



A new, three-dimensionally preserved enantiornithine bird (Aves: Ornithothoraces) from Gansu Province, north-western China

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Received 19 August 2009; accepted for publication 20 April 2010

In recent years, the Lower Cretaceous (Aptian) Xiagou Formation has yielded approximately 100 avian partial skeletons, many with soft-tissue traces, from sites in the Changma Basin of Gansu Province, north-western China. The most abundant taxon amongst these is the ornithuromorph *Gansus yumenensis*, but enantiornithines have also been identified in the sample. Here we describe two incomplete, semi-articulated appendicular skeletons, the first consisting of a partial left pelvic girdle and complete pelvic limb, and the second comprised of a nearly complete right pelvic limb. Both specimens bear characteristics diagnostic of Enantiornithes, and are referred to a new taxon, *Qiliania graffini* gen. et sp. nov. The exceptional, three-dimensional preservation of these specimens (compared to the crushed, nearly two-dimensional condition of most other Early Cretaceous avian fossils) reveals new information regarding enantiornithine anatomy, evolution, and diversity.

© 2011 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2011, **162**, 201–219.
doi: 10.1111/j.1096-3642.2010.00671.x

ADDITIONAL KEYWORDS: anatomy – Aptian – Changma Basin – diversity – Early Cretaceous – Enantiornithes – evolution – phylogeny – *Qiliania graffini* gen. et sp. nov. – Xiagou Formation.

INTRODUCTION

Enantiornithines were the dominant avian clade during the Cretaceous, with over 50 genera named to

date. Fossils belonging to the group have been collected from every continent except Antarctica (Chiappe, 2007). The Early Cretaceous enantiornithine record is largely limited to China and Spain, but accounts for approximately half of the generic diversity of the clade and includes many of the most complete and informative specimens yet discovered (e.g. Chiappe & Walker, 2002; Sanz *et al.*, 2002; Chang *et al.*, 2003). Contributions from China have

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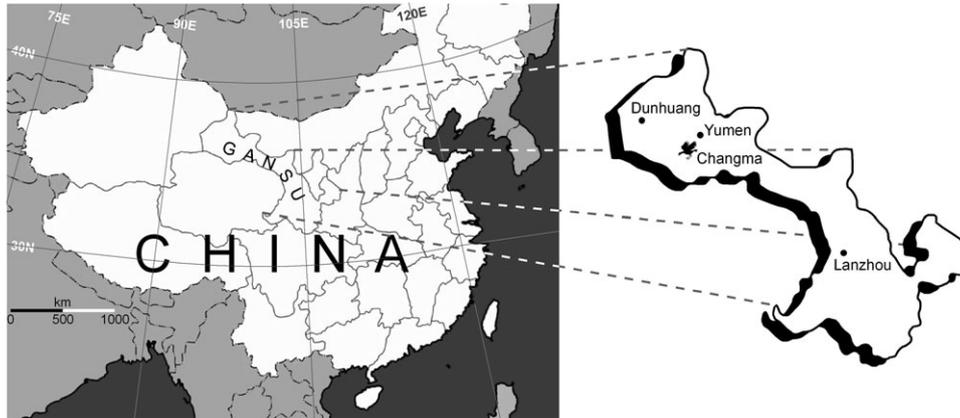


Figure 1. Locality (indicated by avian silhouette) from which FRDC-04-CM-006 and FRDC-05-CM-006 were recovered, near Changma, north-western Gansu Province, China.

been particularly important in revealing enantiornithine diversity, and are largely responsible for the tripling of the number of known species of these birds over the past three decades (Zhou & Hou, 2002; Zhou & Zhang, 2006a; Chiappe, 2007).

The majority of Chinese enantiornithines have come from the Lower Cretaceous Jehol Group, which consists of two units: the Jiufotang Formation and the underlying Yixian Formation. The Jiufotang Formation has produced such enantiornithine taxa as *Sinornis santensis* (Serenó & Rao, 1992; Zhou, Jin & Zhang, 1992; Zhou, 1995a; Sereno, Rao & Li, 2002), *Bolouchia zhengi* (Zhou, 1995b), *Longipteryx chaoyangensis* (Zhang *et al.*, 2001), *Eocathayornis walkeri* (Zhou, 2002), *Dapingfangornis sentisorhinus* (Li *et al.*, 2006), *Alethoalaornis agitornis* (Li *et al.*, 2007), *Pengornis houi* (Zhou, Clarke & Zhang, 2008), and *Rapaxavis pani* (Morschhauser *et al.*, 2009). The Yixian Formation, although most famous for its abundant specimens of the basal pygostylian *Confuciusornis sanctus* (Hou *et al.*, 1995), has also yielded a number of enantiornithines, including *Eoenantiornis buhleri* (Hou *et al.*, 1999), *Longirostravis hani* (Hou *et al.*, 2004), *Vescornis hebeiensis* (Zhang, Ericson & Zhou, 2004), *Dalingheornis liweii* (Zhang *et al.*, 2006b), *Paraprotopteryx gracilis* (Zheng, Zhang & Hou, 2007), and *Shanweinia cooperorum* (O'Connor *et al.*, 2009). Enantiornithine specimens from the Jehol Group, although frequently consisting of complete or nearly complete skeletons, are typically poorly preserved and crushed flat, often with bones broken between a slab and a counterslab. Thus, although this unit has yielded abundant information on the taxonomic diversity and palaeoecological specializations of Enantiornithes during the Early Cretaceous, data regarding the three-dimensional osteology of the clade have been scarcer.

In 1981, exposures of the Lower Cretaceous Xiagou Formation in the Changma Basin of north-western Gansu Province (Fig. 1) produced the first published Mesozoic avian fossil from China: the holotypic distal left pelvic limb of the ornithuromorph *Gansus yumenensis* (Hou & Liu, 1984). Renewed field efforts in the Changma Basin beginning in 2002 have produced dozens of additional bird fossils, predominantly more completely preserved specimens of *G. yumenensis* (You *et al.*, 2006). Enantiornithines have been collected as well, although in comparison to *Gansus*, specimens of these archaic birds have been far fewer in number and generally less complete. Changma enantiornithine specimens described to date include an isolated left pectoral girdle and limb (You *et al.*, 2005), another nearly complete left pectoral limb (Harris *et al.*, 2006), and a third partial skeleton consisting of a fragmentary pelvic girdle and largely complete pelvic limbs (Lamanna *et al.*, 2006b).

The avifauna of the Jehol Biota is diverse, encompassing basal forms such as *Jeholornis prima*, *Sapeornis chaoyangensis*, and *Confuciusornis* alongside a host of more derived enantiornithines and basal ornithuromorphs (Chiappe & Dyke, 2006; Zhou & Zhang, 2006a). Conversely, fossils recovered from Changma thus far suggest that the Xiagou avifauna was overwhelmingly dominated by *Gansus*, with non-ornithothoracine birds absent and enantiornithines present but much less common (You *et al.*, 2006). Moreover, none of the few described enantiornithine specimens from Changma have been considered to be referable to taxa less inclusive than Enantiornithes (You *et al.*, 2005; Harris *et al.*, 2006; Lamanna *et al.*, 2006b). In this context, Changma enantiornithine material that is diagnostic to the species level is of considerable interest. Here we describe a new enantiornithine species based on two semi-articulated,

partial appendicular skeletons recovered from exposures of the Xiagou Formation at Changma. Coupled with previous discoveries of Enantiornithes from these strata and from the Jehol Group, the new taxon indicates that this avian clade was diverse and widespread across northern China during the Early Cretaceous.

GEOLOGICAL SETTING

Cretaceous sedimentary strata exposed in the Changma Basin belong to the Lower Cretaceous Xiagou and Zhonggou formations, which together comprise the Xinminpu Group (Bureau of Geology and Mineral Resources of Gansu Province, 1989, 1997; Editorial Committee of Chinese Stratigraphic Standard: Cretaceous, 2000; Tang *et al.*, 2001). The fossil-bearing beds of the Xiagou Formation exposed at Changma consist mainly of yellowish-brown, fissile mudstones that have yielded specimens of plants, bivalves, gastropods, ostracodes, conchostracans, insects, fishes, a salamander, turtles, and birds (Bureau of Geology and Mineral Resources of Gansu Province, 1989; Lamanna *et al.*, 2006a, b; You *et al.*, 2006; Murray, You & Peng, 2010). In general terms, this assemblage is comparable to the *Eoestheria–Epicharmeropsis–Lycoptera* fauna (Chang *et al.*, 2003; Huang *et al.*, 2007) of the Jehol Biota. However, the abundant Jehol fish *Lycoptera* has not been recorded from the Xiagou Formation, but is present in the underlying Chijinpu Formation, suggesting that the former unit may be slightly younger than the Jehol Group (You *et al.*, 2006). A recent chemostratigraphical study (Suarez *et al.*, 2008) suggests an early Aptian age (Ogg, Ogg & Gradstein, 2008) for the bird fossil-bearing section at Changma, whereas K-Ar radiometric dates taken elsewhere in the basin imply a middle-late Aptian age (~118.8–112.8 Myr; Li & Yang, 2004). Collectively, the evidence indicates that the Cretaceous bird-bearing strata of the Changma Basin are comparable in age to, or perhaps slightly younger than, the upper unit of the Jehol Group, the Jiufotang Formation [Aptian (Eberth *et al.*, 1993; He *et al.*, 2004; Chang *et al.*, 2009)] and younger than the Yixian Formation [Barremian-early Aptian (Smith *et al.*, 1995; Swisher *et al.*, 1999, 2001; Niu *et al.*, 2004; Zhang *et al.*, 2006a; Yang, Li & Jiang, 2007; Chang *et al.*, 2009)].

