

A LARGE COMPSOGNATHID FROM THE EARLY CRETACEOUS YIXIAN FORMATION OF CHINA

Sunny H. Hwang

Division of Paleontology, American Museum of Natural History, 79th Street at Central Park West,
New York, NY 10024, USA

Mark A. Norell

Division of Paleontology, American Museum of Natural History, 79th Street at Central Park West,
New York, NY 10024, USA

Ji Qiang

Chinese Academy of Geological Sciences, 26 Baiwanzhuang, Beijing 100037, People’s Republic of China;
Department of Earth Sciences, Nanjing University, Nanjing 210093, People’s Republic of China

Gao Keqin

School of Earth and Space Sciences, Peking University, Beijing 100871, People’s Republic of China

SYNOPSIS A new, large compsognathid theropod, *Huaxiagnathus orientalis* gen. et sp. nov., from the Early Cretaceous Yixian Formation deposits of Liaoning Province, People’s Republic of China is described. The holotype specimen is nearly complete, lacking only the distal portion of the tail. It is the second largest theropod taxon discovered from Jehol Group sediments. Like all compsognathids, *Huaxiagnathus* has short forelimbs and a relatively unspecialised coelurosaur body plan. Previously, fairly complete skeletons existed for only two small-bodied taxa of compsognathids, *Compsognathus longipes* from the Late Jurassic of Western Europe and *Sinosauropteryx prima*, also from the Yixian. The phylogenetic position of *Huaxiagnathus orientalis* was analysed using an extensive matrix of theropod characters from many taxa. *Huaxiagnathus orientalis* fell out at the base of the Compsognathidae, as it lacks the forelimb adaptations of more derived compsognathids. The addition of *Huaxiagnathus* and the two other compsognathid species to our data matrix resulted in the placement of Compsognathidae near the base of Maniraptora. Furthermore, Alvarezsauridae, Paraves, and a monophyletic Therizinosauroida + Oviraptorosauria clade fall out in an unresolved trichotomy in the strict consensus of our most parsimonious trees.

KEY WORDS Compsognathidae, Theropod, Yixian Formation, Liaoning, Jehol

Contents

Introduction	14
Institutional abbreviations	14
Systematic palaeontology	14
THEROPODA Marsh, 1881	14
COELUROSAURIA von Huene, 1914	14
MANIRAPTORA Gauthier, 1986	14
COMPSOGNATHIDAE Marsh, 1882	14
Genus <i>HUAXIAGNATHUS</i> gen. nov.	14
<i>Huaxiagnathus orientalis</i> gen. et sp. nov.	15
Description	16
Skull	16
Axial skeleton	17
Pectoral girdle	20
Forelimb	20
Pelvic girdle	24
Hindlimb	24

Discussion	26
Phylogenetic analysis	26
Acknowledgments	29
References	29

INTRODUCTION

Compsognathids are a poorly known group of moderately primitive theropods placed in various relatively basal positions within the Coelurosauria (Forster *et al.* 1998; Sereno 1999; Holtz 2000). Most of the information about compsognathids is based on only one European species, *Compsognathus longipes* (Bidar, Demay & Thomel 1972; Ostrom 1978) and one Asian species, *Sinosauropteryx prima* (Ji & Ji 1996; Chen, Dong & Zhen 1998; Currie & Chen 2001). Bidar *et al.* (1972) referred a specimen to a new species, *Compsognathus corrallestris*, but the synonymy of this specimen with *C. longipes*, which was suggested by Ostrom (1978), has been nearly universally accepted (Glut 1997; Norman 1990). *Aristosuchus pusillus* from the Wealden Group of England (Owen 1876; Naish 1999) and a fragmentary unnamed theropod (SMNK 2349 Pal) from the Santana Formation of Brazil (Martill *et al.* 2000) are probably also compsognathids, but both specimens are too incomplete to include in a phylogenetic analysis. Here we describe a new compsognathid, *Huaxiagnathus orientalis* gen. et sp. nov., from the Yixian Formation of China, which is unusual because of its large size. Both *Compsognathus* and *Sinosauropteryx* are small animals (although the size of the French *Compsognathus* specimen is nearly twice the size of the type specimen), as are most of the theropod taxa found in the Early Cretaceous Yixian and Jiufotang Formations of Liaoning Province, China (Ji & Ji 1996; Ji *et al.* 1998, 2001; Xu, Wang & Wu 1999b; Xu, Zhou & Wang 2000; Norell *et al.* 2002; Xu *et al.* 2002b, 2003). The average length of theropods from these Jehol Group sediments, which include the smallest non-avian theropod known, *Microraptor zhaoianus* (Xu *et al.* 2000; Hwang *et al.* 2002a) is about 100 cm. *Huaxiagnathus* is almost twice the size of most Jehol theropods and other compsognathids. The holotype is missing the distal end of the tail, but is otherwise complete and extremely well preserved. A conservative estimate places the animal's length at about 1.6 m, making it second in size only to *Beipiaosaurus inexpectus* (Xu, Tang & Wang 1999a) among Jehol theropods.

The holotype was collected by farmers from a quarry belonging to the village of Dabangou in the Sihetun area, near the city of Beipiao in Liaoning Province. All the specimens of *Sinosauropteryx* were also recovered from quarries in the Sihetun area. The specimen consists of five large slabs pieced together from smaller fragments (Fig. 1). There are no counterslab elements preserved. The edges of the five large slabs match well, as do the edges of the smaller fragments within each slab. Slab junctions were examined to make sure that the bone was firmly embedded in the matrix and matched bones from adjacent slabs. The entire specimen was searched for anomalous bits of matrix and protruding pieces of foreign bone that might have been added to 'complete' the skeleton. The specimen was also examined under ultraviolet light for

any changes in fluorescence that might signal replacement parts. There were no signs of any foreign matrix or skeletal material in the specimen; this specimen is preserved in a very distinctive matrix of sea-green clay that is rarely seen in Liaoning specimens and the bone is a unique light orange colour. There was no plaster present in the specimen that would have indicated heavy reconstruction with mismatched fragments. Extensive time was spent to allay all concerns that this specimen is a chimera.

At first glance, *Huaxiagnathus* looks like a large *Sinosauropteryx* or *Compsognathus*, since they all have the same general skeletal proportions (Table 1). All three taxa have long tails, short forelimbs, relatively large skulls and relatively short distal portions of the hindlimb. These proportions are characteristic of compsognathids, but not of other non-tyrannosaurid coelurosaurs (Gauthier 1986). *Huaxiagnathus orientalis* can be assigned to the Compsognathidae on the basis of the fan-shaped neural spines on its dorsal vertebrae and its robust manual phalanx I-1 (Chen *et al.* 1998).

Institutional abbreviations

Institutional abbreviations used throughout the text, figures and tables are as follows:

- BSP** = Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany.
CAGS = Chinese Academy of Geological Sciences, Beijing.
NIGP = Nanjing Institute of Geology and Palaeontology, Nanjing.
NGMC = National Geological Museum of China, Beijing.
SMNK = Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe, Germany.

SYSTEMATIC PALAEONTOLOGY

- THEROPODA** Marsh, 1881
COELUROSURIA von Huene, 1914
MANIRAPTORA Gauthier, 1986
COMPSOGNATHIDAE Marsh, 1882
 Genus **HUAXIAGNATHUS** gen. nov.

ETYMOLOGY. After *Hua Xia*, an ancient Mandarin name for China and *gnathus*, Greek for jaw.

TYPE SPECIES. *Huaxiagnathus orientalis* gen. et sp. nov. from the Yixian Formation of Liaoning Province, China.

DIAGNOSIS. Differs from other known compsognathids in having a very long posterior process of the premaxilla that

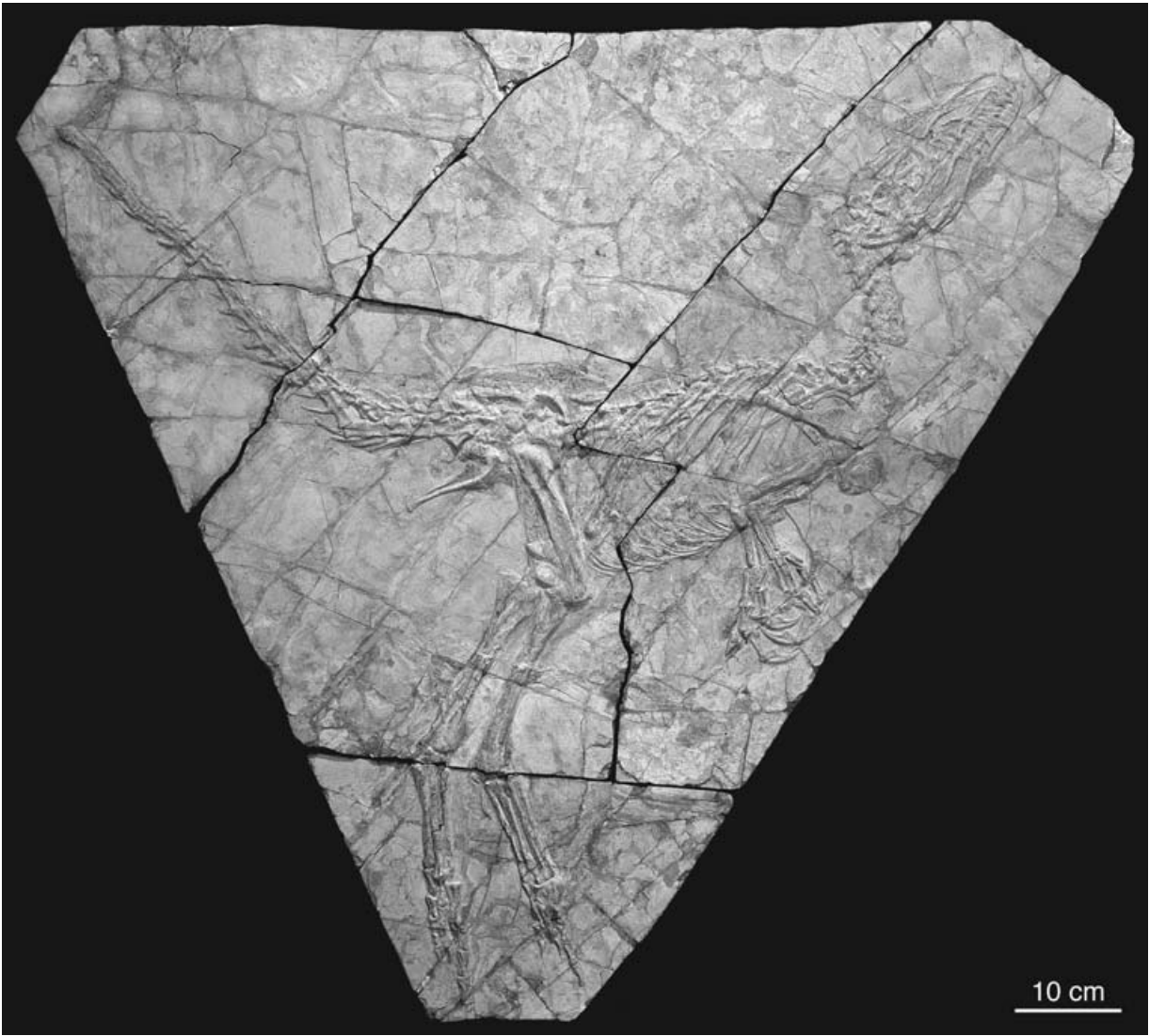


Figure 1 The holotype of *Huaxiagnathus orientalis* (CAGS-IG02-301).

overlaps the antorbital fossa, a manus as long as the lengths of the humerus and radius combined, large manual unguals I and II that are subequal in length and 167% the length of manual ungual III, a first metacarpal that has a smaller proximal transverse width than the second metacarpal and a reduced olecranon process on the ulna.

