Figs 14, 15) is 45% the length of metacarpal III. In dorsal view, it is almost twice the mediolateral width of metacarpal III at mid-shaft (Fig. 11).



**Figure 15.** Left manus of *Aorun zhaoui* (IVPP V15709). **A**, medial view; **B**, lateral view; **C**, line drawing of medial view; **D**, line drawing of lateral view. Dark shading represents unprepared matrix. Abbreviations as in Fig. 14, and: mcIV, metacarpal IV; II-1–IV-4, phalanges of digits two to four. Scale bar equals 1 cm.

The proximal end of the medial surface of metacarpal II is flattened dorsoventrally to form a low, medially projecting flange. A well-developed flange is present on the medial side of the proximal end of metacarpal II in compsognathids (Gishlick & Gauthier 2007), *Haplocheirus* (Choiniere *et al.* 2010b), and *Nqwebasaurus* (de Klerk *et al.* 2000), but in *Aorun* the flange is not as well developed. The proximal end of the ventral surface of metacarpal II is flat ventral to the medial flange, but distal to this flange the ventral surface is concave. The proximal surface has a dorsoventrally oriented notch located on the lateral side of the midline that articulates with the angular distal surface of distal carpal 1. The lateral surface of metacarpal II is closely appressed to the medial surface of metacarpal III along its entire length, although this may be a preservational artefact. The distal condyles are large and the dorsal surfaces of the distal condyles are almost flat. The distal end of metacarpal II is not ginglymoid, a very rare morphology in theropods, but it is abraded and may be missing a portion of the distal condyles. The lateral condyle is closely appressed to metacarpal III and the condyles are subequal in size. The

ventral surfaces of the distal condyles project well below the ventral level of the metacarpal shaft. The ventral projection of the medial condyle gives it a subtriangular shape in medial view.

Metacarpal III (Figs 14, 15) is long and slender, only half the mediolateral width of metacarpal II proximally, and lacks the proximal expansion seen in many basal tetanurans (Rauhut 2003a). The proximal end of metacarpal III is obscured by the displaced lateral edge of distal carpal 1. The shaft and proximal and distal ends of metacarpal III are of subequal width. The distal articular end of metacarpal III is only slightly expanded from the shaft diameter and it lacks a ginglymus and an extensor pit on the dorsal surface.

Metacarpal IV (Fig. 15) is missing the proximal articular end and the proximal third of its shaft. The remaining shaft is extremely slender, and terminates distally nearly level with metacarpal III, unlike in *Haplocheirus* (Choiniere *et al.* 2010b), where metacarpal IV is not as slender and is half, rather than subequal to, the length of metacarpal III. In *Aorun*, metacarpal IV is closely appressed along its length to metacarpal III, and is not laterally bowed as in derived

maniraptorans. The distal surface is semicircular in lateral view, but the dorsal surface is obscured.

**Manual digits.** The digits of the left manus (Figs 3, 15) are nearly complete and preserved in articulation. Phalanges IV-2 and IV-3 are missing, but the fourth digit is otherwise preserved in life position, allowing confident estimation of the lengths of the fingers. The middle digit is the longest, followed by the lateral digit.

Phalanx II-1 is robust, approximately twice the medio-lateral width of the ulna and metacarpal III. The ventral surface bears a proximal depression immediately distal to the flexor processes, but the distal half of the ventral surface is ventrally flat. This morphology is common in theropods and differs from the axial furrow of alvarezsauroids (Novas 1997). Well-developed, paired flexor processes are present on the proximoventral surface, and the medial flexor process is very large, projecting beyond the ventral level of the medial metacarpal condyle. The distal condyles of II-1 are ginglymoid, with a well-developed trochlea extending onto the dorsal surface of the phalanx. In medial view, the distal condyles are ovoid and the collateral ligament pit is located on the anterodorsal corner of the condyle. Ungual II-2 is the longest, tallest, and mediolaterally widest of the manual unguals and it weakly recurves in lateral view. Despite being the longest and tallest unguinal, it is still mediolaterally narrow. The flexor tubercle is large and proximally located. The ventral margin of the flexor tubercle is mediolaterally emarginated by symmetrical circular depressions of the medial and lateral surfaces. These were presumably attachment points for the paired flexor tendons.

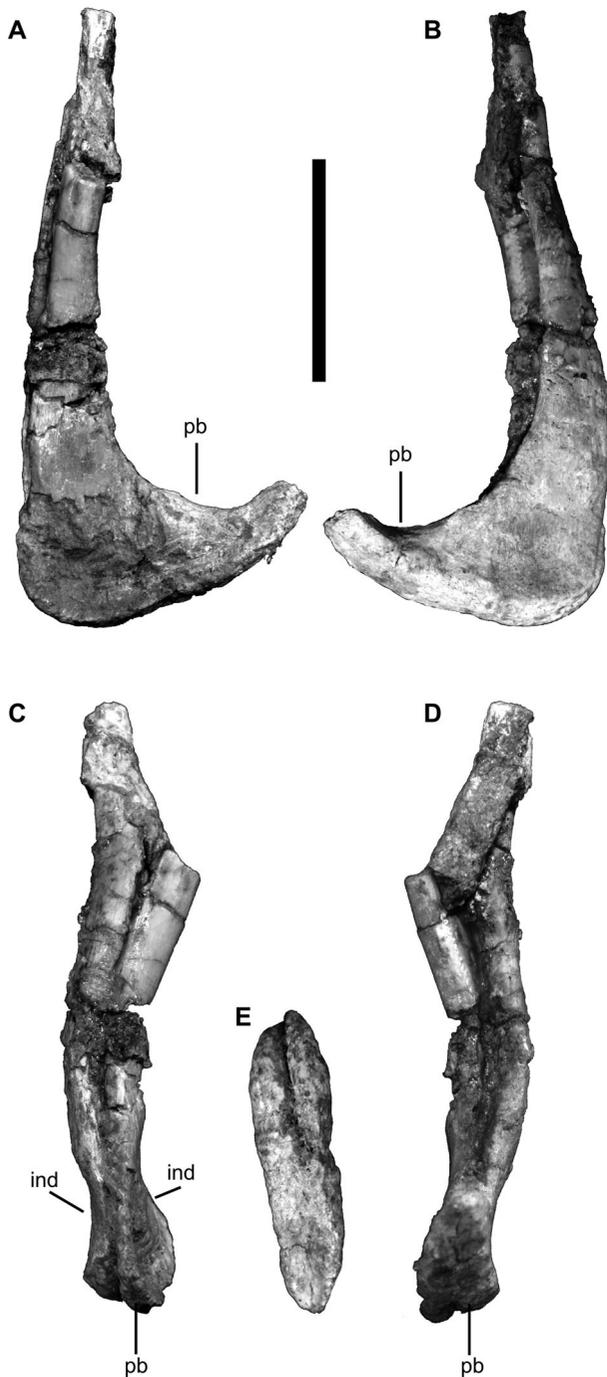
Phalanx III-1 is much shorter than III-2 (62% of its length), and its shaft is long and slender. The distal condyles are separated by a mediolaterally narrow, deep trochlea that extends onto the dorsal surface. The condyles are subcircular in medial view and the collateral ligament pit is located in the middle of the condyle. Phalanx III-2 is long and mediolaterally thin. The proximoventromedial surface of III-2 bears a well-developed flexor process. The presence of a second, paired process cannot be confirmed because the lateroventral surface of the proximal end is poorly preserved. The distal condyles of III-2 are ovoid in lateral view and are separated by a narrow trochlea that extends onto the dorsal surface. Ungual III-3 is proximodistally shorter and dorsoventrally much lower than unguinal II-2. Its ventral margin is almost straight in lateral view. A small piece of missing bone on the proximoventral surface of the unguinal makes it impossible to determine whether the flexor tubercle is absent or very weakly developed, but if it was present it was considerably smaller and located more distally than the flexor tubercle of unguinal II-2 and located more distally.

Phalanxes IV-1 and IV-2 are missing, although their total lengths can be confidently estimated at 10 mm based on the gap between metacarpal IV and phalanx IV-3. Phalanx IV-

3 is long, dorsoventrally low and mediolaterally thin, and longer than both of the more proximal phalanges combined (150% their combined length). Only the proximal portion of unguinal IV-4 is preserved, but it is clearly much smaller than III-3, has either weak or no curvature and bears a weakly developed flexor tubercle that is displaced distally from the proximal articular surface. There is no proximodorsal lip on any of the unguals.

**Pubis.** The joined pubes (Figs 3, 16), including nearly half of the distal shafts and the pubic boot, are preserved. A pubic apron is present extending from the anterior margins of the pubic shafts, which are anteroposteriorly flattened distally. The medial junction of the pubic apron is depressed from the anterior surface of the pubic shaft. The pubic boot is well developed posteriorly but does not project anteriorly. It is ventrally convex in lateral view, and in distal view it is mediolaterally narrow, as in coelurosaurs generally (Benson *et al.* 2010a). The distal pubes are poorly fused anteriorly, but the narrow posterior end of the pubic boot is completely fused. Posteriorly, the pubic boot narrows dorsoventrally and turns dorsally slightly. The lateral surfaces of the pubic shafts are concave along the lateral sides of the pubic boot, forming contralateral indentations that are visible in anterior view as a mediolateral narrowing of the distal pubis.