INSTITUTIONAL ABBREVIATIONS

CAGS-IG, Chinese Academy of Geological Sciences, Institute of Geology, Beijing; DNHM, Dalian Natural History Museum, Dalian; FRDC, Fossil Research and Development Center, Third Geology and Mineral Resources Exploration Academy, Gansu Provincial Bureau of Geo-Exploration and Mineral Development,

Lanzhou; GMV, National Geological Museum of China, Beijing; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; LH, Museo de las Ciencias de Castilla-La Mancha, Cuenca; MTM, Magyar Természettudományi Múzeum, Budapest; NIGP, Nanjing Institute of Geology and Paleontology, Nanjing; PKUP, Peking University Paleontological Collection, Beijing; PVL, Fundación Instituto Miguel Lillo, Tucumán.

SYSTEMATIC PALAEOLOGY

AVES LINNAEUS, 1758

ORNITHOTHORACES CHIAPPE, 1996

ENANTIORNITHES WALKER, 1981

QILIANIA GEN. NOV.

Etymology: Qilian ('heaven' in the language of the Xiongnu, an ancient confederation of nomadic tribes that inhabited central Asia), for the Qilian Mountains that lie to the south of the Changma Basin. The generic name is fashioned after that of the only other fossil bird thus far named from Changma, *Gansus*, in that it refers to a local geographical feature but eschews a traditional avian suffix. Pronunciation: CHEE-lee-AH-nee-uh.

Type species: *Qiliana graffini* sp. nov. (by monotypy).

Diagnosis: As for the type and only known species, given below.

QILIANIA GRAFFINI SP. NOV.

Holotype: FRDC-05-CM-006, a nearly complete left pelvic girdle and limb, lacking only the preacetabular portion of the ilium and the femoral head. The specimen is completely articulated save for the pelvic girdle and femur, which have been slightly displaced (Fig. 2).

Type horizon: Xiagou Formation, Lower Cretaceous [Aptian (Li & Yang, 2004; You *et al.*, 2006; Suarez *et al.*, 2008)].

Type locality: Near the town of Changma, in the Changma Basin of Gansu Province, north-western China. Precise locality information is available to qualified researchers upon request.

Referred material: FRDC-04-CM-006, a partial right pelvic limb consisting of the femur missing its proximal end, the complete tibiotarsus, and the tarsometatarsus lacking its distal end (Figs 3, 4). Upon discovery, the specimen was partially articulated, but it has since been disarticulated and prepared free of matrix to facilitate study.

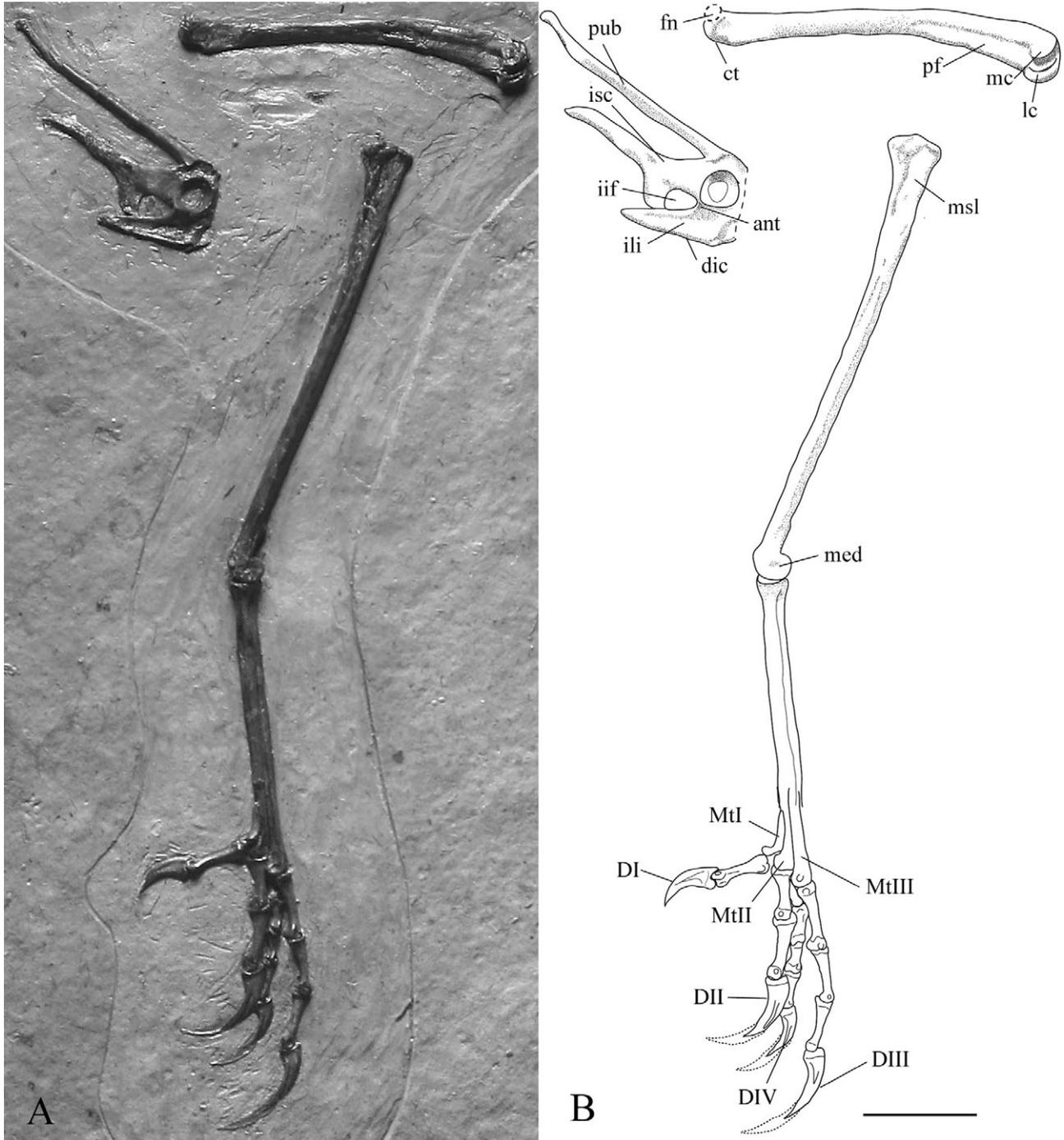


Figure 2. Holotype (FRDC-05-CM-006) of *Qiliania graffini* gen. et sp. nov., a nearly complete left pelvic girdle and limb. A, photograph; B, interpretive drawing. Abbreviations: ant, antitrochanter; ct, caudal trochanter; DI, digit I; DII, digit II; DIII, digit III; DIV, digit IV; dic, dorsal iliac crest; fn, femoral neck; iif, ilioischial foramen; ili, ilium; isc, ischium; lc, lateral condyle; mc, medial condyle; med, medial epicondylar depression; MtI, metatarsal I; MtII, metatarsal II; MtIII, metatarsal III; MtIV, metatarsal IV; pf, popliteal fossa; pub, pubis. Dashed lines indicate areas of broken bone; thin lines extending from the unguals indicate impressions of keratinous claw sheaths. Scale bar = 1 cm.

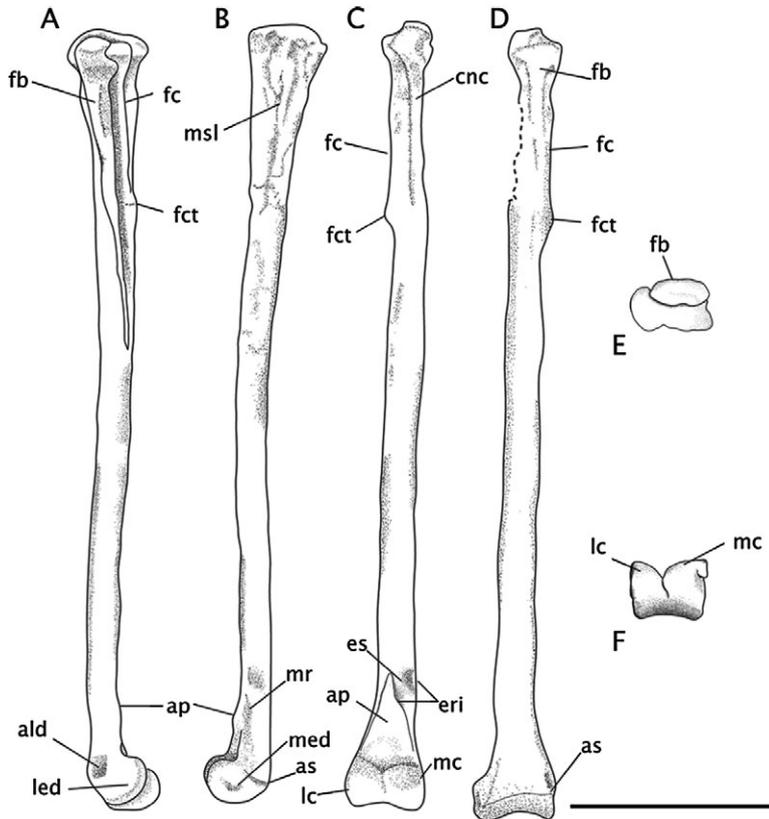


Figure 3. Interpretive drawings of the right tibiotarsus of the referred specimen of *Qiliania graffini* gen. et sp. nov. (FRDC-04-CM-006). A, lateral view; B, medial view; C, cranial view; D, caudal view; E, proximal view; F, distal view. Abbreviations: ald, accessory lateral depression; ap, ascending process of astragalus; as, astragalal synostosis; cnc, cnemial crest; eri, extensor retinaculum insertions; es, extensor sulcus; fb, fibula; fc, fibular crest; fct, fibular crest tubercle; lc, lateral condyle; led, lateral epicondylar depression; mc, medial condyle; med, medial epicondylar depression; mr, medial ridge; msl, medial sulcus. Dashed lines indicate broken bone. Scale bar = 1 cm.