***Huaxiagnathus orientalis* gen. et sp. nov.** (Figs 1–11)

ETYMOLOGY. After the Latin *orientalis* - of or from the east.

HOLOTYPE. CAGS-IG02-301, a nearly complete skeleton lacking only the distal end of the tail. It is preserved on five large slabs, with no counterpart elements retained. This

Table 1 Comparison of skeletal length ratios of *Huaxiagnathus orientalis* (CAGS-IG02-301), *Sinosauropteryx prima* and *Compsognathus longipes*.

	<i>Huaxiagnathus</i> (CAGS-IG02-301)	<i>Sinosauropteryx</i> (NIGP 127587)	<i>Compsognathus</i> (BSP ASI 563)
Skull/presacral column (%)	45	36	30
Forelimb/hindlimb (%)	48	36	39
(Humerus + radius)/(femur + tibia) (%)	39	31	41
Manus/(humerus + radius) (%)	103	84	74
Metatarsus/femur (%)	67	75	76
Femur/tibia (%)	89	89	76

Ratios are based on values from Chen *et al.* (1998) and Currie & Chen (2001) for *Sinosauropteryx* and from Ostrom (1978) for *Compsognathus*.

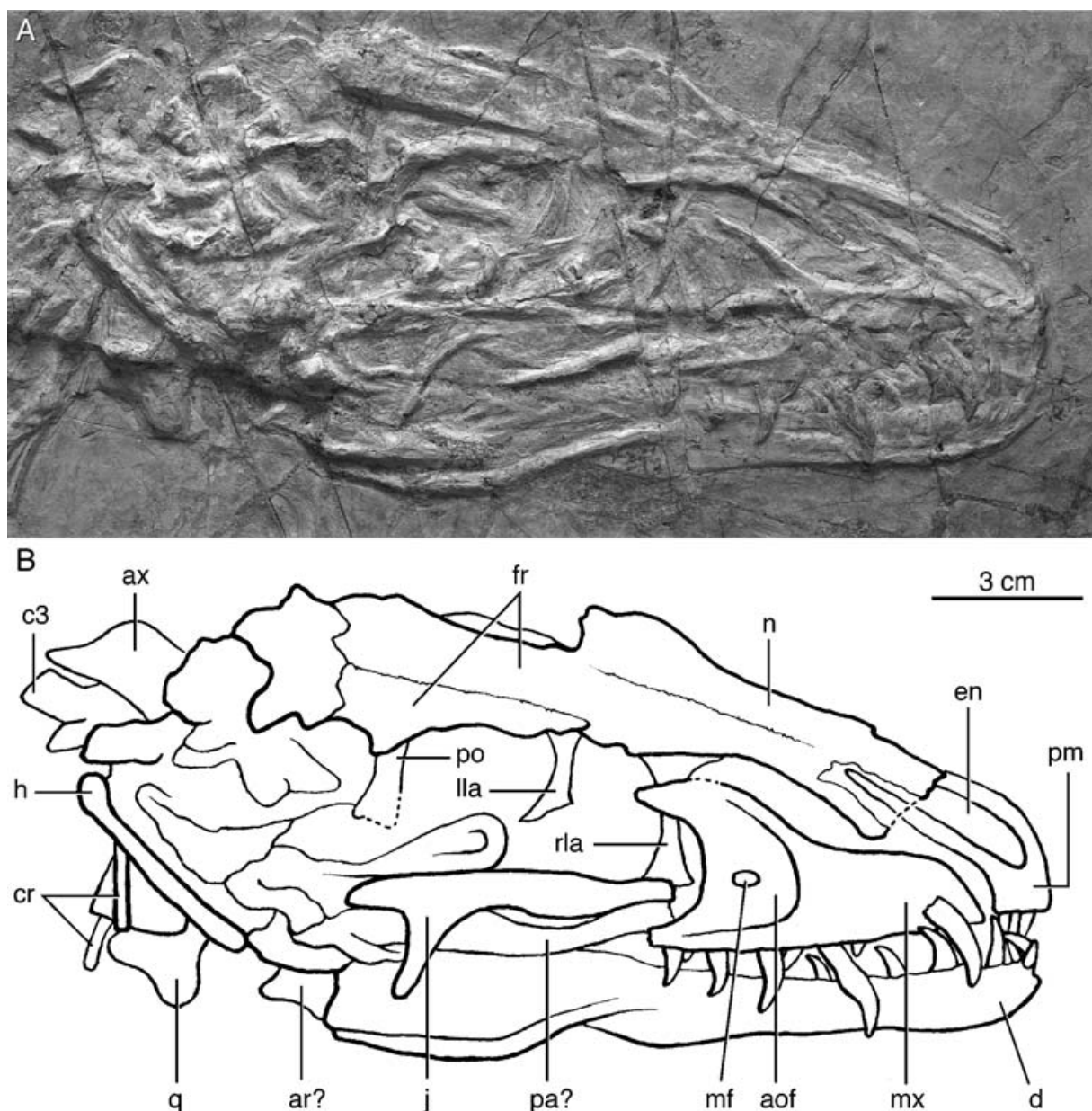


Figure 2 Photograph (A) and interpretive drawing (B) of the skull of CAGS-IGo2-301 in right lateral view. Abbreviations: aof, antorbital fossa; ar, articular; ax, axis; c, cervical vertebra; cr, cervical rib; d, dentary; en, external naris; fr, frontal; h, hyoid; j, jugal; lla, left lacrimal; mf, maxillary fenestra; mx, maxilla; n, nasal; pa, prearticular; pm, premaxilla; po, postorbital; q, quadrate; rla, right lacrimal.

is the specimen referred to in Hwang *et al.* 2002b; it was mistakenly assigned the specimen number CAGS 30-2-035 in the Hwang *et al.* 2002b poster presentation.

DIAGNOSIS. As for genus.

TYPE LOCALITY AND HORIZON. Dabangou village, Sihetun Area, near Beipiao City, Liaoning Province, China; Yixian Formation, Early Cretaceous, 125 Myr (Swisher *et al.* 1999, 2002).

OTHER MATERIAL. NGMC 98-5-003, an almost complete, poorly reconstructed and poorly prepared specimen also from the Yixian Formation in the Sihetun area. Because of the many mistakes in its reconstruction (such as the placement

of the counterpart to the radius and ulna in the hand to mimic phalanges) and copious amounts of plaster filling in the hindlimbs (with pieces of bone stuck randomly into this plaster), this specimen was not considered to be an appropriate holotype.

DESCRIPTION

Skull

The skull is preserved in its entirety, but is compressed so that many details and most of the sutures between the individual bones are not discernable (Fig. 2). The maxillary

process of the premaxilla is elongate and contacts the nasal posteriorly, excluding the maxilla from the narial border, as in dromaeosaurids (Currie 1995; Norell & Makovicky, in press) and ornithomimids (Barsbold & Osmólska 1990). However, unlike the latter two taxa, the maxillary process is not so long that it overlaps the internal antorbital fenestra (it does reach the rostral border of the antorbital fossa, however). The external naris is fairly large, overlapping the antorbital fossa posteriorly. There appears to be a small, circular maxillary fenestra on the maxilla approximately 1 cm posterior to the rostral border of the antorbital fossa, but this may be a preservational artefact. The rostral margins of the antorbital fossa and internal antorbital fenestra are level with the anterior edges of the fifth and seventh maxillary teeth, respectively. The caudal extent of the antorbital fossa is not detectable.

The nasals are exposed dorsally and are expanded posteriorly. The nasals have migrated ventrally, covering the dorsal processes of the lacrimals, so it is uncertain whether the lacrimals are 'T'- or 'L'-shaped. The right frontal tapers anteriorly, but the suture between the left frontal and nasals is not visible. The lateral edge of the right frontal has shifted to cover the dorsal portion of the postorbital, so only the jugal process of the postorbital is visible. The jugal process of the postorbital descends only halfway down the posterior margin of the orbit. The jugal has flipped over so that its medial surface is visible. The postorbital process of the jugal is long, so it and the postorbital contribute equally to the postorbital bar. A long, rod-like bone at the posterior of the skull is probably the hyoid.

The dentary is dorsoventrally short and has subparallel dorsal and ventral margins except at the rostral end, where the ventral margin curves upward to meet the dorsal margin. As reported for *Compsognathus longipes* (Ostrom 1978), no external mandibular fenestra is visible, but this may be due to poor preservation of the posterior part of the mandible.