**Tibia.** The proximal half of the right tibia (Fig. 3) is preserved and the left tibia (Figs 3, 17, 18) is nearly complete, missing only the medial distal condyle. The tibia is long and slender. The cnemial crest does not project far anteriorly from the tibial shaft, but both proximal tibiae have been mediolaterally compressed and the preservation of the cnemial crests is poor. The proximal extension of the cnemial crest is level with the posterior condyles. A well-developed fibular crest is present, which likely was continuous with the proximal end of the tibia, but the proximal extent cannot be determined because of poor preservation. The anterior surface of the distal tibia bears a deep, anterolaterally facing groove for the ascending process of the astragalus. This groove extends proximally from the distal end of the tibia, along the anterolateral side of the tibia for 1.5 cm before grading into the tibial shaft. A groove on the anterior surface of the distal tibia that restricts the ascending process to the lateral side is present in many non-coelurosaurian theropods (e.g. *Allosaurus*: Rauhut 2003a), but within Coelurosauria it has only been reported in *Tugulusaurus* (Rauhut & Xu 2005). In *Tugulusaurus*, the restriction of this groove to the lateral side of the tibia is similar to the condition in *Aorun*. Another similarity to *Tugulusaurus* is that the groove is oriented proximodistally, whereas in non-coelurosaurian theropods the groove curves strongly medially as it extends distally (Rauhut & Xu 2005). However, in *Aorun* the groove is mediolaterally narrower than that of *Tugulusaurus* and, unlike the apomorphically large lateral tibial condyle of *Tugulusaurus* (Rauhut & Xu 2005), the lateral condyle of the tibia is very small in *Aorun*.



**Figure 16.** Pubes of *Aorun zhaoui* (IVPP V15709). **A**, left lateral view; **B**, right lateral view; **C**, anterior view; **D**, posterior view; **E**, ventral view. Abbreviations: ind, indented area; pb, pubic boot. Scale bar equals 2 cm.

The anterolateral surface of the tibia is angled approximately  $45^\circ$  to the plane of the anterior surface, probably serving as an articular surface for the calcaneum, which is not preserved. The posterior surface of the distal tibia is flat. The distal tibia is anteroposteriorly thickest medially, and the step-like offset for the ascending process

of the astragalus yields a marked lateral anteroposterior thinning.

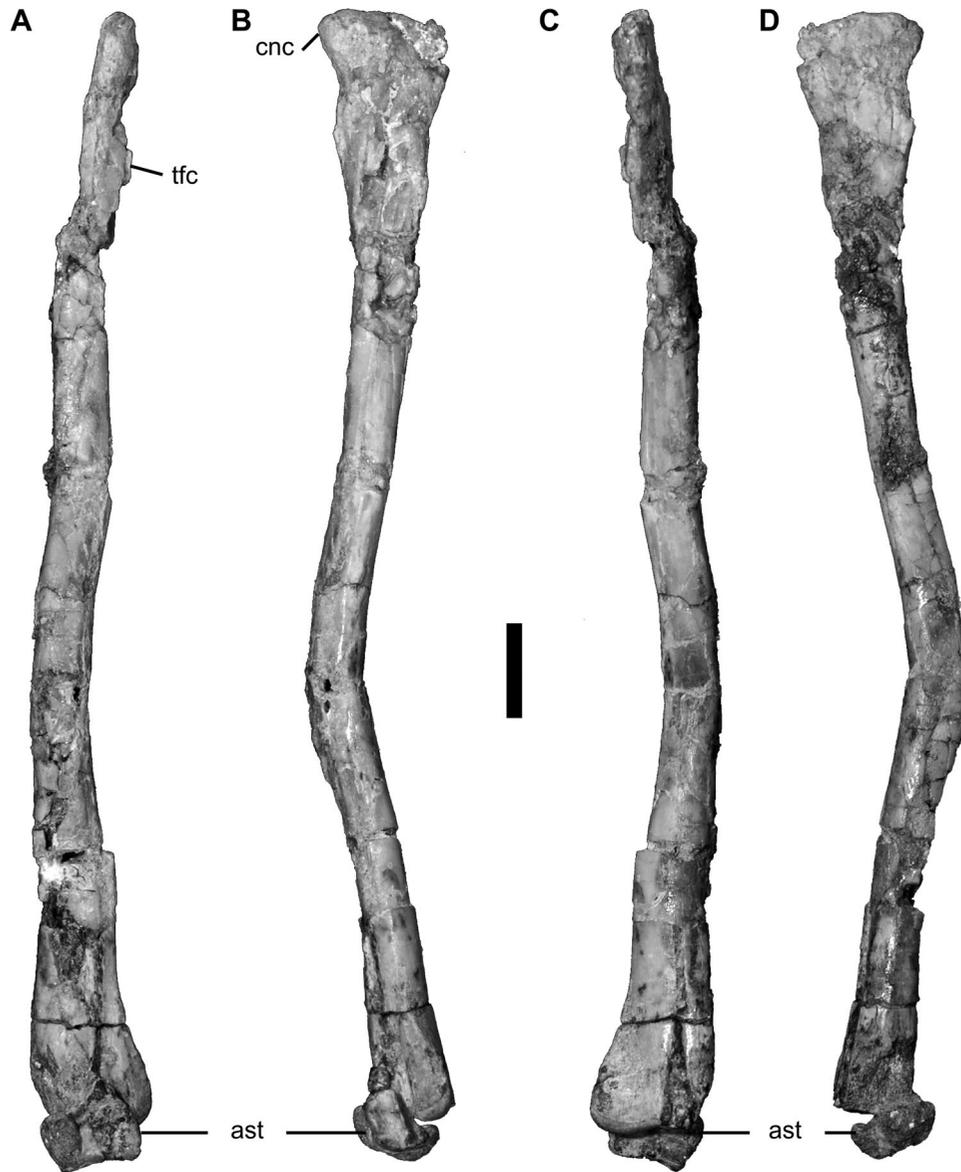
**Fibula.** The proximal end of the right fibula has been lost, but a section of the proximal shaft is preserved lying close to the right tibia. It is only about half the diameter of the tibia, but little can be said about its morphology.

**Astragalus.** The left astragalus (Figs 17, 18) is preserved in partial articulation with the distal end of the left tibia. The astragalus has been displaced distally and offset from the anterior surface of the tibia slightly during preservation, indicating that the astragalus and tibia were not tightly co-ossified. The calcaneum is missing. The medial condyle of the astragalus has been broken off from the astragalus body and is preserved adhering to the astragalus body slightly proximal and lateral to its original position. The lateral condyle is intact and shows that the condyles of the astragalus were fully developed on the anterior surface of the tibia. The ascending process, unlike that of most coelurosaurs (Rauhut 2003a), is mediolaterally narrow and proximodistally short. As preserved, the triangular ascending process is restricted to the lateral side of the astragalus, articulating with the groove on the anterolateral surface of the tibia. It is unclear whether the ascending process in adult animals would have completely filled the tibial groove, but it is possible that the relatively low ascending process merely reflects incomplete ossification. Given the size and shape of the groove in the tibia, if the ascending process completely filled it, the process would be much taller than the astragalus body, as in most coelurosaurs.

**Distal tarsals.** Two distal tarsals (Fig. 3) are preserved and are separate from the proximal ends of the metatarsals. The lateral distal tarsal is the larger of the two, and possesses a deep medial notch for the articulation of the subrectangular and smaller medial distal tarsal. The distal tarsals are both shallowly concave on their proximal aspects and shallowly convex on their distal aspects. The lateral distal tarsal likely articulated with the lateral astragalus condyle and the calcaneum based on its lateral position.

**Metatarsals.** Left metatarsals I–IV are preserved in articulation with the nearly complete pes, and are missing portions of the proximal ends (Fig. 19). Only the distal ends of right metatarsals II–IV are preserved, but right metatarsal I is complete. Metatarsal V is not preserved on either side. The maximum length of the metatarsus is about 66% of the length of the tibia.

Metatarsal I is proximodistally short and has a flattened, blade-like proximal articulating surface that is closely appressed to the medial side of metatarsal II. It articulates on the medial surface of metatarsal II, just distal to the midpoint of its shaft. The dorsal surfaces of the distal condyles of metatarsal I are smooth and the condyles are subsymmetrical. The lateral surface of the lateral condyle is deeply concave where it is closely appressed to metatarsal



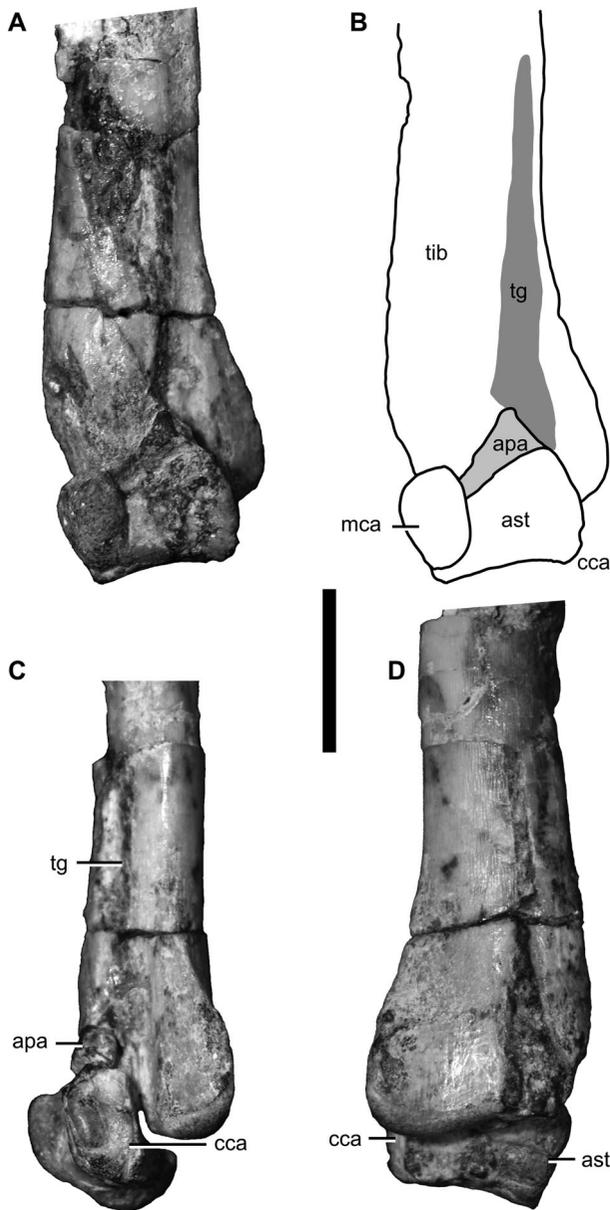
**Figure 17.** Left tibia and astragalus of *Aorun zhaoi* (IVPP V15709). **A**, anterior view; **B**, lateral view; **C**, posterior view; **D**, medial view. Abbreviations: ast, astragalus; cnc, cnemial crest; tfc, tibiofibular crest. Scale bar equals 1 cm.