Etymology: In honour of Dr Gregory Graffin, lecturer at the University of California, Los Angeles and co-founder of the musical group Bad Religion, for his contributions to evolutionary biology, his public outreach through music, and his inspiration to young scientists around the world.

Diagnosis: *Qiliania graffini* is distinguished from other presently known enantiornithines by its possession of the following autapomorphies: distal quarter of pubis deflected ventrally; tibiotarsus very long and slender, with mid-shaft mediolateral width to proximo-distal length ratio of less than 0.05 and proximo-distal length 133% that of femur; tibiotarsus with craniocaudally elongate and subrectangular proximal articular surface, well-developed cnemial crest, and deep distolateral fossa; and tarsometatarsus very long and slender (63% of proximo-distal length of tibiotarsus). The taxon is further diagnosed by the following unique combination of apomorphies that occur, individually or in subsets, in other enantiorni-

thine taxa: deeply excavated medial epicondylar depression and shallower lateral epicondylar depression on the distal tibiotarsus; distinct fibula fully fused to tibiotarsus; plantarily excavated tarsometatarsus; pedal unguals and associated keratinous sheaths relatively straight; and pedal ungual IV reduced (see Comparisons).

DESCRIPTION

GENERAL

Specimen FRDC-04-CM-006 has been prepared entirely free of matrix (and, notably, is one of the very few Early Cretaceous enantiornithine specimens that is currently in such a condition); specimen FRDC-05-CM-006 remains articulated and embedded in matrix, with the pelvic limb exposed in medial view and the pelvic girdle in lateral view. The complete fusion of the proximal tarsals to the tibia in both specimens indicates that they probably pertain to adult individuals.

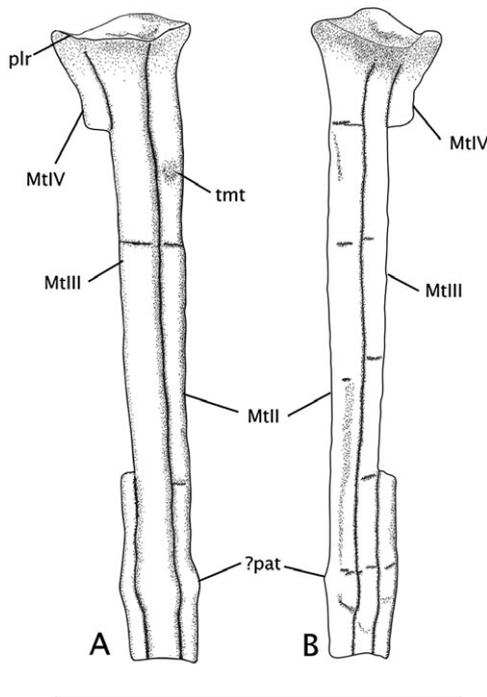


Figure 4. Interpretive drawings of the right tarsometatarsus of the referred specimen of *Qiliania graffini* gen. et sp. nov. (FRDC-04-CM-006). A, dorsal view; B, plantar view. Abbreviations: ?pat, pathologic swelling; MtI, metatarsal I; MtII, metatarsal II; MtIII, metatarsal III; MtIV, metatarsal IV; plr, proximolateral ridge; tmt, tubercle for attachment of the *M. tibialis cranialis*. Scale bar = 2 cm.

Their small sizes are therefore probably not ontogenetic artefacts.

PELVIC GIRDLE

Specimen FRDC-05-CM-006 preserves a nearly complete left pelvic girdle that lacks only the preacetabular portion of the ilium (Fig. 2). The pelvic girdle elements are fully fused. The postacetabular wing of the ilium is subtriangular in lateral view, tapering caudally, and is gently excavated throughout its length, forming a shallow lateral concavity that is bordered dorsally by a straight and delicate dorsal iliac crest. The presence of a laterally projecting supraacetabular tubercle is ambiguous because of the breakage of the cranial portion of the ilium.

A crest circumscribes the margin of the acetabulum, forming a distinct lip. The caudodorsal rim of this lip tapers into a very prominent, strongly laterally projecting antitrochanter. The lateral acetabular opening is greater in diameter than its medial counterpart. The pubic and ischial peduncles of the ilium cannot be clearly distinguished from the proximal extremes of the pubis and ischium, respectively. Caudal to the antitrochanter, the ilioischadic foramen is caudally

demarcated by the prominent dorsal process of the ischium. The dorsal process contacts the ilium ventromedially but remains unfused. The ilioischadic foramen is subtriangular in outline, with a craniocaudal diameter of 2.24 mm and a dorsoventral diameter of 1.78 mm. It is thus considerably smaller than the acetabulum, the lateral margin of which has a roughly uniform diameter of 2.36 mm.

Distal to the dorsal process, the ischium is knife-like, narrowing slightly in craniocaudal dimension distally and lacking an obturator process. The distal-most tip of the ischium is abraded, but it seems unlikely that the bone extended much farther. The distal one-fifth of the ischium is deflected slightly dorsally. There also appears to have been a laterally projecting crest on the ischium that has been obscured by crushing.

The very thin, long, rod-shaped pubis terminates in a small tubercle rather than a distinct boot. Most of the shaft of the pubis is orientated parallel to that of the ischium; however, the distal-most portion of the former is gently ventrally deflected. The pubis is not mediolaterally compressed.

FEMUR

Femora are nearly completely preserved and broken at essentially identical points along the distal shaft in both specimens. The femur of FRDC-05-CM-006 lacks only the head, which has been broken off the small yet distinct femoral neck (Fig. 2); that of FRDC-04-CM-006 is missing the entire proximal end. The caudolateral margin of the proximal femur bears a distinct caudal (=‘posterior’) trochanter, an enantiornithine apomorphy (Chiappe & Walker, 2002). The trochanter angles caudolaterally, away from the head of the femur. The femoral shaft is bowed in the cranial direction, most strongly so distally.

As observed in caudal view, the prominent popliteal fossa extends nearly to midshaft. Distally, this fossa continues as a shallow groove between the two condyles. The distal ends of the femora of both specimens have been crushed caudomedially, rendering the condyles unusually angular and distorting the morphology of the end of the bone. The lateral and medial condyles are prominent in caudal view, subrectangular in shape, and subequal in size. A weakly developed fibular trochlea appears to be present. The distolateral margin of the femur lacks the caudal projection present in some enantiornithines (e.g. PVL 4037; Chiappe & Walker, 2002). A prominent lateral epicondyle is visible on the femur of FRDC-04-CM-006, and is fully distinct from the lateral condyle.

TIBIOTARSUS AND FIBULA

The tibiotarsus of FRDC-05-CM-006 is complete, essentially undamaged, and mainly exposed in medial

Table 1. Measurements (mm) of elements preserved in FRDC-04-CM-006 and FRDC-05-CM-006; all measurements are of proximodistal length unless otherwise specified

Dimension	CAGS-IG-04-CM-006	CAGS-IG-05-CM-006
Pubis	–	17.5
Ischium	–	11.5
Femur	–	24.3
Tibiotarsus	32.4	32.2
Tibiotarsus (craniocaudal width at midshaft)	1.47	1.4
Fibula	7.9	–
Tarsometatarsus	–	20.3
Tarsometatarsus (mediolateral width at midshaft)	2.0	–
Metatarsal I	–	3.2
Metatarsal II	–	19.2
Metatarsal III	–	20.3
Metatarsal IV	–	–
Pedal phalanx I-1	–	4.2
Pedal phalanx I-2 (ungual)	–	4.4
Pedal phalanx I-2 (with sheath)	–	6.8
Pedal phalanx II-1	–	3.7
Pedal phalanx II-2	–	4.8
Pedal phalanx II-3 (ungual)	–	4.9
Pedal phalanx II-3 (with sheath)	–	8.0
Pedal phalanx III-1	–	4.6
Pedal phalanx III-2	–	4.0
Pedal phalanx III-3	–	4.2
Pedal phalanx III-4 (ungual)	–	5.8
Pedal phalanx III-4 (with sheath)	–	9.1
Pedal phalanx IV-1	–	–
Pedal phalanx IV-2	–	2.3
Pedal phalanx IV-3	–	2.4
Pedal phalanx IV-4	–	2.8
Pedal phalanx IV-5 (ungual)	–	4.4
Pedal phalanx IV-5 (with sheath)	–	8.2

view, with some cranial and caudal morphologies also discernable (Fig. 2). The FRDC-04-CM-006 tibiotarsus is also complete, but appears to have been diagenetically distorted to a degree that is difficult to ascertain (Fig. 3). The tibia and proximal tarsals are fully fused, forming a true tibiotarsus. The proximal half of the shaft is widest craniocaudally, whereas the distal portion is broadest mediolaterally. The tibiotarsus of *Qiliania* is long and slender, with a midshaft width to element length ratio of 23:1, and a femoral to tibiotarsal length ratio of 3:4 (Table 1).

