A LARGE COMPSOGNATHID FROM THE EARLY CRETACEOUS YIXIAN FORMATION OF CHINA

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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 Therizinosauroidea + 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

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INTRODUCTION

Compsoognathids 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 compsoognathids 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 corvallestris, 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 compsoognathids, but both specimens are too incomplete to include in a phylogenetic analysis. Here we describe a new compsoognathid, Huaxiagnathus orientalis gen. et sp. nov., from the Xixian Formation of China, which is unusual because of its large size. Both Compsognathus and Sinosauropteryx are small animals (although the size of the French Compsoognathus specimen is nearly twice the size of the type specimen), as are most of the theropod taxa found in the Early Cretaceous Xixian 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. 2002h, 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 compsoognathids. 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 Compsoognathus, 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 compsoognathids, but not of other non-tyrannosaurid coelurosaurians (Gauthier 1986). Huaxiagnathus orientalis can be assigned to the Compsoognathidae 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.
SMNK = Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe, Germany.

SYSTEMATIC PALEONTOLOGY

THEROPODA Marsh, 1881
COELUROSARIA 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 Xixian Formation of Liaoning Province, China.

DIAGNOSIS. Differs from other known compsoognathids in having a very long posterior process of the premaxilla that
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>
<thead>
<tr>
<th></th>
<th>Huaxiagnathus (CAGS-IG02-301)</th>
<th>Sinosauropteryx (NIGP 127587)</th>
<th>Compsognathus (BSP ASI 563)</th>
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<tr>
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<tr>
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</tbody>
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Ratios are based on values from Chen et al. (1998) and Currie & Chen (2001) for *Sinosauropteryx* and from Ostrom (1978) for *Compsognathus*. 

Figure 1  The holotype of *Huaxiagnathus orientalis* (CAGS-IG02-301).
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), *Microceraptor* (Xu et al. 2000) and *Compsognathus* (Ostrom 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 coelurosaurians. 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 as 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 opisthocoelus 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 elongated, 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 vertebrae are not noticeably shorter in length than the more posterior caudals (Fig. 4C & D). The shapes of the anterior caudal vertebrae are similar to those of the posterior caudals in that they are elongate rather than boxy as in dromaeosaurs (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 spines 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 oriented 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 uncinate 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-IG02-301, 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*.†

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† 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-IG02-301, with mystery stomach contents (sc) behind them.

Figure 6  Pectoral girdle of CAGS-IG02-301; 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.
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 tyrannosaurs, alvarezsauds 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...
Huaxiagnathus. 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 metacarpus 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 mediallylateral. It appears triangular in extensor view, with a central peak that articulates with the ulnare and two articulatory surfaces to either side; the medial articulatory 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.
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 II-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 peduncules 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 coelurosaurians 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 ischiadic 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
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 articulatory 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 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 and distally, 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 compsgnathids is not as dramatic as in the dromaeosaurids; for example: *Microsauraptor 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 compsgnathids 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, compsgnathids are difficult to diagnose with autapomorphies other than those that characterise them as compsgnathids. *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 is most readily distinguished from it by the latter. *Compsognathus* does have a higher degree of heterodonty (Stromer 1934) than *Sinosauropteryx*, with sharply bent, un serrated 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 compsgnathids 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, which are 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 compsgnathids 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 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 Therizinosauria + 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, Alvarezsauroidea also fell out in an unresolved trichotomy with Paraves and Therizinosauria + 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 Aves (Chiappe 2001, 2002) and as the sister taxon to ornithimimid (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, Therizinosauridae, Oviraptorosauria and Paraves is supported by at least 11 unambiguous...
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 Alvarezsaur–Paraves grouping is probably the least likely of the three conflicting topologies; as previously mentioned, alcavresaurids have consistently been resolved as basal maniraptorans in our studies and Sereno (2001) noted that basal alcavresaurids are less birdlike than derived ones, suggesting that the avian affinities of derived alcavresaurids were independently acquired. Xu et al. (2002a) also noted that derived members of basal maniraptoran lineages, such as Oviraptorosauria and possibly Alcavresauridae, are more birdlike than the basal taxa.

*Incisivosaurus gauthieri* (Xu et al. 2002a), the taxon added most recently to this matrix prior to the compsgnathids 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 Therizinosauroidea + 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.

**Acknowledgments**

We would like to thank the Chinese Academy of Geological Sciences and National Geological Museum of China for access to the *Huaxiagnathus* specimens. We are grateful to Mick Ellison for his excellent work in preparing the figures and Diego Pol for his NONA expertise. The comments of Oliver Rauhut and an anonymous reviewer were greatly appreciated in improving the quality of this paper. This project was supported by the Division of Paleontology at the American Museum of Natural History.

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“Supplementary data” available on Cambridge Journals Online on: http://www.journals.cup.org/abstract_S1477201903001081