Unfortunately, the margin of the oral cavity of CAGS-IG02-301 is not well-prepared, so it is not possible to tell how many teeth are present in the premaxilla, maxilla and dentary, or whether the anterior teeth in the mouth are serrated or not. There are either three or four narrow, slightly recurved teeth in the premaxilla; the one fully visible tooth has a fore-aft base length (FABL) of 2.58 mm. There are at least eight teeth in the maxilla and six of them occur in pairs consisting of a partially erupted tooth closely appressed to a fully erupted successive tooth (Fig. 2). For example, the fourth visible maxillary tooth has a FABL of 3.76 mm and a crown height of 4.08 mm, while the successive tooth has a FABL of 4.81 mm and a crown height of 11.54 mm. There is a small gap in the tooth row between each fully erupted–partially erupted tooth pair, but these gaps may just be empty alveoli, despite their regular spacing. The dentition of *Huaxiagnathus orientalis* exhibits a typical archosaurian pattern, in which waves of tooth replacement affect every other tooth (Edmund 1960). There does not appear to be a diastema between the premaxilla and maxilla as reported for *Compsognathus* (Ostrom 1978). The maxillary teeth are laterally compressed and strongly posteriorly recurved. There are six teeth visible in the dentary, the most posterior of which is positioned just anterior to the fourth visible maxillary tooth. Where visible, the maxillary and posterior dentary teeth have fine serrations on their posterior carinae only (Fig. 3), as in *Sinosauropteryx* (Currie & Chen 2001), *Microraptor* (Xu *et al.* 2000) and *Compsognathus* (Ostrom



Figure 3 Detail of the first visible maxillary tooth and the third and fourth visible dentary teeth of CAGS-IG02-301.

1978). The dentary and maxillary teeth have the same denticle density, about 7 denticles/mm. The first two dentary teeth are almost cylindrical and resemble the premaxillary teeth, while the more posterior dentary teeth look like the maxillary teeth, as in *Sinosauropteryx* (Currie & Chen 2001). The first dentary tooth has a FABL of 1.54 mm and a crown height of 5.30 mm, while the fourth visible dentary tooth has a FABL of 4.58 mm and a crown height of 8.16 mm. Unfortunately, because their edges are covered by matrix, it is not possible to tell whether the anterior dentary teeth and the premaxillary teeth are completely unserrated as in *Sinosauropteryx* (Currie & Chen 2001), *Compsognathus* (Ostrom 1978) and many other coelurosaurs. The posterior dentary teeth of *Huaxiagnathus* are sharply bent posteriorly, as in *Sinosauropteryx*. All of the teeth are confluent between the crown and the root, not constricted as in some more advanced maniraptorans.

Axial skeleton

There are probably 10 cervical vertebrae and 13 dorsals as in *Sinosauropteryx* (Chen *et al.* 1998) and *Compsognathus* (Ostrom 1978). There are nine vertebrae with prominent neural spines visible in front of the first dorsal (identifiable as such by the pair of long pectoral ribs attached); the atlas is probably hidden in the mass of unidentifiable fragments at the back of the skull. There are 13 dorsal centra visible in front of the ilium. The sacrals are covered by the ilia and matrix, so that the number of sacrals is not determinable. The first 25 caudals are preserved.

The anterior cervical vertebrae have neural spines that are about as tall as, or taller than, they are anteroposteriorly long, giving them a more bladelike appearance than those of the posterior cervicals (Fig. 4A). The axis has the longest and tallest neural spine in the neck, as in all theropods (Makovicky 1997). The posterior cervicals have low neural spines that are about twice as long than they are tall. The postzygapophyses in the anterior cervicals are stout and rounded, with small epipophyses as in *Sinosauropteryx* (Currie & Chen 2001). The postzygapophyses become more elongate and dorsoventrally slender in the posterior cervicals. Prezygapophyses are longer than the postzygapophyses in the anterior cervicals. The centra are difficult to differentiate from one another because of the lack of preparation of the neck, but it appears that the zygapophyses extend beyond the limits of the centra. It is also uncertain whether the cervicals have biconcave centra as in *Sinosauropteryx* (Currie & Chen 2001) or opisthocoeleus centra as reported in the German specimen of *Compsognathus* (Ostrom 1978). It is not possible to see if the cervical centra are pneumatic due to the matrix covering them.

The dorsal vertebrae are overlapped by ribs, so morphological details of the structures between the neural spines and centra (such as the zygapophyses and parapophyses) are not discernable. The centra are amphiplatyan and dorsoventrally constricted midlength, so that the ventral surfaces of the centra are uniformly concave. The centra are fairly elongate, about twice as long as they are tall. The transverse processes in the anterior dorsals have been crushed; the unharmed transverse processes in the posterior dorsals point posteriorly but are held more or less horizontally. The neural spines of the dorsals are anteroposteriorly expanded distally so that they appear fan-shaped in lateral view (Fig. 4B), which is diagnostic of compsognathids (Chen *et al.* 1998). The neural spines increase slightly in height towards the posterior. As with the cervical vertebrae, it is not possible to see whether or not the dorsals are pneumatic because they are obscured by matrix and overlying ribs.

The anterior caudal centra are not noticeably shorter in length than the more posterior caudals (Fig. 4C & D). The shapes of the anterior caudal centra are similar to those of the posterior caudals in that they are elongate rather than boxy as in dromaeosaurids (Ostrom 1969). Although caudal centrum morphology is consistent throughout the tail, there is a discernable transition point. The first 12 caudals have long transverse processes; short, bumpy transverse processes and neural spines persist until the 17th caudal. The neural arches are cleanly detached from the anterior caudals and flipped so that the dorsal surfaces of the transverse processes, zygapophyses and neural spines are visible (Fig. 4C). This indicates that the neural arches were not fused to the centra in the caudal vertebrae and possibly in the rest of the vertebral column as well. Unfused neural arches may indicate that this specimen is a juvenile, which is also supported by the large size of the skull relative to the rest of the body. The transverse processes of the anterior caudals are square and broad in dorsal view and point slightly posteriorly. The height of the neural spines cannot be determined due to the orientation of the neural arches in the slab.

Chevrons first appear between the third and fourth caudal and persist between all of the remaining caudals that are preserved (Fig. 4C & D). They are elongate and

slender, tapering only slightly distally, so that they are rod-like in shape rather than spike-like. This is similar to the condition reported in *Compsognathus* (Ostrom 1978) and unlike that in *Sinosauropteryx*, which has spatulate chevrons (Currie & Chen 2001). As one moves posteriorly along the tail, the chevrons become increasingly posteriorly oriented rather than ventrally orientated and chevron length decreases. However, chevron shape remains consistently rod-like throughout the tail.

Caudal centrum length remains more or less the same until the 14th caudal, at which point centrum length increases slightly and then fluctuates around that slightly higher value for the remainder of the preserved portion of the tail (Table 2). Overall, the gross trend in the tail is an increase in centrum length up to the last caudal preserved. This is the same pattern in caudal centrum length reported in the larger specimen of *Compsognathus* (Bidar *et al.* 1972). In *Sinosauropteryx*, caudal centrum length increases to the sixth caudal but then steadily decreases thereafter, as does centrum height (Currie & Chen 2001). Centrum height in *Huaxiagnathus* follows the trend seen in other compsognathids, peaking at the sixth caudal and then decreasing thereafter. The tail of CAGS-IG02-301 probably contains at least as many vertebrae as that of *Compsognathus*, since the last preserved vertebra is long and tall and the caudal vertebrae follow the length and height trends seen in the larger specimen of *Compsognathus*.

The cervical ribs are very slender, less than 2 mm wide (Fig. 4A) and longer than the centra to which they attach, unlike the short cervical ribs seen in more advanced coelurosaurs (Makovicky 1997). The cervical ribs articulate with the cervical centra at their anteroventral corners.

The anterior dorsal ribs are about the same length as the posteriormost dorsal ribs, with the ribs along the middle of the dorsal series being the longest. The longest pairs of ribs are attached to the fourth through eighth dorsal vertebrae. The anterior ribs have a short tuberculum articulating with the transverse process of a dorsal vertebra and a long capitulum extending to the parapophysis. There is less separation between the tubercula and capitula in the posterior thoracic ribs and the capitula are shorter. The anterior dorsal ribs have shifted from their original positions, so it is uncertain where they articulated with their respective vertebrae. The posterior dorsal ribs articulate above the centra of their corresponding vertebrae, which suggests that the parapophyses of the posterior dorsals were on the neural arch, not at the upper limit of the centra. There are no uncinat processes spanning the ribs.

Gastralia are preserved along the underside of the trunk. The medial gastral segments are longer than the lateral segments. There are some rounded objects present in the abdominal cavity behind the gastralia (Fig. 5). The objects have neither the highly polished appearance nor the high-density occurrence of gastroliths; their texture and colour is the same as the bone of the skeleton. This is not surprising, since CAGS-IG02-301 has a typical carnivorous theropod dentition and gastroliths are most commonly associated with herbivory in dinosaurs (Farlow 1987; Currie 1997; Kobayashi *et al.* 1999). However, de Klerk *et al.* (2000) did report gastroliths in the basal coelurosaur *Nqwebasaurus thwasi*. The objects average 7 mm in diameter; they are too small and too irregularly shaped and placed to be eggs. The objects are most likely chunks of a partially digested meal.