The proximal articular surface of the tibiotarsus is subrectangular in contour and orientated perpendicular to the shaft. Laterally, in FRDC-04-CM-006, the undamaged fibula is articulated with, and fully fused to, the tibiotarsus. Cranial to the fibula lies a pronounced fibular crest that appears to have been slightly crushed cranially. The fibular crest is relatively short, extending distally approximately 8 mm (about one-quarter of the total length of the tibiotar-

sus) and ending in a cranially projecting tubercle for the insertion of the *M. iliofibularis*. The fibula is longer, measuring 13.4 mm in length, but it tapers sharply, becoming narrow and splint-like distal to the fibular crest. There is a well-developed cnemial crest on the craniomedial surface of the proximal tibiotarsus of FRDC-04-CM-006; because the cnemial crest of enantiornithines is typically low and poorly developed, *Q. graffini* is unusual in this respect. Medially, there is a deep sulcus on the proximal end of the tibiotarsal shaft. Although this structure may have been exaggerated by crushing, its presence in both specimens suggests that it is a true feature of this taxon.

Proximal to the distal condyles, on the craniomedial margin of the tibiotarsus, a tubercle medially demarcates a shallow groove that is laterally bordered by the raised ascending process of the astragalus. This is interpreted as the sulcus for the tendon of the *M. extensor digitorum longus* and the *M. tibialis crania-*

lis, with the craniomedial tubercle and the ascending process representing the insertions for the extensor retinaculum. The former of these hypothesized insertion sites lies proximal to the latter; this proximodistal ‘staggering’ lends support to our interpretation of these areas as extensor retinaculum insertion sites because this retinaculum is orientated obliquely in modern birds (Baumel & Witmer, 1993) and possibly also the Cretaceous ornithuromorph *Apsaravis ukhaana* (Clarke & Norell, 2002). The astragalar ascending process is expressed in relief on the cranial margin of the tibiotarsus and is therefore visible in mediolateral view. Distally, in caudal view, the synostosis marking the fusion of the astragalus to the tibia is also faintly visible. In FRDC-04-CM-006, the distal-most portion of the tibiotarsus abruptly expands mediolaterally to nearly twice the width of the shaft.

The medial and lateral distal condyles are prominent in cranial view. The medial condyle is slightly wider mediolaterally and deeper proximodistally than its lateral counterpart, although this difference is subtle. The intercondylar sulcus is present but shallow, and is orientated slightly proximolaterally–distomedially, oblique to the long axis of the tibiotarsal shaft. Because this sulcus is shallow, the distal condyles taper smoothly toward each other, forming an hourglass shape in craniodistal view. The medial surface of the medial condyle is deeply excavated by a circular epicondylar depression. In the FRDC-04-CM-006 tibiotarsus, the lateral surface of the lateral condyle is embayed by a shallower lateral epicondylar depression. As on the medial side, this depression is bordered caudally by an epicondyle; the lateral side, however, bears an additional excavation – much deeper than either of the epicondylar depressions and otherwise unknown within enantiornithines – slightly proximocaudal to the epicondyle. This lateral depression is bordered by a raised, rugose area formed by the fusion of the proximal tarsals and the tibia that is continuous with the lateral margin of the ascending process. The placement of these structures suggests that they are functionally analogous to the *M. fibularis* sulcus and retinacular tubercle of modern birds, respectively.

TARSOMETATARSUS

The tarsometatarsus of FRDC-05-CM-006 is complete and exposed in medial view (Fig. 2). That of FRDC-04-CM-006 is free of matrix but incomplete distally, with metatarsal I and much of the shaft of metatarsal IV also missing (Fig. 4). The mediolateral width of the tarsometatarsus is greatest at the proximal end; it tapers distally, but a distal expansion would presumably be observed were the tarsometatarsus of FRDC-

04-CM-006 complete or that of FRDC-05-CM-006 not embedded in matrix. The proximal ends of metatarsals II–IV are fully fused to the distal tarsals and to each other. Although unfused throughout the remainders of their lengths, these metatarsals firmly abut one another, exhibiting no vascular foramina (at least as far as can be determined, given the incomplete preservation of one tarsometatarsus and the partial exposure of the other; Figs. 2, 4). In proximal view, the articular cotyles of the FRDC-04-CM-006 tarsometatarsus are similar in size, although the medial is slightly larger and the lateral more deeply concave. In addition, the lateral margin of the lateral cotyle is developed into a proximolaterally projecting ridge that extends almost as far proximally as does the intercotylar area.

The tarsometatarsus is slender, with a mid-shaft mediolateral width to total proximodistal length ratio of approximately 10:1 [calculated using the mid-shaft tarsometatarsal width of the referred specimen and the tarsometatarsal length of the holotype, and assuming closely similar tarsometatarsal dimensions in both specimens given their nearly identical tibiotarsal lengths (Table 1)]. Metatarsal IV is mediolaterally thinner than metatarsals II and III, a synapomorphy of Enantiornithes. In plantar aspect, metatarsal II appears to be wider than metatarsal III, and the proximal ends of metatarsals II–IV are flat (Fig. 4). In dorsal view, in contrast, metatarsal III appears wider than metatarsal II, and all metatarsals have significantly more rounded morphologies, although metatarsal III lacks the strong dorsal convexity of some enantiornithines (Chiappe & Walker, 2002). Thus, all three metatarsals are semi-circular in cross-section. Metatarsals II–IV appear dorsoplantarly coplanar throughout most of their lengths. Nevertheless, their distal ends are missing in FRDC-04-CM-006; moreover, in FRDC-05-CM-006, the distal end of metatarsal II is plantarily displaced with respect to that of metatarsal III. The plantar surface of the middle one-third of the tarsometatarsus bears a shallow excavation that is bordered medially by a plantar swelling of the midshaft of metatarsal II. The lateral margin of this excavation is not clearly defined. This morphology may represent a plesiomorphic, incipiently developed homologue of the flexor sulcus seen in modern birds. Metatarsal III is the longest of the metatarsals, but because of the incomplete nature of the tarsometatarsus of FRDC-04-CM-006 and the angle of exposure of that of FRDC-05-CM-006, the lengths of metatarsals II and IV relative to each other cannot be determined. At approximately one-fifth of the length from its proximal end, the dorsal surface of metatarsal II bears a tubercle for the attachment of the *M. tibialis cranialis*. Moreover, near its broken distal extreme, the tarsometatarsus of

FRDC-04-CM-006 exhibits a modest swelling that may be pathologic. A similarly, possibly pathological tarsometatarsus is present, but was not explicitly described, in another avian specimen from Changma: CAGS-IG-04-CM-002, referred to *Gansus yumenensis* by You *et al.* (2006: figs 2a, S1a).

Metatarsal I articulates on the plantaromedial surface of metatarsal II in such a way that digit one is reversed. The first metatarsal is also deflected plantarily, such that its proximal and distal articular surfaces are not in the same plane. This lends metatarsal I a J-shape, another synapomorphy of Enantiornithes (Serenó *et al.*, 2002).

PES

The pes is preserved only in the holotype, FRDC-05-CM-006, in which it is complete, articulated, and exposed in medial view (Fig. 2). The pedal phalangeal formula of *Qiliania* is 2-3-4-5-X; the third digit is the longest. Digit II appears to be more robust than the others, as is common within Enantiornithes; however, including the unguis, the phalanges of digit IV are very small relative to those of other digits. This reduced digit IV unguis is highly unusual amongst enantiornithines.

Phalanges II-2 and II-3 are subequal in length and nearly the longest in the foot (shorter only than the unguis of digit III; Table 1). The proximal phalanx of digit II is shorter than the penultimate phalanx, and is more robust than the proximal phalanges of the other digits. Phalanges III-2 and III-3 are nearly equal in length, each significantly shorter than the proximal phalanx of this digit. Phalanges IV-2, IV-3, and IV-4 are relatively shorter and thinner than the other phalanges; they successively increase in length distally, such that phalanx IV-4 is the longest of the three. The proximal phalanx of digit IV is partially obscured by digits II and III, although it appears that this element is similarly short and thin. The unguis phalanges are morphologically heterogeneous; the unguis of digit I is proximodistally shorter than those of digits II and III, but is dorsoplantarly taller. The unguis of digit II is shorter than that of III but more robust. Relative to the other digits, the unguis of digit IV is significantly reduced in proximal dorsoplantar height, although it is the same length as unguis I.

