The osteology of the wrist of *Heyuannia huangi* (Oviraptorosauria) and its implications for the wrist folding mechanism

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The wrist of extant birds is highly specialized which permits folding of the forelimb, in order to protect the pennaceous feather when they relax. The similar mechanism is absent in most non-avian theropods and unknown in oviraptorosaurs because the specimens with well-preserved wrist are rare. Here we give a detailed description about the wrist of two three-dimensionally preserved oviraptorosaurian *Heyuannia huangi* specimens from the Upper Cretaceous in the Southern China. The wrist of *Heyuannia huangi* is obviously specialized with a strongly dorsoventrally compressed distal ulna, larger radiale angle and strongly convex semilunate carpal. The morphology of its wrist indicates that the distal ulna would not prevent the rotation of the manus, giving the smallest angle between the manus and the ulna smaller than 90°. The combination with the morphology of the wrist of oviraptorosaurs and the phylogenetic result indicates a functional convergence in the wrist of oviraptorids and extant birds.

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Abstract

The wrist of extant birds is highly specialized which permits folding of the forelimb, in order to protect the pennaceous feathers when they relax. The similar mechanism is absent in most non-avian theropods and unknown in oviraptorosaurs because the specimens with well-preserved wrists are rare. Here we give a detailed description about the wrist of two three-dimensionally preserved oviraptorosaurian *Heyuannia huangi* specimens from the Upper Cretaceous in the Southern China. The wrist of *Heyuannia huangi* is obviously specialized with a strongly dorsoventrally compressed distal ulna, larger radiale angle and strongly convex semilunate carpal. The morphology of its wrist indicates that the distal

ulna would not prevent the rotation of the manus, giving the smallest angle between the manus and the ulna smaller than 90°. The combination with the morphology of the wrist of oviraptorosaurs and the phylogenetic result indicates a functional convergence in the wrist of oviraptorids and extant birds.

Introduction

Heyuannia huangi (Fig. 1) is an oviraptorosaurian theropod found from the Upper Cretaceous Zhutian Formation in the Heyuan Basin of Guangdong Province, China (Lü, 2005). Zhutian Formation was originally named as Dalangshan Formation and regarded as the Maastrichtian (Lü, 2002). In the later research, this deposits is revised to Zhutian Formation, and its age is changed to Upper Campanian (Lü, 2005).

Oviraptorosauria is a clade among non-paravian theropods which possesses several morphological characters similar to the primitive birds, including the fused dentary and premaxilla, jugal narrow and rod-shaped, loss of the maxillary and dentary teeth, ectopterygoid connecting lacrimal to the palatine, reduction in the number of caudal vertebrae (Elzanowski, 1999; Maryańska et al., 2002; Lü et al., 2002). The early phylogenetic analyses performed on theropods even recovered oviraptorosaurs as flightless birds rather than non-avian therapods (Maryańska et al., 2002; Lü et al., 2002). Recent studies on coelurosaurian phylogeny have identified oviraptorosaurs as the basal pennaraptorans (Brusatte et al., 2014; Lee et al., 2014). They are found to be more closely related to birds than most theropods, with the exception of deinonychosaurs. Oviraptorosaurs are regarded as the feathered dinosaurs because of the elongated pennaceous feathers covering on the forelimb and tail in the basal species (Ji and Ji. 1997; Zhou et al., 2000; Zhou and Wang, 2000; Qiu et al., 2019) and feather quill knobs on the ulna of derived species (Funston and Currie, 2016). In order to protect the pennaceous feathers on the forelimb when on the ground, the extant volant birds have developed a highly specialized wrist with an increased range of abduction of the manus (Sullivan et al. 2010; Hutson and Hutson, 2014). Although the flexibility of the wrist compared to the extant birds has been discussed in some theropods (Gishilk, 2001; Carpenter, 2002; Senter and Robins, 2005; Senter, 2006), there is no study on the shape and function of the wrist of oviraptorosaurs.

The well-preserved wrist in *Heyuannia huangi* is a good example to study the morphology and function of the wrist in the heyuannine oviraptorids. While the wrist of *Heyuannia huangi* was briefly described by Lü (2002) and a relatively detailed description was given by Lü (2005), the function related to the morphology of the wrist was not studied. In this study, we provide a detailed description of the osteology of the wrist of *Heyuannia huangi* and discuss the function of the wrist based on the careful comparison between the morphology of the wrist of *Heyuannia huangi* and other pennaraptorans with the completed wrist preserved.