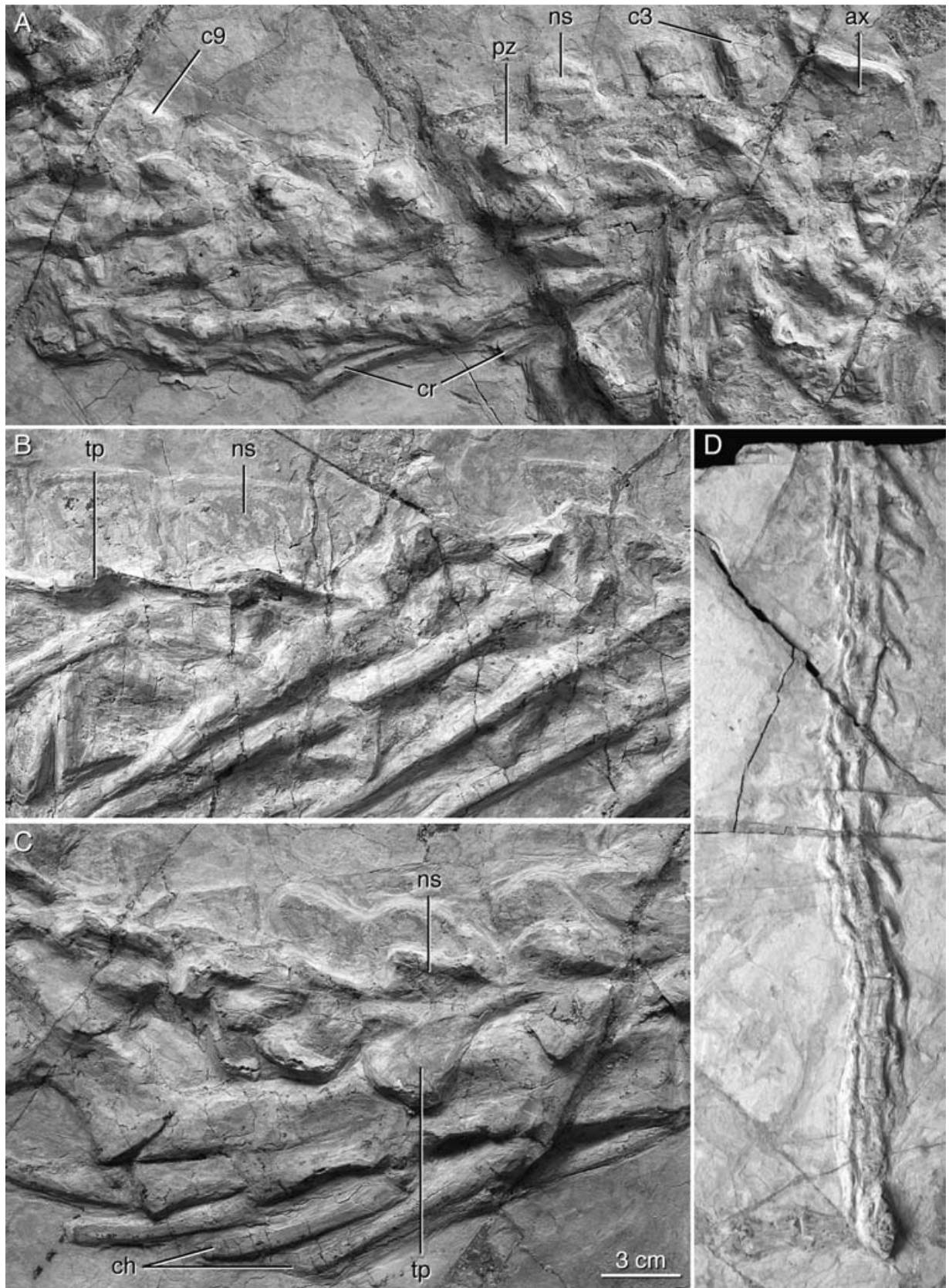


Figure 4 Vertebrae of CAGS-IGo2-301, all in right lateral view. **A**, Anterior cervicals with attached cervical ribs. **B**, Posterior dorsals with fan-shaped neural spines. **C**, Detail of anterior caudals; note the detachment of the neural arches from the centra. **D**, Posterior caudals. Abbreviations: ax, axis; c, cervical vertebra; ch, chevron; cr, cervical rib; ns, neural spine; pz, postzygapophysis; tp, transverse process.

Table 2 Selected measurements (in mm) of the caudal vertebrae of *Huaxiagnathus* (CAGS-IG02-301) and the French specimen of *Compsognathus*.[†]

Caudal number	<i>Huaxiagnathus</i>		<i>Compsognathus</i>	
	Anteroposterior length of centrum	Dorsoventral height of centrum	Anteroposterior length of centrum	Dorsoventral height of centrum
1	20.44	10.93	15.00	11.00
2	21.66	12.37	18.00	15.00
3	20.46	13.12	18.50	
4	20.16	13.08	26.00	18.00
5	19.74	14.07	19.00	14.00
6	19.67	14.38		
7	21.32	13.67		11.00
8	19.60	12.40		
9	20.71	12.35		
10	21.12	11.39		
11	20.66	11.97		
12	20.92	11.30	19.00	11.00
13	20.73	10.66	20.00	10.40
14	20.88	11.18	20.70	9.80
15	22.00	10.40	20.50	9.50
16	21.75	11.00	21.00	10.00
17	22.72	9.41	20.80	10.00
18	21.75	9.21	18.00	9.00
19	21.43	9.20	20.40	9.30
20	22.52	10.03	22.00	9.00
21	23.15	9.75	22.00	9.00
22	22.38	8.99	21.70	8.50
23	20.93	8.91	22.20	8.00
24	22.00	10.15	22.60	8.00
25	23.29	9.27	23.00	7.50
26			22.5	7
27			23.2	6.5
28			22.3	6
29			23	6
30			23.2	6
31			23	5.5
32			23	5.3

[†] Data taken from Bidar *et al.* (1972).

Pectoral girdle

The scapula is slightly longer than the humerus and the width of the scapular blade is slightly less than the diameter of the humeral shaft (Fig. 6). Distally, the blade of the scapula is dorsoventrally expanded to a small extent. The large, triangular acromion process merges smoothly with the anterior margin of the scapular blade. The glenoid fossa is small and directed posteriorly as in more primitive theropods, as opposed to more laterally as in other maniraptorans.

The coracoid, which is not fused to the scapula, is very similar in morphology to that of *Sinosauropteryx* (Currie & Chen 2001). The coracoid is subcircular in lateral view, with a tiny coracoid foramen anterior to the glenoid fossa (Fig. 6). A coracoid tubercle approximately twice the size of the coracoid foramen is positioned anteroventrally to the foramen. The ventral blade of the coracoid is shallow and tapers to a blunt point.

Half of a small, boomerang-shaped furcula is associated but not articulated with the scapulae (Fig. 6). This is the first furcula described for a compsognathid theropod. The furcula is very slender and the ramus that is preserved is slightly

sigmoidal in shape. The furcula is thickened at its rounded apex, which does not bear a hypocleidium. The furcula very closely resembles those in many tyrannosaurids, which also have sigmoid curvatures and tapered ends, except that tyrannosaurid furculae possess hypocleidia (Makovicky & Currie 1998). Enough of the other half of the furcula is preserved to estimate an interclavicular angle of 130°. There is no trace of an ossified sternum; considering the excellent preservation of bone in this specimen, this probably indicates a primitive cartilaginous sternum in *Huaxiagnathus* rather than the non-preservation of an ossified sternum (Padian 1997). Although a sternum was provisionally illustrated for the French specimen of *Compsognathus* (Bidar *et al.* 1972), Ostrom (1978) cautioned that this region of the skeleton is extremely poorly preserved and difficult to interpret.

Forelimb

The forelimbs are short and stout, with hands that are long in comparison to the rest of the forelimb (Figs. 7A & B). The forelimb is 48% of the length of the hindlimb, which

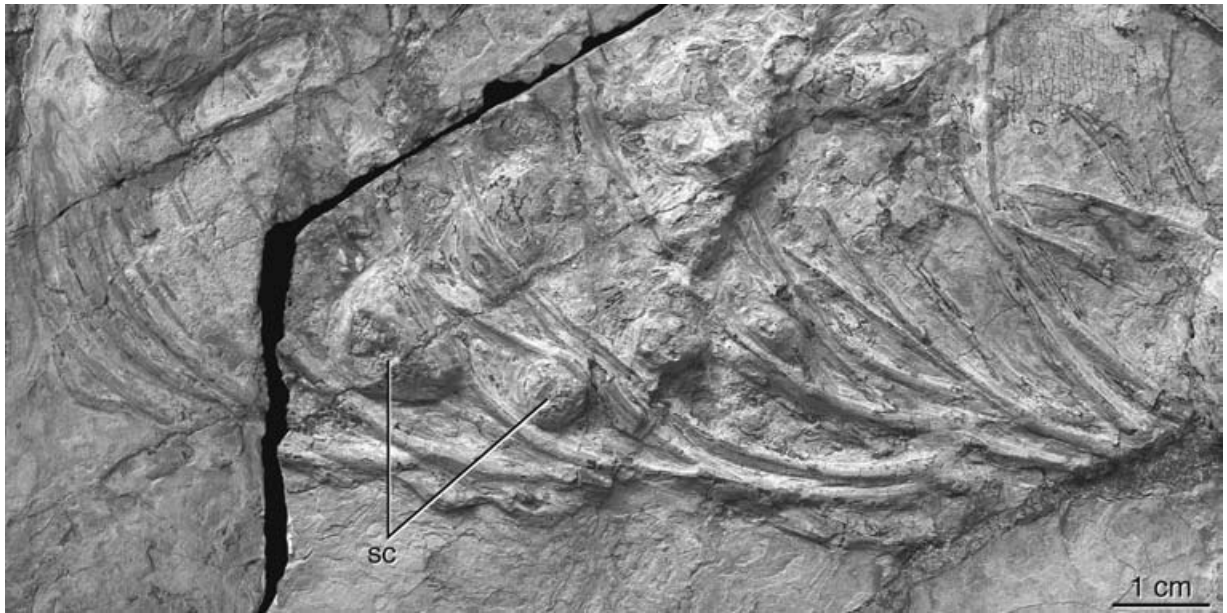


Figure 5 Gastralia of CAGS-IGo2-301, with mystery stomach contents (sc) behind them.



Figure 6 Pectoral girdle of CAGS-IGo2-301; there is no trace of an ossified sternum. Abbreviations: a, acromion process; cfo, coracoid foramen; ct, coracoid tubercle; f, furcula; lc, left coracoid; ls, left scapula; rc, right coracoid; rs, right scapula.