II. The medial condyle has a shallow collateral ligament pit.

Metatarsal II is the same length as metatarsal IV, unlike the metatarsals of troodontids (Makovicky & Norell 2004), some ornithomimosaur (e.g. *Struthiomimus*: Osborn 1916), and many tyrannosaurs where metatarsal II is shorter than metatarsal IV. The distal condyles of metatarsal II are the mediolaterally widest and dorsoventrally tallest of the metatarsus. They are strongly asymmetrical, with the lateral condyle extending further distally and being mediolaterally wider than the medial condyle. The dorsal surface of the distal condyles is smooth. The shaft of metatarsal II is mediolaterally wider than that of metatarsal III, and in

cross section the shaft appears to be wider than dorsoventrally tall, although preservational distortion of the shafts makes this assessment tentative.

The shaft of metatarsal III is triangular in cross section and is exposed in anterior view along the entire metatarsal length, although the anterior exposure becomes mediolaterally narrower proximally. In posterior view, the shaft of metatarsal III is mediolaterally very narrow. The distal condyles of metatarsal III are subsymmetrical, but in distal view, the dorsal surface slopes laterally, so that it is taller medially along the contact with the distal end of metatarsal II than it is laterally along the contact with metatarsal IV. The dorsal surface of the distal condyles is smooth, although



**Figure 18.** Close-up of left distal tibia and astragalus of *Aorun zhaoi* (IVPP V15709). **A**, anterior view; **B**, line drawing of anterior view; **C**, lateral view; **D**, posterior view. Abbreviations as in Fig. 17, and: apa, ascending process of astragalus; cca, calcaneal articular surface; mca, medial condyle of astragalus; tg, tibial groove; tib, tibia. Scale bar equals 1 cm.

there is a very shallow extensor fossa on the anterior surface located immediately proximal to the condylar articulation surface.

Metatarsal IV is mediolaterally narrower than the other metatarsals, a common theropod condition. The shaft of metatarsal IV is dorsoventrally deeper than it is mediolaterally wide. The distal condyles of metatarsal IV are asymmetrical, with the lateral condyle forming a mediolaterally narrow tab projecting ventrolaterally from the distal end of

the metatarsus. The distal end of metatarsal IV is mediolaterally much narrower than the ends of metatarsal II and metatarsal III, as in ceratosaurs (Carrano & Sampson 2008) and some ornithomimosaur (e.g. *Struthiomimus*: Osborn 1916; *Garudimimus*: IGM 100/13–07–7).

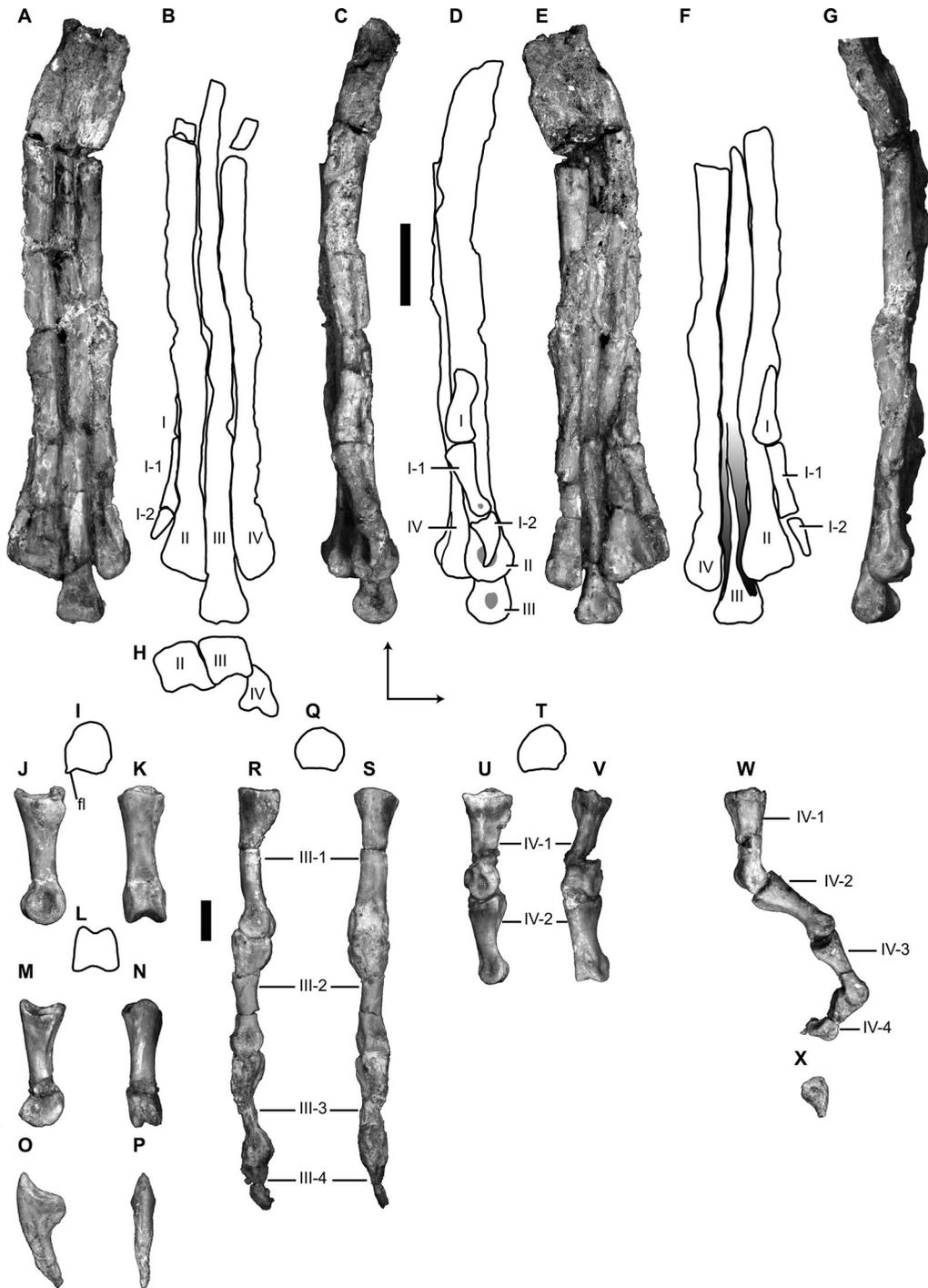
**Pedal digits.** Representatives of nearly every bone of the pedal digits are preserved (Fig. 19H–X). The phalanges and ungual of digit II are more robust than those of the more lateral digits and the phalanges of this digit bear extremely deep extensor ligament pits on their distal dorsal surfaces.

Phalanx I-1 is long and thin. The distal condyles are round in medial view and the collateral ligament pits are located in the middle of the lateral and medial surfaces. The ungual is small and gently recurved.

Phalanx II-1 is the mediolaterally widest pedal phalanx and it is subequal in length to pedal phalanx III-1. The proximal surface is deeply concave and subcircular. A well-developed lip is present on the ventral margin projecting proximally. The dorsal margin bears a small extensor process that projects proximally. The lateroventral edge of the proximal end of the ventral surface of pedal phalanx II-1 bears a small, lateroventrally projecting flange. The symmetric distal condyles of pedal phalanx II-1 are separated by a trochlea that is continuous dorsally with a deep, mediolaterally extensive extensor ligament pit. The medial collateral ligament pit is round, centrally placed, and occupies the majority of the medial surface of the distal condyles. The lateral collateral ligament pit is small, ovoid and dorsally displaced. Pedal phalanx II-2 is nearly equal in length to II-1. The proximal surface is triangular, divided into lateral and medial cotyles for articulation with the ginglymoid end of II-1 and bears a prominent extensor process on the dorsal margin. The distal condyles of II-2 are ovoid in lateral and medial views. Its collateral ligamentous fossae are dorsally displaced and a deep, narrow trochlea separates the condyles, extending far proximally onto the dorsal surface.

Pedal ungual II-3 is the largest pedal ungual, as in *Haplocheirus* (IVPP V15988), dromaeosaurids (Norell & Makovicky 2004) and troodontids (Makovicky & Norell 2004). It is weakly recurved, unlike the hypertrophied, strongly recurved digit II ungual of dromaeosaurids (Norell & Makovicky 2004) and troodontids (Makovicky & Norell 2004). The ventral surface bears a well-developed, proximally located flexor tubercle. The distal end is a spike-like tapering cone, as opposed to the pyramidal shape of the more lateral unguals. The ungual of pedal digit II is much larger than the ungual of digit III, almost twice the length and height at the articular surface, although pedal ungual III-4 is not completely preserved.