Materials & Methods

All the specimens studied here were found from the Upper Cretaceous of Heyuan Basin in Heyuan, Guangdong Province, China. These specimens are housed in Heyuan Museum, a research and educational non-profit museum established in 1982. *Heyuannia huangi* was discovered in 1999 and was the first dinosaur found in Heyuan, with its specimens becoming the initial dinosaur collections of Heyuan Museum. Since then, Heyuan Museum has become a center for the study of the dinosaurs from Southern China. A key laboratory of paleontological research and conservation is affiliated to Heyuan Museum and all its collections are always be available for research.

The following description is based on the nearly completed right forelimb preserved in HYMV (Heyuan Museum) 1-2 (Fig. 2) of *Heyuannia huangi*. The preserved elements include humerus, ulna, radius, radiale, semilunate carpal, and metacarpal I-III. This specimen has been fixed on the showcase of Heyuan Museum and only the lateral view of the right forelimb could be observed. Additionally, an isolated ulna HYMV 2-8 (Fig. 3) is also included in the analysis. It could be assigned to *Heyuannia huangi* because it was found from the same quarry with HYMV 1-2 in Heyuan basin and it shares the similar shape of the ulna with HYMV 1-2, especially the dorsal and ventral margin of olecranon process forming a sharp angle. Though Botelho et al. (2014) termed that the radiale of the birds and non-avian coelurosaurian theropods is a composite bone ‘‘scapholunare’’ derived from the fusion of radiale and intermedium. This paper continues to use radiale rather than scapholunare for simplicity of comparison with other coelurosaurian research.

In order to discuss the change of the wrist during the evolution of oviraptorosaurs, a phylogenetic analysis was performed using the software package TNT 1.5 (Goloboff and Catalano, 2016) on a recently published matrix of oviraptorosaurs (Wei et al., 2022) with three new characters related to the morphology of the wrist and two characters related to the morphology of the manus based on Qiu et al. (2019). We used the “New Technology” search options, with sectorial search, ratchet, tree drift and tree fusion, recovering a minimum tree length in ten replicates. The rogue taxa were identified automatically with prunnelsen in TNT (Goloboff et al., 2008). The data matrix is available in the Supplemental Information.

The potential range of motion of the manus was evaluated by comparing the shape of the articular faces of the carpals and distal forearm of *Heyuannia huangi* and with those of whose movement of the manus has been studied in detail using bone-on-bone approach (Gishilk, 2001; Carpenter, 2002; Senter and Robins, 2005; Senter, 2006; Hutson and Hutson, 2014). This analysis method is adopted because the articular faces on the carpals of *Heyuannia huangi* show no significant difference in shape compared to those of other non-avian pennaraptorans. All pennaraptorans possess a trochlear groove along the proximal side on the proximal semilunate carpal (Ostrom, 1969; Lü, 2002; Burnham, 2004; Xu et al., 2014) and a concave proximal surface on the radiale (Ostrom, 1969; Burnham, 2004; Longrich et al., 2010; Balanoff and Norell, 2012; Tsuihiji et al., 2016). So, the discussion of the factors influencing the range of motion in the radial abduction-ulnar adduction of the manus in different non-avian pennaraptorans mainly focuses on the shape and relative size of the carpal bones and distal forearms. The maximum ulnar adduction of the hand is determined by two factors: the semilunate carpal not dislocated from the radiale; the metacarpals not making contact with the forearm during the movement. The estimation of the angle of hand folding is made without considering the movement of the radius in all species discussed here. Since the soft tissue is not be preserved in all known *Heyuannia huangi* specimens and in order to facilitate comparison with previous studies about the range of motion of the forelimb (Gishilk, 2001; Carpenter, 2002; Senter and Robins, 2005; Senter, 2006; Hutson and Hutson, 2014), the influence of soft tissue was not taken into this study.