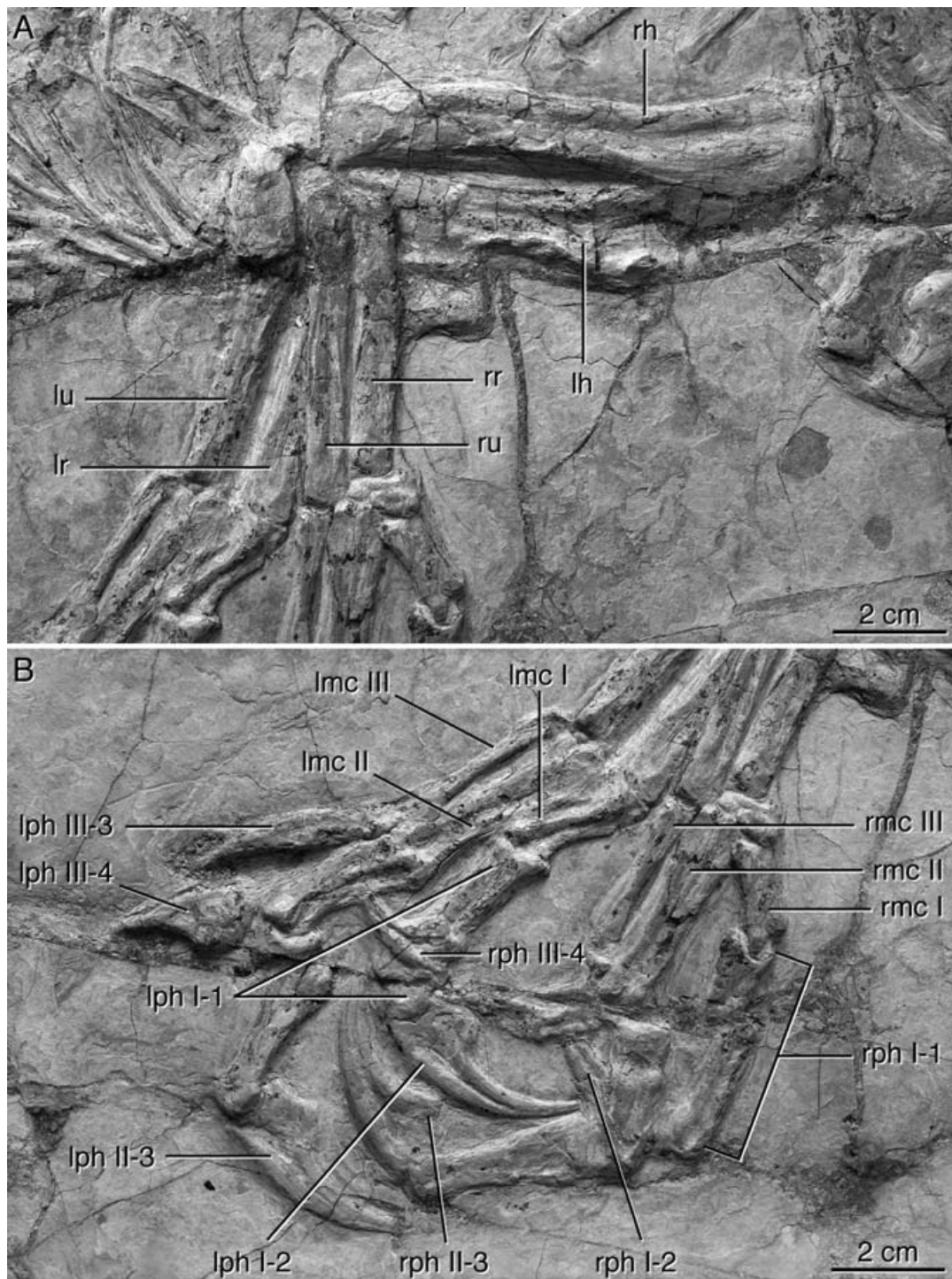


Figure 7 Forelimbs of CAGS-IGo2-301. **A**, Humeri, radii and ulnae. **B**, Hands. Abbreviations: lh, left humerus; lmc, left metacarpal; lph, left phalanx; lr, left radius; lu, left ulna; rh, right humerus; rmc, right metacarpal; rph, right phalanx; rr, right radius; ru, right ulna.

is a larger ratio than for any other compsognathid (36% and 39% for *Sinosauropteryx* and *Compsognathus*, respectively), but still a smaller ratio than for any other coelurosaur except tyrannosaurids, alvarezsaurids and some secondarily flightless avialans (Gauthier 1986). The relatively long length of the forelimb is due to the relatively great length of the manus in *Huaxiagnathus*. The lengths of the humerus plus radius divided by the lengths of the femur plus tibia is about

the same in *Compsognathus* and *Huaxiagnathus* (41% and 39%, respectively), while that for *Sinosauropteryx* is slightly lower (31%). However, the hand length of *Huaxiagnathus* is 103% of the lengths of the humerus plus radius, while in *Sinosauropteryx* and *Compsognathus* the ratios are 84% and 74%, respectively. The length of the hand of *Compsognathus* was estimated from the figures in Ostrom (1978) following Gauthier & Gishlick's (2000) reinterpretation of the manus of

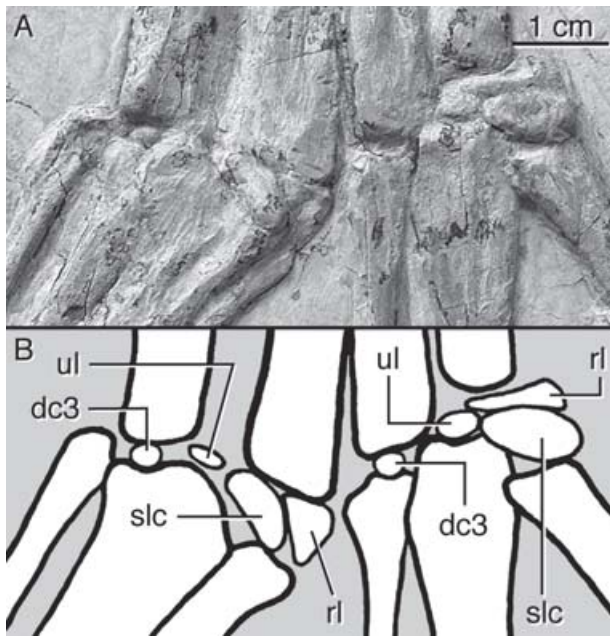


Figure 8 Photograph (A) and interpretive drawing (B) of wrist of CAGS-IGo2-301. Abbreviations: dc3, distal carpal 3; rl, radiale; slc, semilunate carpal; ul, ulnare.

Compsognathus. Therefore the element identified as phalanx I-2 by Ostrom (1978) was considered to be phalanx II-3 and increased the length of the hand to 47 mm from the 39 mm originally proposed by Ostrom (1978).

The humerus is stout and about 160% of the length of the ulna. In both *Compsognathus* (Ostrom 1978) and *Sinosauropteryx* (Currie & Chen 2001) the humerus is approximately 130% of the length of the ulna. This is due to the relatively short length of the ulna in *Huaxiagnathus*. In both *Compsognathus* and *Huaxiagnathus* the humerus is about 55% of the length of the femur, but the ulna is 42% of the length of the femur in *Compsognathus* (Ostrom 1978) and only 34% in *Huaxiagnathus*. The deltopectoral crest expands the width of the proximal end of the humerus to twice its midshaft diameter and extends 40% of the way down the humeral shaft. The anterodistal corner of the deltopectoral crest is rounded. The internal tuberosity is weakly developed, so that the posterior margin of the proximal humerus is straight. The proximal end of the humerus is quadrangular in lateral view. The distal ends of both humeri are covered by other bones or broken, so their morphology is unknown.

The radius and ulna are slender elements that are subequal in diameter. Both forearm bones are slightly expanded proximally and distally. The proximal ends of the ulnae are covered by other bones, but it appears that the olecranon is small and short as in other basal tetanurans. This is different from the condition in other compsognathids, in which the ulna is robust and has a greatly enlarged olecranon process (Ostrom 1978; Chen *et al.* 1998). The radius has a small, laterally-pointing process at its proximal end that articulates with the ulna.

There are at least four carpals in the wrist of *Huaxiagnathus*. A small, wedge-shaped carpal is the most medial one, positioned between the radius and the medial edge of metacarpal I (Fig. 8). This is presumably the radiale. A crescent-shaped carpal approximately twice the size of the

radiale lies just lateral and distal to the radiale, capping the lateral half of the proximal surface of metacarpal I and the medial third of the proximal surface of metacarpal II. This is the largest carpal in the wrist and is probably the semilunate carpal (*sensu* Padian & Chiappe 1998, in which any crescent-shaped, single distal carpal capping digits I and II – formed by the fusion of distal carpals 1 and 2 – is considered to be a semilunate carpal). The small semilunate carpal that incompletely covers metacarpals I and II is the same size as those seen in *Sinosauropteryx* (Currie & Chen 2001) and other less derived tetanurans (Holtz 2000, 2001; Chure 2001). A third, disk-like carpal about half the size of the radiale is positioned between the radius and ulna and may be the ulnare. Finally, a tiny fourth carpal is situated between the ulna and metacarpal III, which is presumably distal carpal 3.

Metacarpal I is short and stout, just under half the length of metacarpal II (Fig. 7B). Metacarpal II is the longest and most robust metacarpal. This is different from the situation in *Sinosauropteryx*, in which the first metacarpal is much broader and shorter than the second (Currie & Chen 2001). In their reinterpretation of the *Compsognathus* holotype, Gauthier & Gishlick (2000) also report a very short metacarpal I. The proximal end of metacarpal II is well-developed and greatly expanded mediolaterally. It appears triangular in extensor view, with a central peak that articulates with the ulnare and two articular surfaces to either side; the medial articular surface articulates with the semilunate carpal and the lateral one with distal carpal 3. Metacarpal III is very slender, as in *Compsognathus* (Ostrom 1978) and is only half the diameter of metacarpals I and II and slightly shorter than metacarpal II. Metacarpal III is slightly bowed laterally. Both the proximal and distal ends are expanded, but the distal end is the wider of the two ends.

Both of the robust first phalanges of manual digit I are preserved in lateral view. The proximal diameter of phalanx I-1 is greater than the diameter of the radius, which is a diagnostic character of compsognathids (the element identified as metacarpal I by Ostrom (1978) was reinterpreted as phalanx I-1 by Gauthier & Gishlick (2000)). It is similar in thickness to, and almost the same length as, metacarpal II, but is slightly shorter. Phalanx I-1 is the longest non-ungual phalanx in the hand. The proximal articular facet of phalanx I-1 is well-developed, with pronounced dorsal and ventral extensions overlapping the distal end of metacarpal I. The ungual of digit I is the largest in the hand, with a large flexor tubercle and a relatively small articular facet; the height of the articular facet is subequal to that of the flexor tubercle. The sharp claws have deep claw sheath grooves and are extremely recurved.

Digit II is the longest in the hand as is typical of theropods and the combined lengths of the phalanges of digit II are greater than the combined lengths of the phalanges of digit I. This is different from the condition reported in *Sinosauropteryx*, in which the combined lengths of the phalanges of the second digit are less than the combined lengths of the phalanges of the first digit, but digit II extends further distally than digit I because of the greater length of metacarpal II (Currie & Chen 2001). The second digit is also robust, with an ungual that is subequal in size to that of digit I. The large second digit ungual is a diagnostic character of *Huaxiagnathus*. The second phalanx of digit II is longer than the first.