Pedal phalanx III-1 is the longest pedal phalanx, but is only marginally longer than II-1. The proximal end of the ventral surface bears two proximodistally short ridges along the lateral and medial margins. The shaft is mediolaterally



**Figure 19.** Left metatarsus and partial left and right pedes of *Aorun zhaoi* (IVPP V15709). **A**, anterior view; **B**, line drawing of anterior view; **C**, medial view; **D**, line drawing of medial view; **E**, posterior view; **F**, line drawing of posterior view; **G**, lateral view; **H**, distal line drawing of left metatarsals; **I–L**, left pedal phalanx II-1 in: **I**, line drawing of proximal surface of pedal phalanx II-1; **J**, lateral view; **K**, dorsal view; **L**, line drawing of distal view; **M, N**, left pedal phalanx II-2 in: **M**, lateral view; **N**, dorsal view; **O, P**, left pedal ungual II-3 in: **O**, lateral view; **P**, dorsal view; **Q**, line drawing of left pedal phalanx III-1 in proximal view; **R, S**, left pedal digit III in: **R**, lateral view; **S**, dorsal view; **T**, line drawing of left pedal phalanx IV-1 in proximal view; **U, V**, left pedal phalanges IV-1 and IV-2 in: **U**, lateral view; **V**, dorsal view; **W**, right pedal digit IV in lateral view; **X**, right pedal ungual IV-5 in lateral view. Arrows refer to **H**, vertical arrow indicates dorsal direction and horizontal arrow indicates lateral. Abbreviations: fl, flexor process; I–IV, metatarsals one to four; I-1–IV-4, pedal phalanges of digits one to four. Scale bar equals: A–H, 1 cm; I–X, 5 mm.

much thinner than II-1 and bears a shallower extensor pit on the distal dorsal surface. The distal condyles are round in lateral and medial view, and the collateral ligamentous fossae are asymmetrically developed, as in II-1. The ventral surface of III-1 is flat. The proximal end of III-2 is mediolaterally wide and anteroposteriorly tall, but the shaft narrows markedly mediolaterally distal to its proximal articulation. The proximal end of the ventral surface bears similar lateral and medial ridges as III-1, although they are less ventrally extensive. The distal condyles are circular in lateral view, with centrally located, symmetric collateral ligament pits. The dorsal surface of the distal condyles is not ginglymoid, but there is a well-developed extensor pit on the dorsal surface just proximal to the condyles. The distal condyles of III-3 appear ginglymoid, but are poorly preserved and this cannot be confirmed on the contralateral side.

The phalanges of pedal digit IV are slender and elongate, with an arched ventral surface and shallow extensor pits. This contrasts with the fourth digit of many theropods, including ornithomimosaurs (Makovicky *et al.* 2004), *Nqwebasaurus* (AM 6040), *Dilophosaurus* (Tykoski & Rowe 2004), *Avimimus* (IGM uncatalogued specimen), and tyrannosaurines (Holtz 2004), where the phalanges of the lateral pedal digit become proximodistally short and dorsoventrally deep with proximally extensive extensor pits and long narrow flexor processes. The extensor processes are small and the ventral surfaces are flat. Only a small portion of the ungual for pedal digit IV is preserved, but it is much smaller than that of digit II.

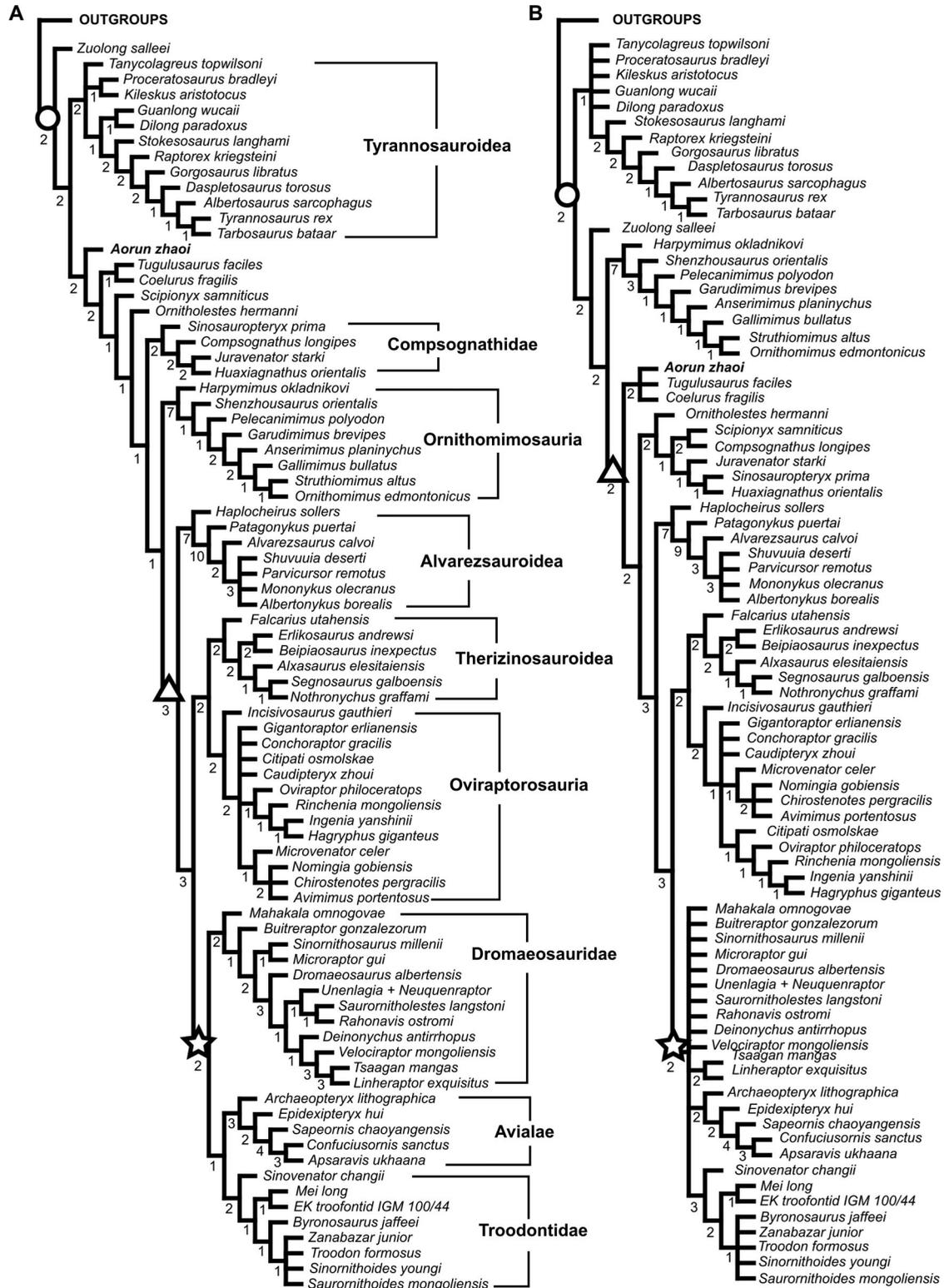
## Phylogenetic analysis

The full phylogenetic analysis produced 80 MPTs of length 3045, Consistency Index (CI) 0.213 and Retention Index (RI) 0.611 (Fig. 20A). The ontogenetic analysis produced 4416 MPTs of length 3036, CI 0.214 and RI 0.614 (Fig. 20B). The phylogenetic position of *Aorun* differs only slightly between the full and the ontogenetic analysis. In the full analysis, *Aorun* is recovered as a member of the Coelurosauria, more derived than Tyrannosauoidea but basal to Compsognathidae, in a grade of relatively basal coelurosaurs that includes *Tugulusaurus* + *Coelurus*, *Scipionyx* and *Ornitholestes*. *Juravenator* is recovered as a derived compsognathid in this analysis, the closest relative of the much larger *Huaxiagnathus*. Several characters unambiguously support a monophyletic grouping of Maniraptora (*sensu* Choiniere *et al.* 2010b), Ornithomimosauria, Compsognathidae and the aforementioned grade of relatively basal coelurosaurs, including: the lack of a suborbital jugal process (character 57, reversed in Ornithomimosauria, Oviraptorosauria and *Archaeopteryx*); a tapering quadratojugal process of the squamosal (character 105, also known in some ceratosaurs, e.g. *Limusaurus*: Xu *et al.* 2009a; and coelophysoids, e.g. *Coelophysis*:

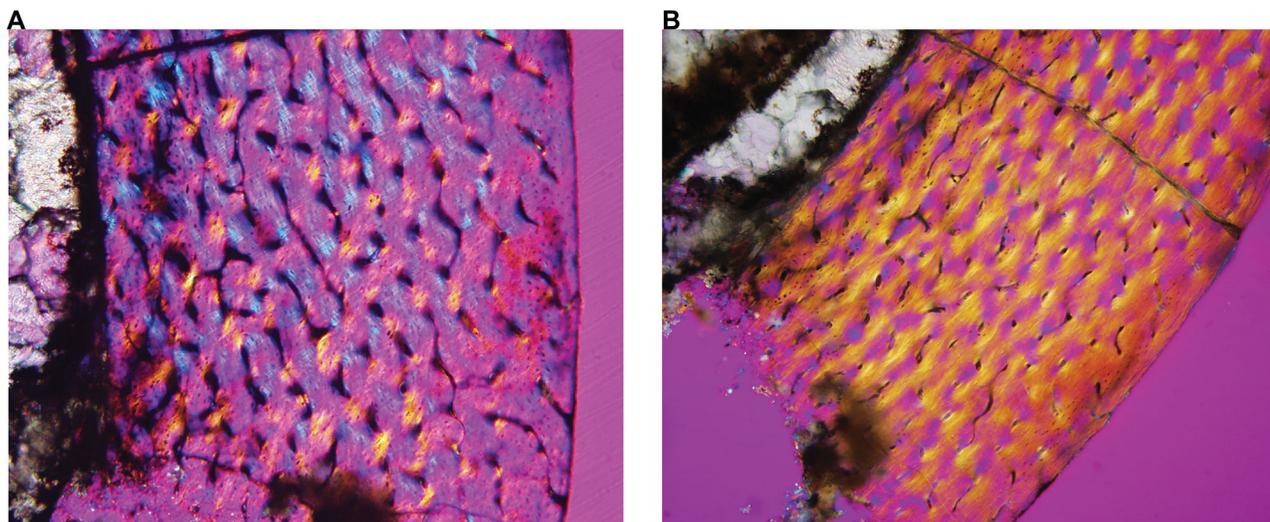
Colbert 1989); a dentary with subparallel dorsal and ventral edges (character 189, highly homoplastic within Theropoda); the loss of premaxillary tooth serrations (character 216, regained in some dromaeosaurids (e.g. *Deinonychus*: Ostrom 1969); loss of the mesial carinae on the maxillary teeth (character 222, regained in some dromaeosaurids, e.g. *Deinonychus*: Ostrom 1969; and in therizinosauroids, e.g. *Falcarius*: Kirkland *et al.* 2005); reduction in the height of the cervical neural spines (character 266, highly homoplastic in Theropoda); posterior dorsal vertebrae with square, rather than high rectangular neural spines (character 289, also present in *Masiakasaurus* (Carrano *et al.* 2002) and some coelophysoids, and reversed in *Harpymimus* (Kobayashi & Barsbold 2005a), some therizinosauroids, some oviraptorosaurs and some dromaeosaurids); shaft diameter of phalanx II-1 greater than that of the radius (character 402, reversed in all maniraptorans other than alvarezsaurids); weakly curved lateral manual unguals (character 412, highly homoplastic within Coelurosauria); and presence of a horizontal groove across the anterior surface of astragalar condyles (character 531, reversed in *Nomingia*: IGM uncatalogued specimen).