In order to evaluate potential range of motion of the manus, the radiale angle is measured. The radiale angle is defined as the angle between the articular surface for the radius and semilunate carpal as Sullivan et al. (2010). The evaluation of whether the semilunate carpal is strongly convex involves multiplying the ratio of the anteroposterior length to the lateromedial length of the semilunate carpal (Figure 2C) by the ratio of the combined widths of the proximal articular surfaces of the first and second metacarpals to the lateromedial length of the semilunate carpal (Table 1).

Results

Systematic paleontology

Dinosauria, Owen, 1842

Theropoda, Marsh, 1881

Maniraptora, Gauthier, 1986

Oviraptorosauria, Barsbold, 1976

Oviraptoridae, Barsbold, 1976

Heyuanninae, Yun, 2019

Heyuannia huangi Lü, 2002

Locality and Horizon: Zhutian Formation, Late Cretaceous, Campanian; Huangsha village, Heyuan City, Guangdong Province, China.

Revised Diagnosis: A oviraptorid dinosaur that can be distinguished from other oviraptorids by a unique combination of characters: quadratojugal articular surface of the quadrate more groove-like; the length of dentary subequal to the length of surangular, the external mandibular fenestra locating at the middle of mandible (sharing with *Yulong*); pneumatic foramina present on the cervical ribs; olecranon process development, the dorsal and ventral margin of olecranon process forming a sharp angle (which is right angle in other caenagnathoids); metacarpal I longer than half the length of metacarpal II; manual phalanx II-1 longer than II-2. It can be distinguished from *Heyuannia yanshini* by dorsal margin of ilium arched; pubis subequal to the length of ischium.

Description of the wrist.

The distal end of radius is ventrally expanded (Fig. 2) as in *Machairasaurus* (Longrich et al., 2010), different from a dorsoventral expansion in *Anzu* (Lamanna et al., 2014), *Nemegtomaia* (Fanti et al., 2012), *Khaan* (Balanoff and Norell, 2012) and *Citipati* (Norell et al., 2018), or the absence of obvious expansion in caudipterids (Zhou and Wang, 2000; Zhou et al., 2000; Qiu et al., 2019). The distal end of radius is triangular in the distal view. The distal end of ulna is strongly dorsoventrally compressed and plate-like (Fig. 3B), similar to other caenagnathoids with well distal ulna preserved, such as *Khaan* (Balanoff and Norell, 2012), Nemegtomaia (Fanti et al., 2012), *Oksoko* (Funston et al., 2020), *Citipati* (Norell et al., 2018), *Anzu* (Lamanna et al., 2014) and *Yulong* (Wei et al., 2022). While the distal ulna of caudipterids possesses no compression (Zhou and Wang, 2000; Zhou et al., 2000; Qiu et al., 2019). There are two carpals preserved. The radiale is trapezoid (Fig. 2). The proximal surface of the radiale is generally concave for the contact with the radius. The radiale angle is approximately 58°, similar to most oviraptorosaurs but larger than other non-avian theropods (Sullivan et al., 2010; Qiu et al., 2019). The semilunate carpal is nearly twice the size of radiale as in *Caudipteryx* and *Oksoko* (Zhou et al., 2000; Funston et al., 2020). The semilunate carpal is nearly triple the size of radiale in *Hagryphus* (Zanno and Sampson, 2005). The radiale and semilunate carpal share the similar size in most oviraptorosaurs with known radiale and semilunate carpal, (Longrich et al., 2010; Balanoff and Norell, 2012; Qiu et al., 2019). In the lateral view, the length of the proximal margin of the radiale in *Heyuannia huangi* is subequal to the height of the distal end of the radius. However, the proximal margin of the radiale is smaller than half the height of the distal end of the radius in the lateral view in *Caudipteryx* and *Oksoko*. These conditions suggest that the semilunate carpal is larger than radiale in *Caudipteryx* and *Oksoko* due to the strong reduction of the radiale, rather than the enlargement of the semilunate carpal as in *Heyuannia huangi*. The semilunate carpal is strongly convex. The ratio between the anteroposterior length and the lateromedial length is approximately 0.51, subequal to that of *Heyuannia yanshini* (0.49). This ratio is larger than those of most oviraptorosaurs (0.44 in *Xingtianosaurus*, 0.42 in *Caudipteryx*, 0.43 in *Hagryphus*, 0.43 in *Khaan*), and smaller than that of *Oksoko* (0.82).. As in other pennaraptorans, a deep transverse groove that runs along the entire arc of the proximal semilunate carpal is present (Xu et al., 2014), which offers a gliding surface for the radiale. The gliding surface for the radiale is symmetrical, differs from an asymmetrical gliding arc for the radiale in *Hagryphus* (Zanno and Sampson, 2005). The distal surface of the semilunate carpal covers the proximal end of metacarpal I and metacarpal II, as in other caenagnathoids except *Oksoko* (Zanno and Sampson, 2005; Longrich et al., 2010; Balanoff and Norell, 2012; Fanti et al., 2012), which means the ratio of the combined widths of the proximal articular surfaces of the first and second metacarpals to the lateromedial length of the semilunate carpal is 1. In *Oksoko*, the semilunate carpal covers only half of the proximal end of metacarpal I (Funston et al., 2020), and the ratio of the combined widths of the proximal articular surfaces of the first and second metacarpals to the lateromedial length of the semilunate carpal is 0.78. In contrast to the description from Lü (2005), the semilunate carpal is not fused with metacarpal I and metacarpal II. An obvious suture between the semilunate carpal and the first two metacarpals is present.