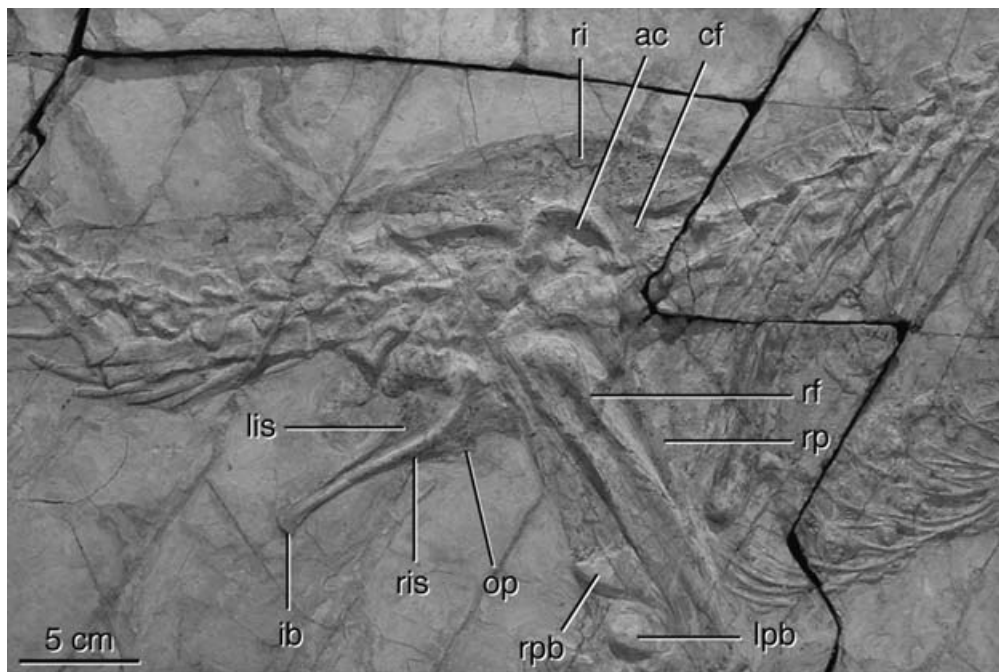


Figure 9 Pelvic girdle and right femur of CAGS-IGo2-301. Abbreviations: ac, acetabulum; cf, cuppedicus fossa; ib, ischial boot; lis, left ischium; lpb, left pubic boot; op, obturator process; rf, right femur; ri, right ilium; ris, right ischium; rp, right pubis; rpb, right pubic boot.

Digit III is the shortest and most slender digit in the hand. The phalanges of digit III are half as thick as those of the other two digits and much shorter. The ungual is small in proportion to the rest of the digit; it is half the size of those of digits I and II. Of the non-ungual phalanges, phalanx III-3 is the longest, phalanx III-1 is the next longest and phalanx III-2 is the shortest.

The manus of *Huaxiagnathus* is less derived than that of *Sinosauropteryx* and more closely resembles the primitive maniraptoran condition, with its first metacarpal of normal proportions and thin, bowed third metacarpal (Gauthier 1986). However, *Huaxiagnathus* does depart from the typical maniraptoran pattern and shows affinities with *Sinosauropteryx* in its large phalanx I-1 and short third digit.

Pelvic girdle

The ilium is very simple in morphology and almost symmetrical in lateral view; the preacetabular wing is only slightly shorter than the postacetabular wing and both ends of the iliac blade terminate in gently rounded edges of the same height (Fig. 9). The postacetabular wing of the ilium does not taper posteriorly in lateral view as in most maniraptorans (see Hutchinson 2001: figs 4, 6; Norell, Clark & Makovicky 2001: 64; this character was considered a synapomorphy for Maniraptora). The acetabulum has a well-defined dorsal rim. The ventral surface of the pubic peduncle of the ilium slopes anteroventrally, while that of the ischiadic peduncle slopes posteroventrally. Both peduncles are subrectangular processes. The ischiadic peduncle has an anteroposterior length of about half that of the pubic peduncle. The cuppedicus fossa is fairly deep, but the antiliac shelf extends only halfway over the pubic peduncle. There is no vertical ridge dividing the lateral surface of the ilium as in some theropods (Hutchinson 2001), but its presence is

known to vary in different individuals of some theropod species (e.g. *Velociraptor mongoliensis*: Norell & Makovicky 1999).

The ischium is slightly more than two-thirds the length of the pubis (Fig. 9). A prominent, triangular obturator process is positioned proximally on the ischium, just distal to the pubic process, as in other less derived coelurosaurs and tetanurans (Hutchinson 2001). The pubic and iliac processes of the ischium are subequal in size and separated by a small, rounded notch that is the ischiadic contribution to the acetabulum. The ischial shaft thins distal to the obturator process, expanding again at its distal extremity. The ischia are fused distally into a moderately expanded symphysis, as in other compsognathids (Ostrom 1978; Chen *et al.* 1998).

The pubis is almost vertical, as in *Sinosauropteryx*, with the proximal portion of the pubis being more or less vertical and the distal end angled slightly anteriorly, approximately 15° from vertical (Fig. 9). The proximal end of the pubis is anteroposteriorly expanded and fan-shaped in lateral view. The ischiadic process of the pubis curls ventrally, forming a small hook at its posteroventral margin. The pubic shaft is very straight. Distally, a well-developed pubic boot that is anteroposteriorly longer than the proximal end is present. There is no anterior expansion of the pubic boot, as in *Compsognathus* (Ostrom 1978), *Aristosuchus* (Owen 1876; Naish 1999), SMNK 2349 Pal (Martill *et al.* 2000) and some other maniraptorans (Gauthier 1986).

Hindlimb

Only the right femur is visible, in lateral view. The femur is a stout element that is only moderately bowed anteroposteriorly (Fig. 9). The proximal half of the femur is slightly crushed, so that the lesser trochanter appears wide and square and the greater trochanter thin and tall; the

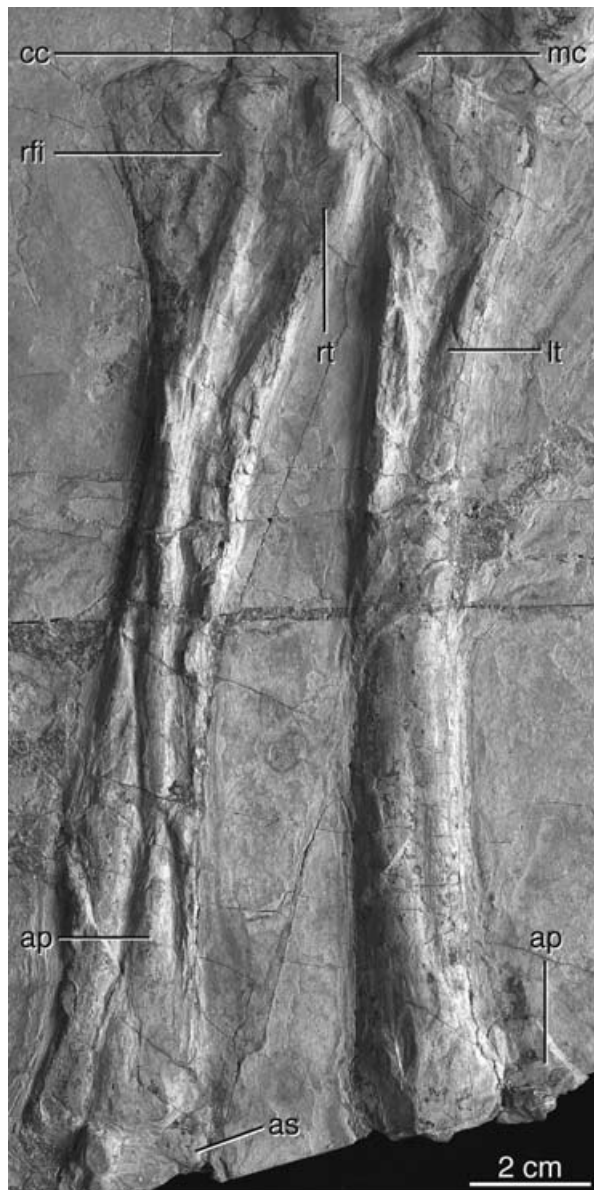


Figure 10 Right tibia of CAGS-IGo2-301 in anterior view, left tibia in medial view, and right fibula in oblique anterolateral view.

Abbreviations: ap, ascending process; as, astragalus; cc, cnemial crest; lt, left tibia; mc, medial condyle; rfi, right fibula; rt, right tibia.

true morphology of the trochanters is uncertain. The lesser trochanter appears to have been separated from the greater trochanter by a deep cleft. Because of the crushing, it is unclear whether the long, sharp ridge at the posterior margin of the shaft below the greater trochanter comprises the posterior trochanter and fourth trochanter, or if it is a deformational artefact. The distal condyles are rounded and separated by a shallow groove.

Both tibiae and fibulae have suffered some crushing and the proximal articular surfaces are covered by other bones or are not well-preserved (Fig. 10). The tibiae are more slender than the femora, but relatively short, only 112% of the length of the femora, as in the larger Nanjing specimen of *Sinosauropteryx* (Currie & Chen 2001). The anterior surface

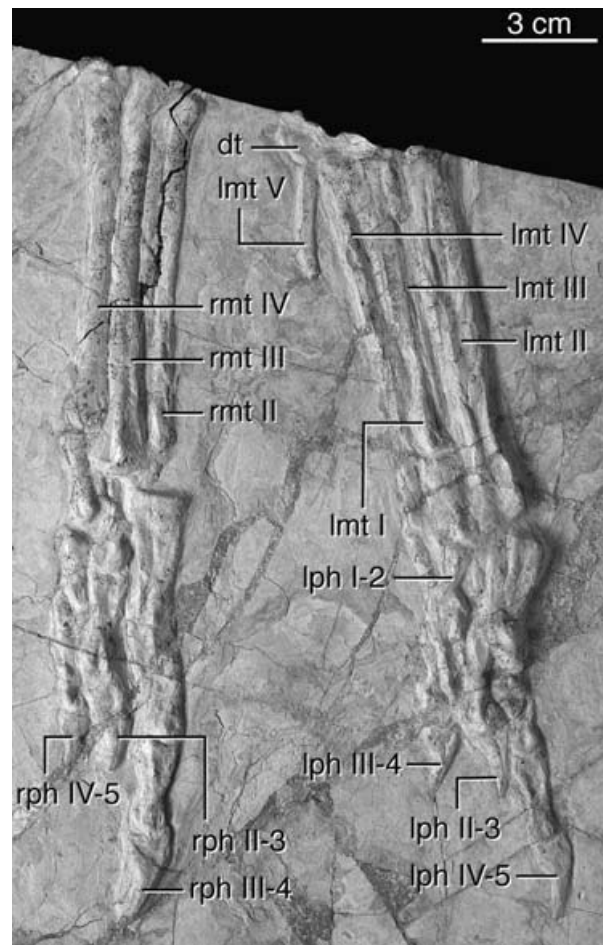


Figure 11 Right pes of CAGS-IGo2-301 in oblique anterior view and left pes in oblique posterior view. Abbreviations: dt, distal tarsal; lmt, left metatarsal; lph, left phalanx; rmt, right metatarsal; rph, right phalanx.