In the ontogenetic analysis, *Aorun* is recovered as a part of a monophyletic group including *Tugulusaurus* and *Coelurus*, and this group (which forms a trichotomy in the strict consensus) is basal to Compsognathidae within Maniraptora. The *Tugulusaurus*–*Coelurus*–*Aorun* group is supported by two characters: the presence of a deep vertical groove on the anterolateral side of the distal end of the tibia, and a mediolaterally narrow ascending process of the astragalus. In the full analysis, the former character is equivocally optimized and the latter character is interpreted as plesiomorphic for Coelurosauria. In the ontogenetic analysis, *Scipionyx* is recovered as a basal member of the Compsognathidae (as found by Dal Sasso & Maganuco 2011), and *Juravenator* is recovered as a derived member of the same group, although it is sister to *Sinosauropteryx* + *Huaxiagnathus*.

Maniraptorans more derived than the *Tugulusaurus*–*Coelurus*–*Aorun* clade (but inclusive of Compsognathidae) are diagnosed in the ontogenetic analysis by nine characters, including: loss of the anterior process of the jugal so that it does not extend ventral to the antorbital fenestra (character 57, reversed in *Citipati* and *Archaeopteryx*); frontal process of postorbital curves anterodorsally making dorsal border of postorbital concave (character 89, reversed in all compsognathids but optimizes to base of clade when *Ornitholestes* is a basal member); loss of posterior pneumatic recess in quadrate (character 113, reversed in *Incisivosaurus*); dentary with subparallel dorsal and ventral margins (character 189, reversed many times within this group); loss of lateral flange along dorsal margin of surangular (character 196, reversed in *Haplocheirus* and some dromaeosaurids); loss of D-shaped premaxillary tooth crowns (character 217, reversed in *Ornitholestes*,



**Figure 20.** Strict consensus trees showing phylogenetic position of *Aorun zhaoi* (IVPP V15709). **A**, full analysis consensus of 80 MPTs, length = 3045, CI = 0.213, RI = 0.611; **B**, ontogenetic analysis consensus of 4416 MPTs, length = 3036, CI = 0.214, RI = 0.614. Open circle at node denotes Coelurosauria, open triangle denotes Maniraptora, open star denotes Paraves. Numbers below selected nodes indicate Bremer support values.



**Figure 21.** Long bone histological sections from *Aorun*. **A**, transverse section of IVPP V15709 femur viewed with polarizing microscopy; **B**, transverse section of IVPP V15709 tibia viewed with polarizing microscopy. The majority of the diaphyseal cortices in both elements are composed of woven fibrolamellar matrix. The deepest cortices (left in **A** and upper left in **B**) show longitudinal, reticular and circumferentially oriented vascularization. Closer to the cortical surface longitudinal vascularization become prevalent. No lines of arrested growth (LAGs) are present in either element. Nevertheless, the outermost bone matrix is avascular, suggesting that IVPP V15709 was in the process of forming an annulus, and perhaps a LAG, at the time of death. Scale bar equals 2 mm.

*Zanabazar* and *Dromaeosaurus*); pronounced hypapophyses in anterior dorsals (character 270, lost in *Microvenator*, *Avialae*, *Sinovenator*, and some dromaeosaurids); presence of a distinct muscle scar on lateral surface of distal end of deltopectoral crest (character 358, highly homoplastic within this group); and manual phalanx II-1 greater in diameter than radius (character 401, reversed in Paraves, Therizinosauroidea and Oviraptorosauria).

### Histological analysis and ontogenetic stage of the holotype

The majority of the diaphyseal cortices are composed of woven fibrolamellar matrix with longitudinal, circumferential and reticular oriented primary vascular canals (Fig. 21). Secondary bone such as Haversian canals are absent, as is endosteal bone. Close to the cortical surface, the bone composition changes to a more parallel-fibred matrix with sparse longitudinal vascularization. No lines of arrested growth (LAGs) were observed on either the tibial or fibular histological sections. Nevertheless, the outermost bone matrix is avascular, suggesting that IVPP V15709 was in the process of forming an annulus, and perhaps a LAG, at the time of death. These observations support a maximum age of one year for the specimen, and in fact probably less given that most extant vertebrates are not hatched/born during the most environmentally stressful climatic conditions when the endogenous growth lines typically form.

The histological analysis is corroborated by the lack of complete fusion of any of the neural arches to the centra in the vertebral column, which suggests that IVPP V15709 is an immature individual, although neural arch fusion is

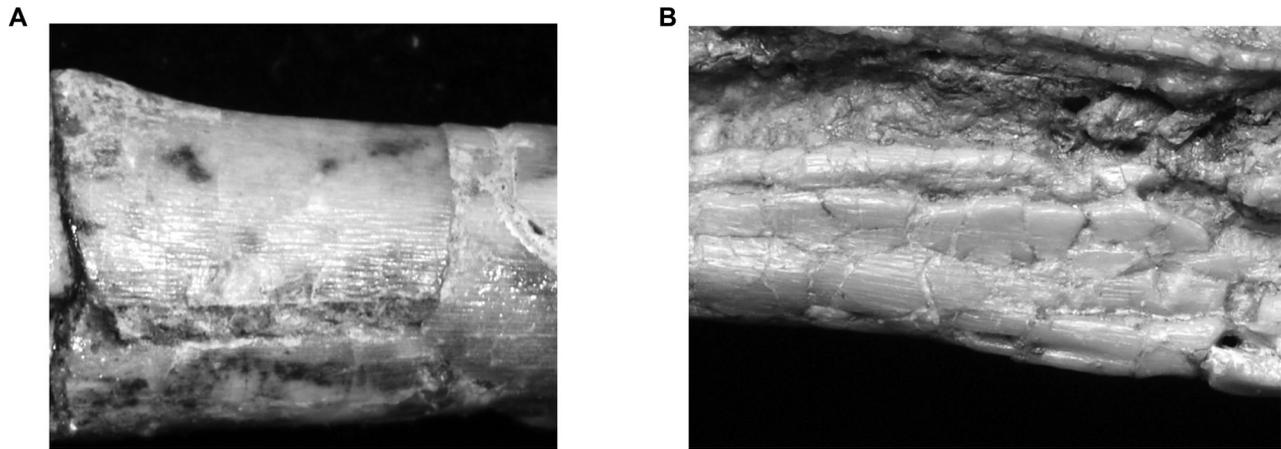
not necessarily a good indicator of developmental stage in archosaurs (Brochu 1996; Irmis 2007). Additionally, the cortical bone preserved on the lower jaw, metatarsus, tibia and femur has the striated, 'scarred' texture (Fig. 22) seen on these bones in many immature archosaurs, including extant crocodylians and birds (Dal Sasso & Maganuco 2011), sauropodomorph embryos (Reisz *et al.* 2005; Salgado *et al.* 2005), and the presumed early juvenile theropods *Scipionyx* (Dal Sasso & Maganuco 2011), *Juravenator* (Göhlich *et al.* 2006) and *Sinosauroptryx* (Currie & Chen 2001). This texture diminishes with increasing ontogenetic age.

A number of other skeletal characteristics, however, show that the holotype of *Aorun* does not represent an especially early ontogenetic stage, such as a perinate or embryo (Bever & Norell 2009). These characteristics are discussed at length by Dal Sasso & Maganuco (2011) and include: nasals longer than frontals, whereas in embryos and perinates they are either shorter or subequal; presence of replacement teeth, whereas very young theropod specimens such as *Scipionyx* do not show replacement teeth; and a relatively long dentary, whereas the dentary is short in very young theropods like *Scipionyx*.

## Discussion

### Implications for theropod diversity in the Middle to Late Jurassic

*Aorun* is the seventh named theropod and the fourth coelurosaur from the Shishugou Formation. The three previously known coelurosaurs (*Guanlong*, *Haplocheirus*



**Figure 22.** Surface texture of cortical bone of *Aorun zhaii* (IVPP V15709) showing longitudinal striations characteristic of early ontogenetic stage. **A**, anterior surface of tibia; **B**, lateral surface of dentary. Figures not to scale.

and *Zuolong*) were also found at Wucuiwan but at higher stratigraphical levels in the Late Jurassic part of the formation. *Aorun* is thus the oldest coelurosaur known from the Shishugou Formation and likely dates to the Middle Jurassic, although the radiometric dates for this part of the Shishugou Formation fall within the error of the Middle–Late Jurassic boundary on the world geological timescale (Gradstein *et al.* 2004). The adult size of *Aorun* is unknown, and based on the extremely small size of the Guimarota *Allosaurus* maxilla relative to the adult size of that taxon (Rauhut & Fechner 2005), it is possible that an *Aorun* adult could have been as large as *Sinraptor* or *Monolophosaurus*. However, the coelurosaurian record of the Shishugou Fm. is limited to small–medium bodied taxa (Xu *et al.* 2006; Choiniere *et al.* 2010a, b; Han *et al.* 2011), and the coelurosaurian status of *Aorun* thus suggests that adults of this species were only of moderate size. *Aorun* differs in overall skull dimensions from *Zuolong* and *Guanlong*, with a proportionately longer maxilla and a lower rostrum. Although the overall skull dimensions and hand morphology are similar to the basal Shishugou alvarezsaurid *Haplocheirus*, *Aorun* can be readily differentiated from that taxon based on both cranial and postcranial morphology.