Unguis II–IV retain remnants of their keratinous sheaths; a faint impression of a sheath is also visible surrounding the unguis of digit I. The keratinous sheaths increase the lengths of the claws by up to 57% (Table 1). Surprisingly, the sheaths lack strong curvature and are thin and uniform in diameter, tapering only very distally to fine points.

COMPARISONS

Specimens FRDC-04-CM-006 and FRDC-05-CM-006 are referred to a single avian species based on their essentially identical morphologies and sizes. Moreover, these specimens possess a unique combination of features that justify the erection of the new taxon *Q. graffini*. *Qiliania* can be included within the ornithothoracine clade Enantiornithes because it possesses characters widely regarded as synapomorphies of that group, including a caudal trochanter on the femur (Chiappe & Walker, 2002), a fibular crest that extends approximately one-quarter of the length of the tibiotarsus, a medial distal tibiotarsal condyle that is larger than its lateral counterpart (although in this instance only slightly; Molnar, 1986), a J-shaped metatarsal I (Serenó *et al.*, 2002), a metatarsal III that is proximodistally longer than metatarsals II and IV (Zhang & Zhou, 2000), and a metatarsal IV that is mediolaterally narrower than either metatarsal II or metatarsal III (Zhang *et al.*, 2004).

The vast majority of avian fossils from the Changma Basin pertain to Ornithomorphs, and almost all of these to *Ga. yumenensis* (You *et al.*, 2010), although, as mentioned above, several generically indeterminate enantiornithine specimens have also been reported from this locality. Two of these specimens, CAGS-IG-02-CM-0901 (You *et al.*, 2005) and CAGS-IG-04-CM-023 (Harris *et al.*, 2006), are represented only by pectoral elements and thus cannot be directly compared to *Qiliania*, although it remains possible that one or both pertain to this taxon. In contrast, CAGS-IG-04-CM-007 (Lamanna *et al.*, 2006b), like known specimens of *Qiliania*, consists of pelvic girdle and limb elements. Although *Qiliania* and CAGS-IG-04-CM-007 are similar in several respects (e.g. pubic boot absent; pelvic limb proportions comparable; tarsometatarsus elongate, slender, and plantarily excavated; pedal unguis not strongly recurved), these forms are distinguished by the presence of the following characteristics in *Qiliania*: femur cranially bowed and with distinct neck; tibiotarsus with craniocaudally elongate proximal surface orientated perpendicular to the shaft and a medial epicondylar depression; tarsometatarsus with proportionately greater proximal mediolateral width relative to mid-shaft width; and pedal unguis IV reduced. Therefore, there are probably at least two different enantiornithine taxa in the Xiagou avifauna, as suggested by Lamanna *et al.* (2006b).

Amongst fossils of Enantiornithes from China, FRDC-04-CM-006 and FRDC-05-CM-006 are exceptional. Although slightly diagenetically compressed, the specimens are three-dimensionally preserved, yielding morphological information that was unknown in previously described Chinese representa-

tives of this clade. This preservation allows for unusually extensive comparisons with material from the latest Cretaceous Lecho Formation of El Brete, Argentina – the basis for the erection of Enantiornithes (Walker, 1981) – and other three-dimensional enantiornithine specimens (e.g. the holotypic tibiotarsus of *Nanantius eos* from Australia; Molnar, 1986). Nevertheless, we excluded several purported enantiornithine taxa from the comparisons below because, although they preserve elements that overlap with those of *Qiliania*, their validity is not universally accepted (Chiappe & Walker, 2002). These taxa include the following: ‘*Cathayornis*’ *aberrans* and ‘*Cathayornis*’ sp. (Hou *et al.*, 2002); ‘*Cathayornis*’ *caudatus*, *Cuspirostrornis houi*, *Jibeinia luanhera*, *Largirostrornis sexdentoris*, and *Longchengornis sanyanensis* (Hou, 1997); and *Sazavis prisca* (Nesov & Jarkov, 1989). Additionally, we follow recent studies (Cau & Arduini, 2008; Zhou *et al.*, 2008) in regarding the alleged large-bodied enantiornithine *Aberratioodontus wui* (Gong, Hou & Wang, 2004) as a probable ornithuromorph; hence, this taxon will not be further considered here.

The fully fused pelvic girdle of *Qiliania* is an enantiornithine character previously known only in the El Brete collection. The pelvis of other Early Cretaceous Chinese enantiornithines range from completely unfused [e.g. *Shenqiornis mengi* (Wang *et al.*, 2010), some specimens of *Sinornis santensis* (Zhou *et al.*, 1992), and GMV-2158, a generically indeterminate juvenile enantiornithine (Chiappe, Ji & Ji, 2007)] to fused but with discernible lines of synostosis [e.g. the holotypic specimen of *Sinornis* (Sereno & Rao, 1992; Sereno *et al.*, 2002)]. The postacetabular wing of the ilium is subtriangular in lateral view, tapering caudally, as in *Eoalulavis hoyasi* (Sanz *et al.*, 2002), *Sinornis* (Sereno *et al.*, 2002; Zhou & Hou, 2002), and PVL-4032-3, a generically indeterminate euenantiornithine pelvis from El Brete (Chiappe & Walker, 2002). In the morphology of the ilioischadic foramen, *Qiliania* most strongly resembles *Sinornis* and PVL-4032-3: in all three of these forms, this fenestra is present but not completely circumscribed by the fusion of the ilium and ischium seen in modern birds. Instead, the dorsal process of the ischium contacts the ilium medially, such that the dorsal end of the process is obscured in lateral view. The ischial blade of *Qiliania* resembles those of *Eoenantiornis buhleri* (Zhou, Chiappe & Zhang, 2005) and *Sinornis* in its ‘knife-like’ morphology and lack of an obturator process, opposing the condition reported in *Concornis lacustris* (Sanz, Chiappe & Buscalioni, 1995; Sanz *et al.*, 2002). As in *Gobipteryx minuta* (Kurochkin, 1996), GMV-2158, and GMV-2159 (another indeterminate juvenile enantiornithine from the Early Cretaceous of China; Chiappe *et al.*, 2007) but in contrast to *Longipteryx*

chaoyangensis (Zhang *et al.*, 2001), *Pengornis houi* (Zhou *et al.*, 2008), *Protopteryx fengningensis* (Zhang & Zhou, 2000), *Shenqiornis*, *Sinornis* (Sereno *et al.*, 2002), ‘bird 1’ of a probable regurgitated pellet from the Early Cretaceous of Spain (LH 11 386; Sanz *et al.*, 2001; Chiappe, 2007), and possibly *Bolouchia zhengi* (Zhou, 1995b), the distal end of the pubis of *Qiliania* lacks a boot. *Eoenantiornis* does possess a pubic boot, although it is proportionately smaller than in *Pengornis*, *Shenqiornis*, and *Sinornis*. The absence of the pubic boot [as above, also noted in the indeterminate Changma enantiornithine CAGS-IG-04-CM-007 (Lamanna *et al.*, 2006b)] may represent an evolutionary stage in the reduction of the pubic symphysis approaching the wholly separate pubes of more derived enantiornithine taxa and, convergently, ornithurans (e.g. Hesperornithes, *Ichthyornis* spp., and Neornithes).

The proportions of the pelvic limb (i.e. the relative proximodistal lengths of the femur, tibiotarsus, and tarsometatarsus) of *Qiliania* recall those of several enantiornithines, particularly *Concornis* and *Eoenantiornis*. In the new taxon from Changma, the femur is gently bowed cranially, as in most other enantiornithines including ‘*Cathayornis*’ *chabuensis* (Li *et al.*, 2008), *Concornis*, *Dapingfangornis sentisorhinus* (Li *et al.*, 2006), *Eoenantiornis*, *Gobipteryx*, *Longipteryx*, *Neuquenornis volans* (Chiappe & Calvo, 1994), *Pengornis*, *Sinornis*, *Vescornis hebeiensis* (Zhang *et al.*, 2004), PVL-4037, a generically indeterminate enantiornithine femur from El Brete (Chiappe & Walker, 2002), and MTM V.2002.05, a generically indeterminate enantiornithine femur from Iharút, Hungary (Ösi, 2008). Conversely, a few other enantiornithine femora [e.g. those of ‘bird 1’ of LH 11 386, GMV-2158, GMV-2159, and NIGP-130723 [a third juvenile from the Early Cretaceous of China (Hou & Chen, 1999; Ji & Ji, 1999; Chiappe *et al.*, 2007)]; PVL-4038, another indeterminate El Brete femur (Chiappe & Walker, 2002)] are straight in mediolateral view. That several juvenile enantiornithine skeletons (e.g. ‘bird 1’ of LH 11 386, GMV-2158, GMV-2159, NIGP-130723) exhibit relatively straight femora suggests that the curvature of this element may have increased through the ontogeny of these birds.