of the right tibia is exposed. Most of the right fibula is shifted medially from its normal position, so that it is visible in oblique anterolateral view; only its distal end is still in place. A well-developed single cnemial crest curves laterally towards the fibula at the proximal end of the tibia. Because the fibula has shifted medially, the fibular crest of the tibia is not visible. The proximal fibula is fan-shaped in lateral view, but quickly attenuates to a thin rod of bone. The calcaneum is missing, so it was probably not fused to the astragalus. The astragalus has a high ascending process and well-rounded condyles that are separated from the ascending process by a pronounced horizontal sulcus. The area between the two condyles of the astragalus is covered by matrix, so it is difficult to determine which of the two is larger, but they are approximately the same size. The astragalus is approximately 20% of the length of the tibia and covers about 75% of the anterior width of the distal tibia.

Unfortunately, one of the slab junctions is located between the metatarsals and the tibiotarsus, so some of the tarsals may have been lost. At least one distal tarsal is present at the lateral margin of the ankle, capping metatarsal IV (Fig. 11). This distal tarsal is not fused to the metatarsus. The metatarsus is symmetrical and does not show the

arctometatarsalian condition (Holtz 1994), with metatarsals II, III and IV subequal in width to one another. Metatarsal III is the longest metatarsal, while metatarsals II and IV are almost exactly the same length (metatarsal IV is longer by barely a millimetre). Metatarsal V is approximately one-third of the width and length of metatarsal IV. Metatarsal V tapers distally and is bent medially approximately halfway along its length. Metatarsal I is preserved on the posterior surface of the metatarsus, but it has shifted from its original position and is no longer in contact with the second metatarsal. It is probably at approximately the same horizontal position as it was in life, about halfway down the shaft of metatarsal II. The first metatarsal is reduced proximally to a blunt point and has a narrow distal articulatory surface.

The pedal digits follow the typical theropod phalangeal formula of 2–3–4–5–0 (Fig. 11). Digit I is slender, with the smallest ungual of the pedal phalanges. Digit III is the longest and most robust pedal digit. Digits II and IV are subequal in length and width, with unguals of subequal size. The pedal unguals are weakly recurved, with large flexor tubercles.

DISCUSSION

While *Huaxiagnathus orientalis* is the second largest coelurosaur to come out of the Liaoning deposits, it is only about half a metre longer than the larger French specimen of *Compsognathus* and the largest specimens of *Sinosauropteryx*. Size variation within the known compsognathids is not as dramatic as in the dromaeosaurids; for example: *Microraptor zhaoianus* is only 55 cm long as an adult (Hwang *et al.* 2002b), while *Utahraptor ostrommaysi* is over 5 m long (Kirkland, Gaston & Burge 1993). *Huaxiagnathus* and other compsognathids are relatively unspecialised (Holtz 2000), like the basal coelurosaurian *Scipionyx samniticus* (dal Sasso & Signore 1998) and retain a basic coelurosaurian body plan. As a result, compsognathids are difficult to diagnose with autapomorphies other than those that characterise them as compsognathids. *Huaxiagnathus*, although possessing a few autapomorphic characters, is most notable for its large size and primitive proportions, neither of which is technically diagnostic. Diagnostic characters are also scarce in *Sinosauropteryx* and *Compsognathus*; the Asian distribution of the former most readily distinguishes it from the latter. *Compsognathus* does have a higher degree of heterodonty (Stromer 1934) than *Sinosauropteryx*, with sharply bent, unserrated premaxillary and anterior dentary teeth, and more typically recurved maxillary and posterior dentary teeth with serrations on the posterior carinae. Currie & Chen (2001) state that the primary features that differentiate *Sinosauropteryx* from *Compsognathus* are relatively shorter forelimbs and shorter cervical ribs, both of which are vague sorts of characters that could easily be affected by ontogeny. Currie & Chen (2001) also noted that *Sinosauropteryx* has caudal transverse processes and integumentary structures, while *Compsognathus* does not, but they also stated that this could just be due to the poorer preservation of the known *Compsognathus* specimens. However, because compsognathids are so unspecialised, they may offer a glimpse of the ancestral maniraptoriform and maniraptoran condition (Holtz 2000).

A very poorly preserved, badly reconstructed, but unusually large specimen, National Geological Museum of China (NGMC) 98-5-003 (Hwang *et al.* 2001), is tentatively identified as *Huaxiagnathus orientalis*. Despite the poor condition of NGMC 98-5-003, there is strong evidence that makes this connection plausible. Both specimens were found in the Sihetun area, in identical facies and they are of similar size. Although size is not technically diagnostic, the small size of the vast majority of theropods excavated from the Sihetun area makes the large size of NGMC 98-5-003 very distinctive. NGMC 98-5-003 has the same basic coelurosaurian body plan as CAGS-IG02-301 and the bones that are preserved in their entirety in NGMC 98-5-003 are the same in morphology as those in CAGS-IG02-301. For example, the shape and relative size of the distal carpals, metacarpals and visible unguals match those of CAGS-IG02-301. In both taxa, the short first metacarpal is half the length and the width of the long, proximally expanded second metacarpal, while the third metacarpal is very slender. The unguals of the first and second manual digits are subequal in size in NGMC 98-5-003, which is a diagnostic character of *Huaxiagnathus*. In addition, the radius and ulna of NGMC 98-5-003 are short and slender, as in CAGS-IG02-301. The forelimbs of NGMC 98-5-003 are completely different from those of *Sinosauropteryx*, which has a very short metacarpal I that is wider than metacarpal II, a small ungual on phalanx II and much shorter arms in proportion to its legs, eliminating the possibility that NGMC 98-5-003 is a very large individual of *Sinosauropteryx*. Elements of the pes in NGMC 98-5-003 are also identical to those in the *Huaxiagnathus* holotype. The small, disk-like, distal tarsals are not fused to the metatarsals as in CAGS-IG02-301. The short, proximally tapering metatarsal I, long, slender metatarsal V and phalanx I-1 have the same morphology and are the same relative size to one another as those in CAGS-IG02-301.

If these two specimens are the same species, then the slightly larger NGMC 98-5-003 may represent an older individual, while the holotype may represent a subadult individual. While the carpals and tarsals are well-ossified in the holotype, the skull is relatively large in proportion to the rest of the body and the neural arches of the vertebrae, where visible, are not fused to the centra. The general proportions of NGMC 98-5-003 are similar to those of CAGS-IG02-301, except that the skull of NGMC 98-5-003 is shorter in proportion to the presacral vertebral column – 34% as opposed to 45% in CAGS-IG02-301. Because the extent of neural arch fusion could not be determined in NGMC 98-5-003, it is uncertain whether or not NGMC 98-5-003 is fully adult.

PHYLOGENETIC ANALYSIS

Analysis of the systematic position of CAGS-IG02-301 and other compsognathids was undertaken using the evolving theropod data matrix created by our research group, which first appeared in Norell *et al.* (2001). It has subsequently been used to analyse the phylogenetic position of several new theropod taxa (Hwang *et al.* 2002a; Xu *et al.* 2002a, b) and new taxa and characters are continuously incorporated into it. The current matrix consists of 222 characters and 55 taxa coded at the species level (2 outgroups and 53 ingroups). Both the matrix and character list are available as

supplementary data on the *Journal of Systematic Palaeontology* website (http://www.journals.cup.org/abstract_S1477201903001081).

Sinosauropteryx prima was coded from the excellent descriptions and figures in Currie & Chen (2001). *Compsognathus longipes* posed more of a problem, because we were unable to examine the specimens firsthand and descriptions of the European specimens vary; it was not included in the original Norell *et al.* (2001) study for these reasons. However, we wanted to include *Compsognathus* in this study in order to see how the well-known species of compsognathids related to one another. Therefore, *Compsognathus longipes* was coded conservatively using figures and the most objective, non-interpretive descriptions from Bidar *et al.* (1972) and Ostrom (1978). Gauthier & Gishlick's (2000) interpretation of the manus of *Compsognathus* was accepted as correct, since Currie & Chen (2001) used the same interpretation of the hand of *Compsognathus* when comparing it to that of *Sinosauropteryx*. For problematic characters about which different authors disagree, such as the number of digits in the manus and whether or not the cervical vertebrae are opisthocoelic, codings were left as unknown ('?'). All analysis was carried out using NONA v.1.9 (Goloboff 1993). A heuristic search using 1000 replicates of tree bisection and reconnection (TBR) branch-swapping was performed. The 10 shortest trees from each replicate were kept and then additional branch-swapping was performed among the shortest of the retained trees. This found 2592 most parsimonious trees (MPTs), each with 629 steps, Consistency Index (CI) = 0.43 and Retention Index (RI) = 0.74: a strict consensus of these trees is shown in Fig. 12.