The discovery of *Aorun* and its recognition as a coelurosaur provides more evidence for the remarkable theropod diversity of the Shishugou Formation (reviewed in Eberth *et al.* 2010). This fauna spans a range of body sizes, from the 2 m long *Haplocheirus* (Choiniere *et al.* 2010b) to the 6 m long *Sinraptor* (Currie & Zhao 1993), and a range of trophic levels, from the edentulous (and presumably herbivorous) ceratosaur *Limusaurus* (Xu *et al.* 2009a) to the hypercarnivorous basal tyrannosauroid *Guanlong* (Xu *et al.* 2006). In its phylogenetic diversity and taxonomic composition, the theropod fauna of the Shishugou Formation is broadly similar to other well-sampled terrestrial Laurasian Late Jurassic theropod faunas. For example,

the Shishugou Fm., the Morrison Fm. of the western USA, and the Lourinhã and Alcoçoça formations of Portugal have fauna composed of basal neotheropods, non-coelurosaurian tetanurans, basal tyrannosauroids, and other coelurosaurs (Dodson *et al.* 1980; Mateus 2006; Mateus *et al.* 2006). Although penecontemporaneous theropod faunas from the UK are known primarily from marine deposits with sparse fossils of terrestrial animals, there is at least some indication that they had similar phylogenetic breadth (Benson & Barrett 2009).

The Late Jurassic theropod faunas of Portugal and the western USA share several genera and relatively closely related taxon pairs (Mateus 2006), including the basal tyrannosauroids *Aviatyrannus* and *Stokesosaurus* (Rauhut 2003b). Although the Shishugou basal ceratosaur *Limusaurus* appears to be closely related to the basal Tendaguru ceratosaur genus *Elaphrosaurus* (Xu *et al.* 2009a), which may also be present in the Morrison Formation (Galton 1982), the coelurosaurs and tetanurans from the Shishugou have no generic overlap, and are not hypothesized to form exclusive sister-group relationships with coelurosaurs from these formations. This difference may be a reflection of endemism of Asian dinosaur faunas during the Middle to Late Jurassic (Mateus 2006; Upchurch *et al.* 2002), or merely a function of the time difference between the Shishugou (Oxfordian/Callovian) and the Morrison and Lourinhã (Kimmeridgian/Tithonian) formations. There are few geographical areas worldwide that sample both the earliest and the latest Late Jurassic to test these hypotheses. However, the close phylogenetic affinities of the Oxfordian taxon *Metriacanthosaurus* with Asian metriacanthosaurids, including *Sinraptor* (Carrano *et al.* 2012), may support the latter hypothesis. If this is the case, then theropod faunal differences in Laurasian Jurassic deposits are a function of time rather than geographic barriers to dispersal.

Gondwanan Late Jurassic localities such as the Tendaguru Beds (Rauhut 2005, 2011) generally are missing

the coelurosaurian faunal component present in contemporaneous beds in Laurasia. The reasons for this distribution of Jurassic coelurosaurs remain unclear. While some authors (e.g. Rauhut 2011) have argued that it reflects a true difference in coelurosaur biogeography, other research suggests sampling bias, perhaps based on body size. Eberth *et al.* (2010) have hypothesized that frequent and 'good' fossil representation of small theropods may require unusual preservational opportunities. This idea is supported by the recent discoveries of Lagerstätten in the shallow lacustrine Daohugou Beds of north-east China (Zhang *et al.* 2002, 2008; Hu *et al.* 2009; Xu *et al.* 2010b, 2011), which clearly show that paravian taxonomic diversity was high in the Middle–Late Jurassic, despite the poor sampling of these taxa in contemporaneous terrestrial beds. Therefore, while the diverse coelurosaurian fauna of the Shishugou supports the hypothesis that coelurosaurs were widespread in the Late Jurassic of Laurasia, testing whether Gondwana was depauperate of coelurosaurs during this time period will require denser sampling of Jurassic deposits in the southern hemisphere.

Ghost lineages (Norell 1992, 1993) demonstrate that the origins of all major coelurosaurian clades date at least to the earliest Late Jurassic (Rauhut 2003a; Hu *et al.* 2009; Choiniere *et al.* 2010b; Xu *et al.* 2010b), but robust hypotheses of coelurosaurian relationships and morphological evolution within the group have been hampered by a lack of stratigraphically older, basal taxa. These taxa are important because they have the potential to preserve plesiomorphic morphologies that change character polarities at the base of clades. For example, the recent discovery of a spate of Middle–Late Jurassic basal paravians in China (e.g. Zhang *et al.* 2008; Hu *et al.* 2009) has led to bold new hypotheses of relationships within this group (e.g. Xu *et al.* 2011). Similarly, the recognition of the Middle Jurassic *Proceratosaurus* as a basal tyrannosauroid and the descriptions of the Jurassic tyrannosauroids *Stokesosaurus langhami* (Benson 2008), *Guanlong* (Xu *et al.* 2006) and *Kileskus* (Averianov *et al.* 2010) have surprisingly shown that the earliest tyrannosauroids differed greatly in body proportions from their better-known Late Cretaceous descendants (Brusatte *et al.* 2010b). Although our understanding of early paravian diversification has been revolutionized by discoveries of Jurassic taxa, long ghost lineages still exist for some more basal coelurosaurian groups (Ji *et al.* 2003; Eberth *et al.* 2010). For example, the oldest known ornithomimosaur material is Hauterivian–Barremian (Buffetaut *et al.* 2009; Allain *et al.* 2011) and the earliest therizinosauroids (Xu *et al.* 1999) and oviraptorosaurs (Xu *et al.* 2002) are from the Barremian (although *Eshanosaurus* may date to the Jurassic; Barrett 2009), at least 25 million years after these groups are inferred to have originated. This underscores the importance of including taxa like *Aorun* in comprehensive analyses of coelurosaurian relationships.

### Implications for hypotheses of coelurosaur dietary shifts

Zanno and colleagues (Zanno *et al.* 2009; Zanno & Makovicky 2011) proposed that early coelurosaurian diversification was coincident with a shift in feeding strategy from hypercarnivory to omnivory and in some coelurosaurian clades to obligate herbivory. They hypothesized that the common ancestor of all coelurosaurs more derived than Tyrannosauroidea should show morphological correlates of dietary diversification. Although our phylogenetic results differ from these authors in finding Compsognathidae in a derived position, we recover *Aorun* as the sister taxon to all coelurosaurs more derived than Tyrannosauroidea. Thus, *Aorun* occupies an important position on the coelurosaurian tree for testing this hypothesis.

Interestingly, some features of the anatomy of *Aorun* are consistent with morphological changes predicted by Zanno *et al.* (2009), including the loss of premaxillary tooth serrations and non-raptorial lateral manual unguals. It is therefore possible that the anatomical features of *Aorun* are representative of morphofunctional correlates of dietary plasticity close to the base of Coelurosauria.

### Implications of ontogenetic stage for phylogenetic position of *Aorun*

The phylogenetic placement of *Aorun* is due to its lack of synapomorphies that provide evidence of affinity with higher coelurosaurian taxa. It is possible that *Aorun* lacks these apomorphic features because it is a juvenile. Ideally, semaphoronts chosen as terminal taxa in a phylogenetic analysis are from the same ontogenetic stage (Hennig 1966; Wiley 1981; Kluge 1985). Taxa represented by immature exemplars pose a problem for phylogenetic analysis when mixed indiscriminately with mature exemplars because character states for a given taxon may change over ontogeny, and in the case of ontogenetic changes that evolve by terminal addition, immature specimens may lack a derived character state that only develops late in the sequence (Mabee 2000). Although invertebrate systematists have had success incorporating data from a variety of life stages in their analyses (e.g. Meier & Lim 2009), the detailed growth series needed to include this sort of data in a phylogenetic analysis is not available for almost all fossil taxa, particularly vertebrates, and is limited to skeletal features that mineralize relatively late in ontogeny. When attempting to assess the phylogenetic position of a new taxon known only from an immature specimen, dinosaurian researchers have generally taken two approaches: listing the diagnostic apomorphies of higher taxa that are identifiable in the immature specimen and assigning the new taxon to the least inclusive group it can be referred to (hereafter 'apomorphy approach'; e.g. Dal Sasso & Signore 1998; Norell *et al.* 2001a; Balanoff *et al.* 2008; Kundrat *et al.* 2008; Tsuihiji *et al.* 2011), or simply including the new immature taxon in a phylogenetic

analysis (e.g. Currie 2003; Göhlich & Chiappe 2006; Allain *et al.* 2007; Choiniere *et al.* 2010a), often with characters suspected of varying over ontogeny scored as missing data (question marks). The apomorphy approach has the disadvantage of not testing the en suite character distribution of the new taxon in a phylogenetic analysis and thus requires ad hoc judgments when conflicting character suites are present, but may be appropriate where the reliable diagnostic characters are present that narrow the identification of the new taxon to a desired taxonomic level. The second approach has the advantage of explaining the phylogenetic position of the new taxon in light of the suite of character evidence it bears, but the phylogenetic results must be interpreted with caution because juvenile semaphoronts may differ from adult semaphoronts of the same taxon.