Phylogenetic Analysis

The phylogenetic position of *Heyuannia huangi* has been analyzed in several papers and all of them recovered it as a member of the Heyuanninae (Funston and Currie, 2016; Lü et al., 2016, 2017; Qiu et al., 2019; Funston et al., 2020). However, there are few morphological characters about the change of the wrist in the data matrix of the previous studies. In order to analyses the evolution of the wrist in this clade, three following characters about the change of the wrist are added in the new data matrix:

Character 249. Distal end of ulna: (0) not strongly dorsoventrally compressed; (1) strongly dorsoventrally compressed.

Character 250. Radiale: (0) smaller than 40 degrees; (1) 40 degrees or larger.

Character 251. Semilunate carpal, the product of multiplying the ratio of the anteroposterior length to the lateromedial length of the semilunate carpal by the ratio of the combined widths of the proximal articular surfaces of the first and second metacarpals to the lateromedial length of the semilunate carpal: (0) <0.4, semilunate carpal not strongly convex; (1) >0.4, semilunate carpal strongly convex.

Our phylogenetic analysis produces a reduced strict consensus tree based on 49 most parsimonious trees (tree length = 696, retention index = 0.41, consistency index = 0.65), which support *Heyuannia huangi* is most close to *Heyuannia yanshini* (Fig. 4), giving a similar result about the evolution of oviraptorosaurs as the previous results (Funston and Currie, 2016; Lü et al., 2016, 2017; Qiu et al., 2019; Funston et al., 2020). Heyuanninae is the sister taxa of Citipatiinae and supported by two synapomorphies: 7-8 vertebrae included in the synsacrum in adults (character 113: 2) and anteroposterior length of the pubic peduncle about the same as that of the ischial peduncle (character 148: 0).

The reduced strict consensus tree shows that a strongly dorsoventrally compressed distal ulna (character 249: 1), radiale angle 40 degrees or larger (character 250: 1) are the synapomorphies of Caenagnathoidea. Though the radiale angle is larger than 70 degrees in *Caudipteryx*, the combination of a radiale angle smaller than 40 degrees in the basal caudipterid *Xingtianosaurus* (Qiu et al., 2019) and the absence of strongly convex semilunate carpal and strongly dorsoventrally compressed distal ulna indicate that the similarity in the relatively large radiale angle between *Caudipteryx* and Caenagnathoidea is convergently evolved in these taxa. A strongly convex semilunate carpal (character 251: 1) is only found in caenagnathoids among oviraptorosaurs based on the strict consensus tree. It is not recognized as the synapomorphy of Caenagnathoidea because the semilunate carpal is unknown in most basal oviraptorosaurs except caudipterids (Zhou et al., 2000; Qiu et al., 2019).