Huaxiagnathus orientalis falls out as the sister taxon to a *Sinosauropteryx*–*Compsognathus* clade and the three taxa together form a monophyletic Compsognathidae. The position of the compsognathids near the base of Maniraptora is the same as that obtained by Gauthier (1986) and Holtz (2000), differing from the alternate view that compsognathids are more primitive than ornithomimids (Forster *et al.* 1998; Sereno 1999). Maniraptora is supported by six unambiguous synapomorphies, including dorsally convex parietals with a low sagittal crest, large hypapophyses on the anterior dorsal vertebrae, separated hyposphenes on the dorsal vertebrae, absence of neural spines on the distal caudals, a shortened cuppedicus fossa that ends posteriorly on the pubic peduncle and a vertically oriented pubis (characters 46, 102, 105, 119, 163 and 175). Characters 102, 105, 119, 163 and 175 were all synapomorphies for Maniraptora in the original Norell *et al.* (2001) analysis. The four maniraptoran synapomorphies from Norell *et al.* (2001) that were lost with the addition of new taxa to the dataset are a greatly reduced prefrontal, a lateral tab on the quadrate that contacts the squamosal and quadratojugal, short, deep paroccipital processes and a tapered postacetabular process of the ilium (characters 41, 51, 57 and 158 in this version of the dataset). *Sinosauropteryx* possesses the primitive character state ('0') for character 41, while the most basal maniraptoran, *Ornitholestes*, has state '1' and more advanced maniraptorans tend to have state '2'. This causes a greatly reduced prefrontal (state '1' of character 41) to become an autapomorphy of *Ornitholestes*. Missing data causes the ambiguous optimisation of characters 54 and 57, since the state of character 54 is unknown ('?') in *Huaxiagnathus* and *Compsognathus* and character 57 is unknown in all three compsognathids included in the matrix. The tapered

postacetabular process of the ilium (character 158) is ambiguously optimised because a recently added, undescribed, basal ornithomimid has a tapered postacetabular process, unlike more derived ornithomimids, which have the primitive squared process. The shape of the postacetabular process is unknown in the most basal ornithomimid, *Pelecanimimus*, but is tapered in *Ornitholestes* and squared in *Huaxiagnathus* and *Sinosauropteryx*.

Compsognathids are united with more derived maniraptoran clades by the presence of fused parietals, premaxillary tooth crowns with suboval to subcircular cross-sections and the absence of a separate supra-acetabular crest on the ilium (characters 47, 91 and 157). It takes only one additional step for compsognathids to be placed at the base of the Maniraptora and three additional steps for them to fall outside the Maniraptoriformes; however, most of the clades in our tree, including some that are supported by more than 10 unambiguous characters (such as Paraves and the clade comprised of Alvarezsauridae, Therizinosauroidea + Oviraptorosauria and Paraves), collapse in just one step. Compsognathidae itself is a relatively robust clade, with a Bremer support of 3.

Huaxiagnathus orientalis is the most basal compsognathid, as shown by its relatively unspecialised forearm; it shares with *Sinosauropteryx* and *Compsognathus* a robust phalanx I-1 (character 207; this is an unambiguous synapomorphy for compsognathids only in the trees in which Alvarezsauridae clusters with Paraves or the Therizinosauroidea + Oviraptorosauria clade) but does not have a large olecranon process on the ulna (character 142). The lack of specialisation in the forearm of *Huaxiagnathus* may also explain its greater relative length compared to those of other compsognathids – the short length of the forearm in compsognathids is considered to be a secondary modification (Gauthier 1986).

For the most part, the rest of the tree agrees with recent phylogenies obtained from our group's dataset (Hwang *et al.* 2002a; Xu *et al.* 2002a, b). The topology of the consensus tree is almost identical to that obtained by Xu *et al.* (2002a); in that study, Alvarezsauridae also fell out in an unresolved trichotomy with Paraves and Therizinosauroidea + Oviraptorosauria (TO). This trichotomy is somewhat surprising because alvarezsaurids landed near the base of Maniraptora in almost all of the studies using this data matrix (Norell *et al.* 2001; Hwang *et al.* 2002a; Xu *et al.* 2002b) and independently in Novas & Pol (2002). Because alvarezsaurids show affinities to myriad groups, the phylogenetic position of the group is uncertain. Alvarezsauridae was originally considered to be an avialan group sister to Ornithothoraces (Perle *et al.* 1993; Chiappe, Norell & Clark 1996), but has more recently been posited as the sister taxon to Avialae (Chiappe 2001, 2002) and as the sister taxon to ornithomimids (Sereno 1999, 2001).

The unresolved trichotomy between Alvarezsauridae, TO and Paraves in the consensus tree from this study is due to the uncertain position of Alvarezsauridae. In a third of the resulting MPTs, alvarezsaurids fall out as basal to a monophyletic Paraves + TO clade. In another third of the MPTs, alvarezsaurids + TO are a monophyletic group that is the sister taxon to Paraves, while in the remaining third of the MPTs alvarezsaurids form a monophyletic clade with Paraves that is sister to TO. The higher maniraptoran clade comprised of Alvarezsauridae, Therizinosauroidea, Oviraptorosauria and Paraves is supported by at least 11 unambiguous

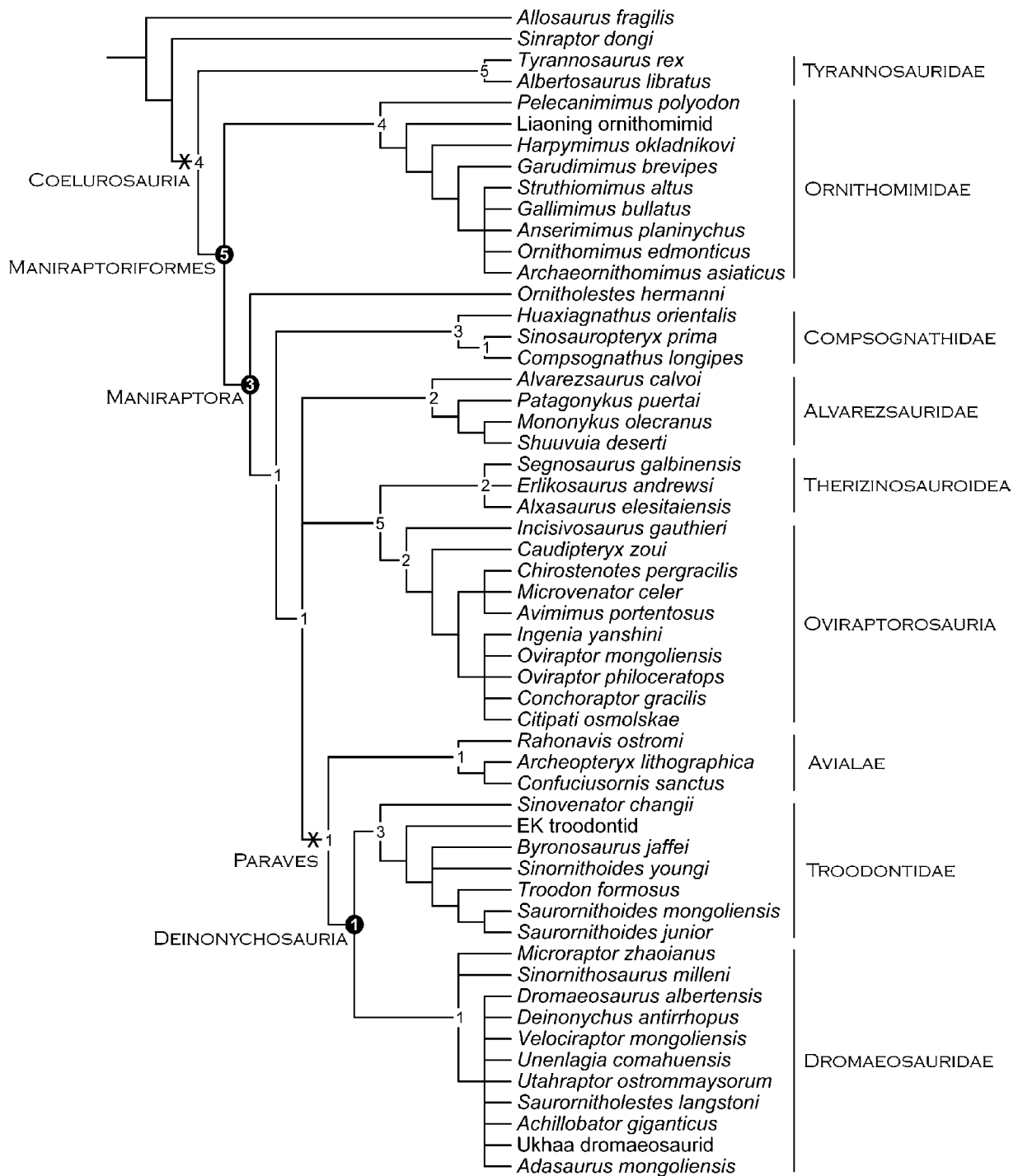


Figure 12 Strict consensus of the 2592 most parsimonious trees obtained, each with 629 steps, Consistency index (CI) = 0.43, retention index (RI) = 0.74. The numbers at major nodes represent the Bremer support for the clade stemming from that node. Undescribed taxa are not italicised and referred to by a descriptive term only. •, node-based taxon; X, stem-based taxon.

synapomorphies in all three topologies, with eight being common to all three, including teeth that are constricted between the root and crown (character 88), a transition point in the tail proximal to the tenth caudal (116), absence of an obturator notch (169) and ischial boot (173) and widely separated ischia (172). However, only two unambiguous synapomorphies support the next higher node in all three topologies. A TO-Paraves grouping is supported by a sternum with

lateral xiphoid processes and with anteriorly positioned articular facets for the coracoids (characters 129 and 131). An Alvarezsaurid-TO grouping is supported by a downturned dentary and the absence of a foramen in the lateral surface of the surangular (characters 67 and 75). Finally, an Alvarezsaurid-Paraves grouping is supported by an external naris that has a caudal margin farther rostral than the rostral border of the antorbital fossa and the presence of carotid

processes on the posterior cervical vertebrae (characters 23 and 97). An Alvarezsaurid–Paraves grouping is probably the least likely of the three conflicting topologies; as previously mentioned, alvarezsaurids have consistently been resolved as basal maniraptorans in our studies and Sereno (2001) noted that basal alvarezsaurids are less birdlike than derived ones, suggesting that the avian affinities of derived alvarezsaurids were independently acquired. Xu *et al.* (2002a) also noted that derived members of basal maniraptoran lineages, such as Oviraptorosauria and possibly Alvarezsauridae, are more birdlike than the basal taxa.

Incisivosaurus gauthieri (Xu *et al.* 2002a), the taxon added most recently to this matrix prior to the compsoognathids of this study, is missing almost all of its postcrania (only a partial cervical is preserved for the taxon). Discovery of postcranial material for this taxon could easily affect the arrangement of our tree. Paraves, Deinonychosauria and the Therizinosauridae + Oviraptorosauria clade remain stable in this study, although neither Paraves nor Deinonychosauria appeared in the initial analysis using this dataset (Norell *et al.* 2001). The continuously fluctuating topology of the consensus trees obtained from this dataset shows how important new taxa are in influencing our understanding of coelurosaur evolution.

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