The apomorphy approach is potentially problematical for discerning the phylogenetic position of *Aorun*. The Middle–Late Jurassic date of the Shishugou Formation makes it penecontemporaneous with the hypothesized time of earliest coelurosaurian diversification (Rauhut 2003a; Choiniere *et al.* 2010a, b; Rauhut *et al.* 2010), and thus coelurosaurs preserved within it may lack the full suite of apomorphies of higher coelurosaurian taxonomic groups (e.g. *Haplocheirus*: Choiniere *et al.* 2010b). It follows that *Aorun* might only preserve a few diagnostic apomorphies and that even fewer of these would be manifested in immature individuals. Furthermore, the characters diagnosing higher theropod taxa, particularly Coelurosauria, are in a state of flux (Choiniere *et al.* 2010a), and new taxa (particularly basal taxa from geologically older formations) are important for assessing these diagnostic character distributions.

The phylogenetic approach is also potentially problematical for elucidating the relationships of *Aorun*. There has been little research on the effects of including semaphoronts of differing ontogenetic stages in phylogenetic analyses. Tykoski (2005) analysed the influence of ontogenetically variable characters in a phylogenetic analysis of the Coelophysoidea and showed that when immature taxa are coded as adults in a phylogenetic analysis, the immature taxa were recovered in artificially basal positions relative to adults of the same taxon. Similarly, Kammerer (2010) conducted a phylogenetic analysis of anteosaurian therapsids where juveniles and adults were coded as separate operational taxonomic units (OTUs) and found that when known juvenile or subadult specimens of a given taxon were included in the analysis, these specimens were recovered in more basal position on the tree than the adults. Recently, Tsuihiji *et al.* (2011) showed that a juvenile specimen of the derived tyrannosauroid *Tarbosaurus bataar* (identified as such based on the apomorphy approach) was recovered in a more basal position when coded as an exemplar in an analysis of tyrannosauroid relationships. These results are supported by the observation that in centrarchid fish approximately 75% of developmental changes are the product of

terminal addition (Mabee 2000), thus the appearance of derived character states late in ontogeny would result in an immature taxon scored for the plesiomorphic state in the majority of instances. Based on these limited studies, *Aorun* might be expected to occupy an artificially basal position in phylogenetic analyses.

Although *Aorun* shows characters suggesting coelurosaur affinities, such as features of the hand, it has other features, such as a short ascending process of the astragalus, that imply a more basal phylogenetic position. Incorporating *Aorun* into a phylogenetic analysis is the most rigorous means of assessing the relative importance and hierarchal nature of these characters. Varrichio (1997) and Bever & Norell (2009) listed morphological characters that are likely to change ontogenetically in dinosaurs and troodontids, respectively. These characters are possibly misleading when immature specimens are included in a phylogenetic analysis, but remain useful as phylogenetic markers for adults.

The phylogenetic position of *Aorun* differs when ontogenetically variable character codings are excluded from the analysis. Deletion of these characters moves *Aorun* into a more derived position on the theropod tree, above Ornithomimosauria rather than basal to it. *Scipionyx* is also recovered in a more derived position when ontogenetically variable characters are excluded, where it is hypothesized as a basal compsognathid rather than part of a coelurosaurian grade basal to the Compsognathidae. The placement of *Juravenator* within Compsognathidae is robust to the exclusion of ontogenetically variable character scorings. At least for *Aorun* and *Scipionyx*, it therefore seems likely that ontogenetically variable characters are responsible for an artificially basal position for these taxa if they are included as exemplars without consideration of ontogenetically variable characters. In the case of *Scipionyx*, these characters may be obscuring higher taxonomic affinities, presumably due to the retention of plesiomorphies in the juvenile. However, because adults of *Scipionyx* and *Aorun* are unknown and because developmental trajectories are so incomplete for most theropods, we are unable to determine a hypothesis of relationships for these taxa. Nevertheless, the hypothesis that *Aorun* is a relatively basal member of the Coelurosauria is robust to the exclusion of developmentally labile character scorings.

### **Morphological implications of ontogenetic stage of the holotype**

The lack of a complete growth series for almost all non-avian coelurosaurian taxa makes separating skeletal characteristics that are developmentally labile from those that are stable problematic. Embryos are known for several coelurosaurian taxa, including therizinosauroids (Kundrat *et al.* 2008), oviraptorosaurs (Norell *et al.* 2001a) and troodontids (Varrichio *et al.* 2002), but postembryonic

juvenile skeletal material of non-avian coelurosaurs is rare. The discovery of *Archaeornithoides* (Elzanowski & Wellnhofer 1993) and *Scipionyx* (Dal Sasso & Signore 1998) provided some of the first information on the juvenile coelurosaur skeleton, and recent morphological descriptions of the early ontogenetic skeletal stages of the non-coelurosaurian tetanuran *Allosaurus* (Rauhut & Fechner 2005), the tyrannosauroid *Tarbosaurus* (Tsuihiji *et al.* 2011) and the paravian theropods *Byronosaurus* (Bever & Norell 2009) and *Mei* (Xu & Norell 2004), are beginning to fill in this information gap. The work of Carr (1999) and Carr & Williamson (2004) on craniofacial ontogeny in tyrannosaurids remains the most thorough investigation of developmental changes in the morphology of the bones of the skull for coelurosaurs. Unfortunately, these studies are limited by the lack of very early tyrannosaurid ontogenetic stages (i.e. perinates and embryos), and tyrannosaurids are highly specialized, gigantic coelurosaurs (Holtz 2004) that probably do not reflect the primitive coelurosaurian morphology or ontogenetic trajectory (Xu *et al.* 2006; Benson 2008; Choiniere *et al.* 2010a). We discuss below some of the morphologies of *Aorun* in light of the available information on ontogenetic shape change.

Relative size of the orbit in comparison to skull length decreases during development in theropods (Colbert 1989; Varrichio 1997; Carr 1999; Chure 2000), in keeping with a general pattern in almost all vertebrates (Emerson & Bramble 1993). In *Aorun*, the maximum length of the orbit is about 29% of maximum skull length, approximately the same as that of presumed juvenile specimens of *Coelophysus* and *Compsognathus* (Colbert 1989). Therefore, the relatively large orbit of *Aorun* is likely not indicative of the adult morphology. In the co-occurring Shishugou theropod taxa *Haplocheirus*, *Guanlong* and *Limusaurus*, all of which are at least subadults (Xu *et al.* 2006, 2009a; Choiniere *et al.* 2010b), maximum orbital length is 20, 18 and 31% of maximum skull length, respectively. However, *Limusaurus* has an unusually short rostrum, related to its edentulous beak.

In dinosaurs in general ontogenetically young specimens are characterized by a short, high rostrum, and the rostrum increases in length relative to the height of the skull during development (Coombs 1982; Horner & Currie 1994; Rauhut & Fechner 2005; Bever & Norell 2009; Tsuihiji *et al.* 2011). The plesiomorphic condition for tetanurans is to elongate the maxilla during development, as evidenced by the short, high maxilla of hatchling *Allosaurus* (Rauhut & Fechner 2005). In the longirostrine basal tyrannosauroid *Guanlong*, the maxilla becomes more elongate during development (Xu *et al.* 2006), apparently retaining the plesiomorphic tetanuran developmental trajectory, but in derived tyrannosaurids the maxilla becomes relatively dorsoventrally higher and anteroposteriorly shorter with increasing ontogenetic age (Carr 1999; Brusatte *et al.* 2009, 2012). In the derived coelurosaur *Byronosaurus*, the maxilla also becomes relatively anteroposteriorly longer

during development, but its shape in early ontogeny is longer and lower than that of more primitive tetanurans, such as *Allosaurus* (Rauhut & Fechner 2005; Bever & Norell 2009). In the one-year-old specimen of *Aorun*, the rostrum is already longer and lower than in some other juvenile coelurosaurs, such as *Scipionyx* (Dal Sasso & Signore 1998). *Aorun* lacks any synapomorphies with tyrannosauroids, and it can be assumed that its maxillary growth trajectory would have been similar to the plesiomorphic condition for tetanurans, i.e. with an anteroposterior lengthening of the rostrum coupled with little dorsoventral expansion. Without an adult specimen to assess the full extent of this shape change, it is unclear what the endpoint of rostral elongation was in *Aorun*, but we speculate that the adult skull was even longer and lower than that of the juvenile, which would indicate a longirostrine adult morphology perhaps similar to *Haplocheirus*.

The maxillary fenestra of *Aorun* is particularly large, occupying more than 50% of the recessed area of the anterior end of the antorbital fossa. The size of this fenestra is more similar to those of some maniraptorans (e.g. *Erlikosaurus*: Clark *et al.* 1994) than to other basal coelurosaurs and non-coelurosaurian tetanurans. In *Allosaurus* the relative size of the maxillary fenestra decreases during ontogeny (Rauhut & Fechner 2005). In tyrannosaurids the maxillary fenestra increases in relative size during ontogeny (Carr 1999). In troodontids the fenestra becomes anteroposteriorly long and dorsoventrally low during ontogeny, commensurate with changes in rostrum shape, but the overall amount of fenestrated maxilla remains approximately constant. Because of this variation in the development of the maxillary fenestra in tetanurans, it is impossible to predict its relative size in adult specimens of *Aorun*.