The proximal articular surface of the tibiotarsus of *Qiliania* is subrectangular in outline, contrasting with the more circular shape typical of other enantiornithine taxa [e.g. *Concornis*, *Flexomornis howei* (Tykoski & Fiorillo, 2010), *Iberomesornis romerali* (Sanz *et al.*, 2002), *Nanantius eos* (Molnar, 1986), *Nanantius* sp. (Kurochkin & Molnar, 1997), *Sinornis* (Sereno *et al.*, 2002), *Soroavisaurus australis* (Chiappe & Walker, 2002), *Vescornis*]. The El Brete taxon *Lectavis bretincola* (Chiappe, 1993; Chiappe & Walker, 2002) and a generically indeterminate

tibiotarsus from the latest Cretaceous of France (Mechin collection 606; Buffetaut, Mechin & Mechin-Salessy, 2000) also exhibit a subrectangular contour, but in these forms the proximal tibiotarsus is elongate mediolaterally, rather than craniocaudally as in *Qiliania*. Moreover, in the new Gansu taxon, the tibiotarsal proximal surface is orientated perpendicular to the shaft, rather than canted distolaterally as in *Alexornis antecedens* (Brodkorb, 1976), *Concornis*, *Gobipteryx*, *Nanantius* spp., and *Soroavisaurus*. The prominent cnemial crest of *Qiliania* has not previously been reported in Enantiornithes (see Discussion). In this genus, the fibular crest is proximally positioned, more so than in *Soroavisaurus* and Mechin collection 606 but similar to the condition in *Concornis* and *Lectavis*. This crest is less prominent in *Qiliania* than in *Alexornis*, *Nanantius eos*, and *Concornis*, although it terminates in a tubercle as in the latter taxon. The gracile tibiotarsal shaft of *Qiliania* is reminiscent of that in *Concornis*, *Lectavis*, and *Nanantius eos* and dissimilar to the mediolaterally broader shaft of Mechin collection 606.

In *Qiliania*, the ascending process of the astragalus is firmly co-ossified with the tibia, contrasting with the condition reported in *Dalingheornis liwei* (Zhang *et al.*, 2006b), *Iberomesornis* (Sanz & Bonaparte, 1992; Sanz *et al.*, 2002; *contra* Sereno, 2000), *Longipteryx*, *Paraprotapteryx gracilis* (Zheng *et al.*, 2007), *Protopteryx*, *Shenqiornis*, *Vescornis*, GMV-2158, and GMV-2159, where the tibia and proximal tarsals are said to be unfused (this latter morphology may well be a result of the ontogenetic immaturity of these forms; see Chiappe *et al.*, 2007). Nevertheless, in *Qiliania*, the margins of the ascending process may still be discerned, as in *Gobipteryx*, *Na. eos*, and Mechin collection 606, but not *Concornis*. At the distal extreme of the tibiotarsus, the condyles of the Gansu bird are nearly equal in size, as in *Bolouchia* but unlike the condition in most other enantiornithines, including *Concornis*, *Dapingfangornis*, *Gobipteryx*, *Lectavis*, *Na. eos*, *Sinornis* (Zhou & Hou, 2002), *Soroavisaurus*, and Mechin collection 606, in which the medial condyle is substantially larger than its lateral counterpart. Furthermore, the condyles are not divided by a deep sulcus as in *Gobipteryx*; rather, they taper gently toward each other, rendering them hourglass-shaped in craniodistal view, as in *Concornis*, *Lectavis*, *Na. eos*, and *Soroavisaurus*. The distal tibiotarsal condyles of *Qiliania* do not project as far cranially as in *Lectavis*, more closely resembling other enantiornithines (e.g. *Gobipteryx*, *Na. eos*, Mechin collection 606) in this aspect. The medial epicondyle and epicondylar depression of *Qiliania* are also present in *Lectavis*, *Na. eos*, *Soroavisaurus*, and Mechin collection 606; a lateral epicondylar depression is also observed in *Soroavisaurus* and the Mechin tibiotarsus.

As in several enantiornithines [e.g. *Longipteryx*, *Longirostravis hani* (Hou *et al.*, 2004), *Paraprotapteryx*, *Sinornis*], the fibula of *Qiliania* is approximately one-third of the length of the tibiotarsus, and therefore proportionately much shorter than those of *Pengornis* and possibly *Protopteryx* [Zhang & Zhou (2000) described the fibula of the latter taxon simply as 'long'].

The tarsometatarsus is represented in many enantiornithine taxa, enabling extensive comparisons with that of *Qiliania*. In overall morphology, the tarsometatarsus of the new Gansu enantiornithine is most similar to that of slender-limbed taxa like *Concornis*, *Lectavis*, and *Neuquenornis*. It also bears some resemblance to the tarsometatarsi of forms with relatively unspecialized pelvic limbs such as *Bolouchia*, '*Cathayornis*' *chabuensis*, *Dapingfangornis*, *Enantiophoenix electrophyla* (Dalla Vecchia & Chiappe, 2002; Cau & Arduini, 2008), *Eoenantiornis*, *Iberomesornis*, *Paraprotapteryx*, *Pengornis*, *Protopteryx*, *Shenqiornis*, *Sinornis*, *Vescornis*, IVPP V 13 939 (a generically unassigned enantiornithine specimen with pelvic limb feathers; Zhang & Zhou, 2004), and various juvenile Enantiornithes (e.g. 'bird 1' and 'bird 2' of LH 11386, GMV-2158, GMV-2159, NIGP-130723). Conversely, it does not closely resemble the more robust tarsometatarsi of *Avisaurus archibaldi* (Brett-Surman & Paul, 1985), *Avisaurus glorieae* (Varricchio & Chiappe, 1995), *Gobipteryx* (Kurochkin, 1996), *Longipteryx*, *Longirostravis*, *Soroavisaurus*, MTM Gyn 439 (a generically unassigned enantiornithine tarsometatarsus from Iharkút, Hungary; Ösi, 2008), and especially the aberrant, possibly amphibious *Yungavolucris brevipedalis* (Walker, 1981; Chiappe, 1993). Also, the as-yet undescribed 'Kaiparowits avisauid' (Chiappe & Walker, 2002) is reported to possess a 'short robust tarsometatarsus' (Hutchison, 1993); as such, the proportions of this element presumably differ significantly from those of the new Changma bird.

In *Qiliania*, as in nearly all other enantiornithines, the distal tarsals are firmly co-ossified with the fused proximal ends of metatarsals II–IV; in contrast, separate distal tarsals are reported in *Iberomesornis* (Sanz & Bonaparte, 1992; Sanz *et al.*, 2002; *contra* Sereno, 2000), *Protopteryx*, *Shenqiornis*, and the indeterminate juvenile GMV-2158. The uniform size of the proximal articular cotyles in *Qiliania* is unusual compared to the condition in many other enantiornithines (e.g. *Avisaurus* spp., *Gobipteryx*, *Lectavis*, *Yungavolucris*, MTM Gyn 439) in which the medial cotyle is distinctly larger than the lateral (Chiappe, 1993; Varricchio & Chiappe, 1995; Kurochkin, 1996; Ösi, 2008). The attenuated, proximally projecting lateral edge of the lateral cotyle is comparable to the conditions in *Bolouchia*, *Lectavis*, and at least one specimen

of *Yungavolucris* (PVL-4692; Chiappe, 1993), although in *Bolouchia* a similar ridge is present on the proximal-medial tarsometatarsal margin as well (Zhou, 1995b). The proximal articular surface does not appear to be dorsally inclined, differing from the condition in the avisaurids *Avisaurus* spp. and *Soroavisaurus* (Chiappe, 1993). There is no hypotarsus, as in nearly all other Enantiornithes with the exception of *Lectavis*.

In *Qiliana*, the tubercle for the insertion of the M. tibialis cranialis on metatarsal II is less prominent and more proximally placed than those of many other enantiornithines, including *Avisaurus archibaldi*, *Enantiophoenix*, *Gobipteryx*, *Soroavisaurus*, possibly *Pengornis* (in which this tubercle is described as 'prominent'; Zhou *et al.*, 2008), and especially *Avisaurus glorieae* and *Yungavolucris*, in which the tubercle is both strongly developed and relatively distally situated. Only in *Lectavis* is the M. tibialis cranialis tubercle more proximally positioned than it is in *Qiliana*. The Changma bird shares with certain New World avisaurids (*Avisaurus archibaldi*, *Neuquenornis*, *Soroavisaurus*) a mediolaterally convex dorsal surface of metatarsal III and a plantarily excavated tarsometatarsus (Chiappe, 1993; Chiappe & Calvo, 1994). The first of these characters is also shared with *Avisaurus glorieae* and *Concornis*, and the second with *Lectavis* (Chiappe, 1993; Sanz *et al.*, 1995). The proximal mediolateral width of the tarsometatarsus of the new Changma form is substantially greater than that at the midshaft; this character is also found in *Bolouchia*, *Eoenantiornis*, and *Lectavis*. The distal end of metatarsal II of the Gansu bird does not appear to be strongly deflected medially, contrasting with the condition in *Gobipteryx* and the avisaurids *Avisaurus* spp. and *Soroavisaurus*. In *Qiliana*, as in most other enantiornithines, metatarsal III is the longest in the pes; in contrast, in *Alethoalaornis agitornis* (Li *et al.*, 2007) and *Bolouchia*, metatarsals II–IV are subequal in length, in *Gobipteryx* metatarsals II and III are subequal, and in *Longipteryx* and MTM Gyn 439 metatarsal IV is the longest. In *Qiliana*, as in other Enantiornithes, metatarsal IV is mediolaterally narrower than metatarsals II and III.