The holotype of *Aorun* has approximately 12 maxillary tooth positions, a number similar to hatchling *Allosaurus* (Rauhut & Fechner 2005) and *Byronosaurus* (Bever & Norell 2009) specimens. In *Allosaurus* tooth count increases moderately from 13 in the hatchling to 16 in the adult (Rauhut & Fechner 2005). Embryonic therizinosauroids described by Kundrat *et al.* (2008) have eight dentary tooth positions, whereas adult therizinosauroids have at least 20 (e.g. *Erlikosaurus*: Clark *et al.* 1994; *Falcarius*: Kirkland *et al.* 2005), suggesting that tooth count increases greatly during ontogeny in this group. Likewise, if the perinate *Byronosaurus* specimens described by Bever & Norell (2009) are conspecific with *B. jaffeei*, then maxillary tooth count increases at least two-fold during development in that taxon. Ontogeny in the hyperdentate coelurosaur groups Ornithomimosauria (e.g. *Pelecanimimus*: LH 777) and Alvarezsaurioidea is poorly known, but based on the information from therizinosauroids and troodontids, it seems likely that an increase in tooth number occurred during their ontogeny. In contrast, in some members of Tyrannosauridae tooth count decreases

by three or four maxillary positions during ontogeny (Carr 1999), but in *Tarbosaurus bataar* tooth count is preserved throughout ontogeny (Tsuihiji *et al.* 2011). Although *Aorun* lacks apomorphies that would place it within Troodontidae, Ornithomimosauria or Therizinosauroida, it bears relatively small teeth, as in hyperdentate coelurosaur groups. It is therefore possible that adult specimens of this taxon had many more teeth, potentially up to double the number observed in the holotype, and this could in the future be phylogenetically informative.

The low, laterally restricted ascending process of the astragalus is of particular interest in *Aorun* because this feature is generally a characteristic of non-coelurosaurian theropods. Oddly, in *Aorun* the ascending process does not completely fill the astragal groove on the anterior surface of the tibia. An incompletely ossified ascending process of the astragalus is common in hatchling palaeognath birds (Maxwell & Larsson 2009), and it is possible that the ascending process of the astragalus in the holotype of *Aorun* is incompletely ossified, and that the cartilaginous section of this bone creates a facet on the anterior tibia prior to complete ossification. If this is the case in *Aorun*, adult animals might be expected to have a very tall ascending process, as is more typical of coelurosaurs, albeit one that is restricted to the lateral half of the anterior tibia. However, embryonic specimens of *Troodon formosus* have the distinctly flat anterior tibial surface that is a synapomorphy of coelurosaurian theropods (Varrichio *et al.* 2002; Rauhut 2003a). Therefore, it is unlikely that the morphology of the tibiotarsal region in *Aorun* underwent dramatic postnatal changes that would have resulted in a more typical coelurosaurian morphology in adults.

### Anatomical discussion

*Aorun* presents an intriguing mixture of plesiomorphic and derived features within Coelurosauria. Features of the astragalus and distal tibia are among the most important for distinguishing coelurosaurs from non-coelurosaurian tetanurans (Rauhut 2003a; Choiniere *et al.* 2010a), and *Aorun* presents potentially apomorphic morphology in this region as well as features that are suggestive of phylogenetic affinities not recovered in our phylogenetic analysis.

The anterolateral surface of the tibia of *Aorun* bears a deep, mediolaterally narrow groove extending far proximally and partially occupied by the ascending process of the astragalus. The anterior surfaces of the tibiae in the Australian theropod *Kakuru* (Molnar & Pledge 1980), the Chinese theropod *Tugulusaurus* (Rauhut & Xu 2005), and the London (NHMUK 37001) but not the Thermopolis *Archaeopteryx* (Mayr *et al.* 2005) bear similarly tall, mediolaterally narrow grooves. The ascending process of the astragalus of *Aorun* is low and restricted to the lateral side of the tibia, similar to the condition of most non-coelurosaurian theropods, e.g. *Megapnosaurus* (Raath 1977), *Abelisauroida* (Rauhut 2005) and *Neovenator*

(Brusatte *et al.* 2008). In contrast, most coelurosaurs have a mediolaterally wide, proximodistally tall ascending process (Rauhut 2003a), but similar to most coelurosaurs including *Tugulusaurus* (Rauhut & Xu 2005), the ascending process of the astragalus in *Aorun* is separated from the astragal condyles by a groove. In *Tugulusaurus*, regarded as the basalmost coelurosaur by Rauhut & Xu (2005), the ascending process is laterally restricted and low. In *Guanlong* (IVPP V14531) and *Coelurus* (YPM 2010) the ascending process is limited to the lateral half of the anterior tibia by a rounded medial tibial ridge. It is possible that the anterior tibial groove in *Aorun* articulates with a cartilaginous extension of the ascending process of the astragalus that had yet to fully ossify in the holotype. If the ascending process indeed filled the groove, then the morphology of the adult form of the ascending process of *Aorun* would be autapomorphically tall proximodistally, and thin mediolaterally, more similar to derived coelurosaurs like *Archaeopteryx* than non-coelurosaurian theropods. Thus, the tibia and astragalus present a conflicting suite of characters for determining the phylogenetic affinities of *Aorun*.

Other features of the skeleton of *Aorun* are suggestive of a relatively derived position within Coelurosauria. The dorsoventrally flat nasal processes of the premaxilla are only known in maniraptoran theropods, e.g. *Haplocheirus* (Choiniere *et al.* 2010b). The teeth of *Aorun* are distinctive, either bearing no serrations (premaxillary and some dentary teeth), or bearing very fine serrations (~10/mm) only on the distal carinae (maxillary teeth and some dentary teeth). Although the distribution of serrations on the teeth of *Aorun* may only represent a transient juvenile morphology, in embryonic therizinosauroids (Kundrat *et al.* 2008) and in *Byronosaurus* perinates (Bever & Norell 2009) the teeth closely resemble those of adults in the pattern of dental serrations. Within Coelurosauria, serrations are absent on the teeth of avialans (e.g., *Archaeopteryx*: Elzanowski & Wellnhofer 1996), many troodontids (Makovicky & Norell 2004), basal ornithomimosaurids (e.g., *Pelecanimimus*: Perez-Moreno *et al.* 1994; *Shenzhousaurus*: Ji *et al.* 2003; and *Harpymimus*: Kobayashi & Barsbold 2005a), the oviraptorosaur *Caudipteryx* (Ji *et al.* 1998), and parvicursorine alvarezsauroids (Perle *et al.* 1993; Chiappe *et al.* 1998), and this may argue for affinities of *Aorun* to one of these groups if serrations are lost during ontogeny. However, the distal carinae of the maxillary teeth of *Megapnosaurus rhodesiensis* also bear very fine serrations (M. Carrano, pers. comm.), and thus if serrations are not lost during ontogeny in *Aorun*, then the dental morphology is not necessarily evidence for its coelurosaurian affinities.

Opisthocoelous cervical vertebrae are present in a number of large-bodied basal tetanurans, but among small-bodied theropods they are only known in *Aorun*, some alvarezsauroids (Chiappe *et al.* 2002) and *Compsognathus* (Ostrom 1978; Peyer 2006). The condition in *Aorun* more closely resembles the weakly opisthocoelous condition of

the latter taxon. Based on the phylogenetic position recovered in this analysis, the condition in *Aorun* is independently derived.

The manus of *Aorun* is of particular interest. The gracile hand of *Aorun* with particularly thin metacarpals III and IV is more similar to the hands of derived non-avian coelurosaurs (Gishlick & Gauthier 2007) than to the hands of more basal theropods, where digit III is generally robust and proximally expanded (Rauhut 2003a). Metacarpal II is mediolaterally wider than the other metacarpals, and its first phalanx has a diameter greater than that of the radius, as in alvarezsauroids (Choiniere *et al.* 2010b) and compsognathids (Currie & Chen 2001; Hwang *et al.* 2004; Dal Sasso & Maganuco 2011). Manual ungual II-2 is much larger than the other manual unguals, a feature characteristic of all alvarezsauroids (Choiniere *et al.* 2010b). Manual unguals III-3 and IV-4 have reduced curvature, a feature only known in derived therizinosauroids (Clark *et al.* 2004; Zanno 2010), ornithomimosaurids (Makovicky *et al.* 2004) and parvicursorine alvarezsauroids (Suzuki *et al.* 2002). Although developmental changes in the ungual are a possibility, in embryonic therizinosauroids the ungual morphology is nearly identical to the adult phenotype (Kundrat *et al.* 2008).

Although our phylogenetic analysis did not recover a position for *Aorun* within any established coelurosaurian higher taxon, the holotype presents a suite of features that suggest membership in Alvarezsauroida or perhaps Ornithomimosauria. The long, low skull and hyperdentate dentary suggest alvarezsauroid (Choiniere *et al.* 2010b) or basal ornithomimosaurian (Perez-Moreno *et al.* 1994) affinities. The presence of opisthocoelous cervical vertebrae is only known for alvarezsauroids within Coelurosauria (Choiniere *et al.* 2010b). The increase in size of the first manual digit and the reduction in curvature and size of the lateral manual unguals are features known in alvarezsauroids (Perle *et al.* 1993, 1994; Suzuki *et al.* 2002; Choiniere *et al.* 2010b). Because some of these features are present in other coelurosaurian groups, their presence in *Aorun* does not necessarily argue for membership in Alvarezsauroida. Nevertheless, should more skeletal material of this taxon be uncovered, it would be unsurprising if it showed alvarezsauroid or ornithomimosaurian features.

## Conclusions

Although its exact phylogenetic affinities are unclear, perhaps because of its early ontogenetic stage, we hypothesize *Aorun* to be a relatively basal coelurosaur. *Aorun* provides new information on the morphology of basal coelurosaurs from the Middle–Late Jurassic. It lends insight into the morphology of ontogenetically young basal coelurosaurs, which is poorly documented. *Aorun* is the

seventh theropod and fourth coelurosaur known from the Shishugou Formation, and is a member of one of the most phylogenetically and trophically diverse late Middle to early Late Jurassic theropod faunas known. The fauna of the Shishugou Formation differs markedly in its composition from other Late Jurassic theropod faunas worldwide.

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## Supplementary material

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