Metatarsal I of *Qiliana* is J-shaped, as in several enantiornithines; this element is straighter in *Concornis* and perhaps *Neuquenornis*. The pedal unguis of the Gansu bird are less recurved than in many enantiornithine taxa (e.g. *Bolouchia*, 'Cathayornis' *chabuensis*, *Concornis*, *Enantiophoenix*, *Neuquenornis*, *Pengornis*, *Sinornis*, *Soroavisaurus*, *Vescornis*), more closely resembling those of *Dalingheornis*, *Elsornis keni* (Chiappe *et al.*, 2006), *Eoenantiornis*, *Gobipteryx*, *Iberomesornis*, GMV-2158, and GMV-2159 in this regard. In contrast to at least some avisaurids (*Enantiophoenix*, *Neuquenornis*, *Soroavisaurus*), the hallux unguis is not hypertro-

phied; accordingly, the distal articular surface of pedal phalanx I-1 is not conspicuously expanded. Finally, the reduced unguis of digit IV in *Qiliana* is a distinctive characteristic within Enantiornithes, seen elsewhere only in *Vescornis*.

PHYLOGENETIC ANALYSIS

To investigate the evolutionary relationships of *Q. graffini*, we performed a phylogenetic analysis using a modified version of the data set published by O'Connor *et al.* (2009). Four operational taxonomic units (OTUs) from the Xiagou Formation of the Changma Basin were added to this data set: *Qiliana* and three undescribed enantiornithine specimens (FRDC-05-CM-004, FRDC-06-CM-012, and FRDC-07-CM-001). Unlike most previously published enantiornithines from Changma (You *et al.*, 2005; Harris *et al.*, 2006), these three undescribed specimens preserve pelvic girdle and limb elements and are thus directly comparable to known material of *Qiliana*. *Soroavisaurus australis* (Chiappe, 1993) and *Archaeorhynchus spathula* (Zhou & Zhang, 2006b) were also added to the data set, and DNHM D2522 (the holotype of *Rapaxavis pani*; Morschhauser *et al.*, 2009) and PKUP-V1069 (the holotype of the basal ornithuromorph *Longicrusavis houi*; O'Connor, Gao & Chiappe, 2010) were removed (see Supporting Information). Neornithes was represented by *Anas platyrhynchos* and *Gallus gallus*; Dromaeosauridae was scored as the outgroup. A matrix of 214 characters (31 ordered; 28 uninformative characters removed from original data set of 242, see Supporting Information) and 33 OTUs was evaluated using NONA v. 2.0 (Goloboff, 1993); optimal trees were identified by a heuristic search implementing 1000 replicates of the tree bisection and reconnection (TBR) algorithm, retaining the ten shortest trees from each replication. Additional TBR branch-swapping was not required. The analysis yielded three most parsimonious trees (MPTs) of 597 steps (Consistency (C) = 47; Consistency Index (CI) = 47; Retention Index (R) = 67), which differ only in the arrangement of taxa within the enantiornithine clade.

The relationships amongst non-ornithothoracine birds hypothesized in the strict consensus tree (Fig. 5) are consistent with those recovered using the original version of this data set (O'Connor *et al.*, 2009). The basal pygostylians *Sapeornis chaoyangensis* and Confuciusornithidae (*Confuciusornis sanctus* + *Changchengornis hengdaoziensis*) form successive outgroups to Ornithothoraces; *Zhongornis haoae*, *Jeholornis prima*, and *Archaeopteryx lithographica* form sequential outgroups to Pygostylia. These results differ slightly from those of some other analyses, in which confuciusornithids are resolved as closer to Orni-

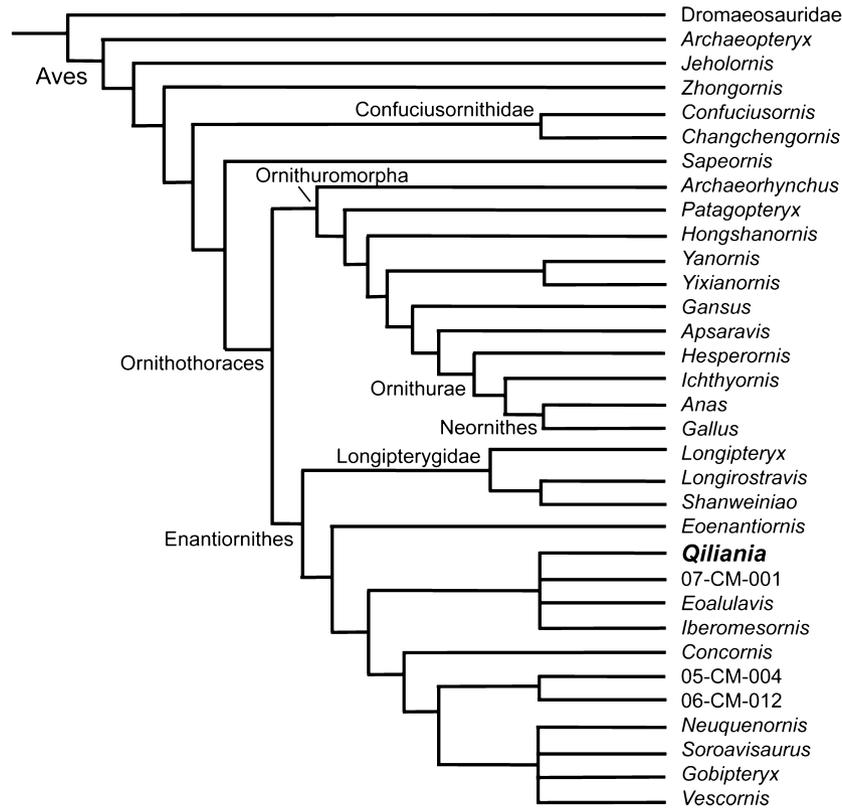


Figure 5. Strict consensus tree (length = 597 steps; C = 47; Ci = 47; R = 67) recovered by the present analysis showing proposed phylogenetic position of *Qiliania graffini* gen. et sp. nov.

thoraces than is *Sapeornis* (Clarke, Zhou & Zhang, 2006) or are even placed as the outgroup to Enantiornithes within Ornithothoraces (Zhou & Zhang, 2006b). The ornithothoracine clade is composed of Enantiornithes and Ornithuromorpha. Relationships within both of these clades are weakly supported, collapsing in trees only one or two steps longer (see Supporting Information). Within Ornithuromorpha, *Ichthyornis* spp., *Hesperornis* spp., *Apsaravis ukhaana*, *Ga. yumenensis*, *Yixianornis grabaui* + *Yanornis martini*, *Hongshanornis longicresta*, *Patagopteryx deferrariisi*, and *Archaeorhynchus* form successive outgroups to Neornithes. The relative positions of basal ornithuromorphs proposed here are similar to those presented by Clarke *et al.* (2006) and Zhou & Zhang (2006b), but differ from those recovered by You *et al.* (2006), whose analysis placed *Gansus* within Ornithurae, closer to Neornithes than is *Hesperornis*. Nevertheless, the former two analyses did not include *Gansus*, possibly because this taxon had been described only from a distal pelvic limb at the time these works were performed. As abundant new specimens from Changma continue to reveal additional morphological information on *Gansus*, the phylogenetic position of this taxon within Ornithuro-

morpha will probably become more conclusively resolved (You *et al.*, 2006; J. D. Harris & M. C. Lamanna, pers. observ.).

The consensus tree confirms the phylogenetic placement of *Qiliania* within Enantiornithes. *Soroavisaurus*, *Neuquenornis volans*, *Vescornis hebeiensis*, and *Gobipteryx minuta* form a derived polytomy within this clade. FRDC-05-CM-004 and FRDC-06-CM-012 (together comprising a clade) and *Concornis lacustris* form successive outgroups to the *Soroavisaurus*–*Neuquenornis*–*Vescornis*–*Gobipteryx* polytomy. This more inclusive clade forms a dichotomy with a polytomy composed of *Qiliania*, *Eoalulavis hoyasi*, *Iberomesornis romerali*, and FRDC-07-CM-001; *Eoenantiornis buhleri* is the outgroup of this dichotomy. Longipterygidae [*Longipteryx chaoyangensis* + (*Longirostravis hani* + *Shanweiniaos cooperorum*)] occupies the basal-most position within Enantiornithes.

The three MPTs differ only in the structure of the polytomous clade in which *Qiliania* occurs. As is the strict consensus, the first MPT is characterized by a four-way polytomy amongst *Qiliania*, *Eoalulavis*, *Iberomesornis*, and FRDC-07-CM-001. In the second MPT, *Qiliania* forms the outgroup to an

Eoalulavis + *Iberomesornis* + FRDC-07-CM-001 polytomy, and in the third, *Iberomesornis* + FRDC-07-CM-001 form a more exclusive relationship with each other than with either *Qiliania* or *Eoalulavis*.

Many of the enantiornithine inter-relationships hypothesized here have been proposed by previous authors (e.g. the existence of a monophyletic Longipterygidae has been supported by multiple analyses [Chiappe *et al.*, 2006; Cau & Arduini, 2008; O'Connor *et al.*, 2009]). However, other aspects of these relationships are more controversial. For example, prior to the discovery of many enantiornithine taxa from the Jehol Group, *Iberomesornis* had been resolved as a basal form that resided outside Euenantiornithes (Chiappe, 2002; Chiappe & Walker, 2002). As novel enantiornithine diversity has been discovered, and the distribution of apomorphies has become less consistent, the purported basal status of *Iberomesornis* has not been supported by some recent analyses (O'Connor *et al.*, 2009) but continues to be upheld by others (Cau & Arduini, 2008). Indeed, phylogenetic relationships within Enantiornithes are typically inconsistent amongst analyses (e.g. Clarke *et al.*, 2006; Zhou & Zhang, 2006b; Cau & Arduini, 2008; Zhou *et al.*, 2008; O'Connor *et al.*, 2009). This long-recognized problem in enantiornithine systematics has resulted from a combination of factors, including the scarcity of comparable fossil material amongst taxa, the highly incomplete nature of most Late Cretaceous forms, the close morphological similarity of many small-bodied species, and the different taxa included in various analyses (such that the results of these analyses are not directly comparable to one another).

DISCUSSION

CNEMIAL CREST EVOLUTION IN BASAL AVIANS

The tibiotarsus of *Qiliania graffini* exhibits several characters that are currently optimized as autapomorphies of this taxon. In particular, the prominent cnemial crest is a remarkable feature. Like *Qiliania*, most enantiornithines (e.g. *Concornis lacustris*, *Flexormornis howei*, *Na. eos*, *Neuquenornis volans*, *Sinornis santensis*, *Soroavisaurus australis*) possess a single cnemial crest positioned at the craniomedial edge of the proximal tibiotarsus, but in these taxa this crest is only very weakly developed. Several non-ornithothoracine birds that are considered to be more derived than Archaeopterygidae, including *Zhongornis haoae* (Gao *et al.*, 2008), *Zhongjianornis yangi* (Zhou, Zhang & Li, 2009), and *Sapeornis chaoyangensis* (Zhou & Zhang, 2001, 2003a), reportedly either lack or possess similarly weak cnemial crests. In contrast, archaeopterygids (e.g. Mayr *et al.*, 2007;

Wellnhofer, 2008) and non-avian theropods (e.g. Hwang *et al.*, 2002) exhibit single, well-developed, craniomedially positioned cnemial crests on the proximal ends of their tibiae. Consequently, following the phylogenetic relationships amongst basal avians proposed by Gao *et al.* (2008), a rudimentary cnemial crest may be a synapomorphy of *Zhongornis* + Pygostylia, or at least the less inclusive clade Ornithothoraces. Regrettably, the lack of published information on the condition of the cnemial crest in many nonpygostylian birds [e.g. *Dalianraptor cuhe* (Gao & Liu, 2005), *Jeholornis prima* (Zhou & Zhang, 2002; Ji *et al.*, 2002a, b, 2003), *Jixiangornis orientalis* (Ji *et al.*, 2002b)] and Confuciusornithidae (e.g. Hou *et al.*, 1995; Chiappe *et al.*, 1999; Ji, Chiappe & Ji, 1999) renders this hypothesis tentative. In any case, however, it is probable that the prominent cnemial crest of *Qiliania* is an apomorphic reversal that is presently unique to this taxon within Enantiornithes.

The development of the cnemial crest in *Qiliania* is interesting in light of the evolution, apparently in parallel, of a comparable condition in Ornithurae – the avian clade that encompasses modern birds (Neornithes) and their closest extinct relatives. In ornithurans, the proximal end of the tibiotarsus bears two distinct cnemial crests, termed the cranial and lateral cnemial crests (Baumel & Witmer, 1993). In many taxa, the cranial cnemial crest is strongly developed, often extending proximally beyond the proximal articular surface of the tibiotarsus and projecting strongly cranially. Indeed, in some aquatic or semi-aquatic ornithurans [e.g. Hesperornithes, Gaviidae (loons), Podicipedidae (grebes)], this crest can be extremely elongate, projecting proximally well beyond the knee joint.

Although it does not extend far proximally, the single cnemial crest of *Qiliania* resembles the cranial cnemial crests of some ornithurans in its degree of cranial projection. Nevertheless, based on its position on the tibia, and the development of the cranial cnemial crest during neornithine embryogenesis, the cnemial crest of enantiornithines and more basal theropods is inferred to be homologous to the lateral cnemial crest of ornithurans (Chiappe, 1996; Hutchinson, 2002). Consequently, the well-developed cnemial crest of *Qiliania* and the comparable expansion of the cranial cnemial crest of Ornithurae are here considered independently derived. The cnemial crest of *Qiliania* thus represents a previously undocumented morphology within Ornithothoraces, in which the lateral cnemial crest became enlarged in parallel to the ossification and expansion of the cranial cnemial crest in ornithurans. In modern birds, the cnemial crests function as attachment sites for the common tendon of the M. femorotibialis musculature, amplifying the moment arm of these muscles about

the knee (Hutchinson, 2002). The enlarged lateral cnemial crest of *Qiliania* may have served a similar function in this Early Cretaceous enantiornithine.

Most recent works (e.g. Chiappe, 1996; Hutchinson, 2002) have interpreted the presence of two cnemial crests (cranial and lateral) on the proximal end of the tibiotarsus as a synapomorphy of Ornithurae. Interestingly, however, a comparable condition has been described in several tibiotarsi attributed to Enantiornithes, namely those of *Alexornis antecedens* (Brodtkorb, 1976) and *Nanantius* sp. (Kurochkin & Molnar, 1997) and the generically unassigned tibiotarsus Mechin collection 606 (Buffetaut *et al.*, 2000). In addition to the single, craniomedially positioned cnemial crest of other enantiornithines, the proximal ends of each of these tibiotarsi are reported to exhibit more laterally placed crests as well. Perhaps, as suggested by Kurochkin & Molnar (1997), one or more enantiornithines evolved a second cnemial crest independent of the development of the cranial cnemial crest in ornithurans. If so, along with the cranially expanded lateral cnemial crest of *Qiliania*, this would constitute another example of convergence between Enantiornithes and Ornithurae in the evolution of the proximal tibiotarsus.

PALAEOECOLOGY OF *QILANIA*

Several recent studies (e.g. Hopson, 2001; Glen & Bennett, 2007) have used ecomorphological data from modern birds to propose methods for generating palaeoecological inferences for extinct avians based on the morphologies of these taxa as preserved in their fossils. One such method (Hopson, 2001) involves the use of non-ungual pedal phalangeal proportions, in which specific patterns of non-ungual phalangeal proximodistal length are hypothesized to be indicative of particular lifestyles (e.g. an avian pes in which the non-ungual phalanges progressively increase in length distally is proposed to be indicative of perching). *Qiliania*, however, exhibits no clear trends in non-ungual phalangeal length; therefore, robust inferences cannot be made regarding the habits of this enantiornithine based on the morphology of its non-ungual phalanges alone.

Avian pedal unguis morphology, especially the curvature of such unguis [e.g. the 'claw angle' of Glen & Bennett (2007)], has also been used as a proxy for palaeoecology. Following the methods of Glen & Bennett (2007), we measured the 'claw angle' of the third pedal unguis of *Qiliania* at approximately 95°. The Changma taxon therefore resides, although somewhat ambiguously, within the groups that Glen & Bennett (2007) designated as 'predominantly ground foragers' and 'predominantly arboreal foragers' niches that today are dominated

by Columbiformes (doves and pigeons) and Cuculiformes (cuckoos and allies). *Qiliania* was therefore perhaps an Early Cretaceous analogue of these extant ecological generalists.

Interestingly, however, Dyke & Nudds (2008) noted that the pelvic limb proportions of many enantiornithine taxa differ significantly from those of extant avians. It is therefore reasonable to expect that the pedal morphology of at least some enantiornithines might fall outside of the range exhibited by modern birds as well. If so, and if *Qiliania* was one such taxon, then this might explain the difficulty we have encountered in attempting to reconstruct the palaeoecology of this form using the proportions of its non-ungual pedal phalanges, as well as our inability to easily 'shoehorn' the taxon into one of the proposed ecological categories of Glen & Bennett (2007) based on the curvature of its pedal unguis. In conclusion, we follow Dyke & Nudds (2008) in considering the possibility that the morphologies and palaeoecologies of *Qiliania*, and at least some other enantiornithines, may not be directly comparable to those of modern birds.

NOTE ADDED IN PROOF

As this paper went to press, the specimens described herein, FRDC-04-CM-006 AND FRDC-05-CM-006, were transferred to the Gansu Geological Museum (GSGM; Lanzhou, Gansu Province, China). They now bear the specimen numbers GSGM-F00003 and GSGM-F00004 respectively.

ACKNOWLEDGEMENTS

We are grateful to personnel of the former Fossil Research and Development Center of the Third Geology and Mineral Resources Exploration Academy of the Gansu Provincial Bureau of Geo-Exploration and Mineral Development (now the Gansu Geological Museum) for discovering the specimens, and Yu-Qing Zhang of the Institute of Geology of the Chinese Academy of Geological Sciences for preparation. Funding was provided by grants from the Ministry of Science and Technology and the National Natural Science Foundation of China (40672007) to Hai-Lu You and Shu-An Ji, the Gansu Provincial Bureau of Geo-Exploration and Mineral Development to Da-Qing Li, Carnegie Museum of Natural History to Matthew Lamanna, and the University of Pennsylvania Paleobiology Research Fund to Jessie Atterholt. We also thank Barbara Marrs of Creative Imaging Photography for photographing the specimens.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. 3 trees of steps = 597 retained.

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