Discussion

In order to protect the pennaceous feathers on the forelimb from damage, the wrist joint of the extant volant birds is so specialized that the avian carpus possess a large range of abduction (Sullivan et al. 2010). The smallest angle between the manus and the ulna is lesser than 60° in extant birds even without the movement of radius (Fig. 5A; Carpenter, 2001; Sullivan et al. 2010). The evolution of this function from non-avian theropods to birds has been discussed by the studies on the range of motion of the wrist in kinds of theropods, including *Deinonychus*, *Bambiraptor*, *Mononykus*, *Acrocanthosaurus* and *Australovenator* (Gishilk, 2001; Carpenter, 2002; Senter and Robins, 2005; Senter, 2005, 2006; White et al., 2015). Compared with other theropods, the wrist of oviraptorids is obviously specialized. The distal end of radius of oviraptorids is strongly ventrally or dorsoventrally expanded, and the distal end of ulna is strongly dorsoventrally compressed. In the lateral view, the distal end of ulna is far lower than the distal end of radius (Longrich et al., 2010; Balanoff and Norell, 2012; Fanti et al., 2012; Norell et al., 2018; Funston et al., 2020; Wei et al., 2022). In birds and other non-avian theropods, the distal end of ulna is higher than or subequal to the distal end of radius (Gishilk, 2001; Carpenter, 2002; Senter, 2006). While there is no study to discuss the range of motion of the wrist of oviraptorids. The change of the range of motion of the wrist caused by the change of the shape of the wrist in oviraptorids is discussed here based on the comparison between the wrist of other non-avian pennaraptorans and the preserved elements of the wrist of *Heyuannia huangi*.

The shape and arrangement of the carpal in *Heyuannia huangi* are more similar to non-avian paravians rather than extant birds (Fig. 5). The semilunate carpal is relatively enlarged and not fused with metacarpals. The strongly convex proximal surface of the semilunate carpal possesses a deep transverse groove and a developed trochlea (Hutson and Hutson, 2014; Xu et al., 2014). The proximal surface of radiale possesses a concavity at its center in order to contact the radius. It could be easily distinguished from the radiale of the extant birds whose proximal surface possesses a sharp ridge, dividing the surface into two facets for contacting the radius and ulna, respectively (Livezey and Zusi, 2006; Mayr, 2014). Since the radiale contacts only the radius in *Heyuannia huangi*, other oviraptorids and non-avian paraves, the center of rotation of the wrist abduction is located higher than or near the joint of the ulna and radius on the lateromedial axis. While in the extant birds, radiale contacts both the radius and ulna causing the center of rotation of the wrist abduction to be located at the center of the distal ulna on the lateromedial axis.

Though the oviraptorids and non-avian paraves share the similar structure on the articular faces of the carpus, the specialized distal end of the forearm in *Heyuannia huangi* indicates a different movement mode of its wrist. In dromaeosaurids, the rotation of the hand will be restricted by the dorsoventrally expanded distal ulna because the center of rotation of the wrist abduction is located higher than or near the joint of the ulna and radius on the lateromedial axis. So, the smallest angle between the manus and the ulna should not be smaller than 100° in these species (Fig. 5B; Gishilk, 2001; Carpenter, 2002; Senter, 2006). Though the distal ulna is also higher than the distal radius in extant birds, the distal ulna should not be an obstacle of the movement of their manus, because the center of rotation of the wrist abduction is located at the center of the distal ulna on the lateromedial axis. The distal end of radius of *Heyuannia* is strongly dorsoventrally expanded and the distal end of ulna is strongly dorsoventrally compressed. In the lateral view, the distal end of ulna is far lower than the distal end of radius, even narrower than the proximal surface of the semilunate carpal. This condition is different from most theropods whose distal end of radius and ulna share the similar height or the distal ulna higher than the distal radius, and the semilunate carpal is narrower than the distal ulna (Gishilk, 2001; Carpenter, 2002). The analysis of joint movement indicates though the center of rotation of the wrist is still located at the joint of the ulna and radius on the lateromedial axis as in other no-avian pennaraptorans, the flat distal ulna would not impede the rotation of the manus. The smallest angle between the manus and the ulna might be smaller than 90°in *Heyuannia huangi* (Fig. 5C), smaller than most non-avian theropods. According to the phylogenetic result, a strongly dorsoventrally compressed distal ulna and a larger radiale angle are the synapomorphies of Caenagnathoidea, and a strongly convex semilunate carpal (character 251: 1) is only found in caenagnathoids among oviraptorosaurs. The shapes of the carpal and forearm in some oviraptorid specimens with well-preserved forelimb also support a development wrist abduction as in *Heyuannia huangi* (Balanoff and Norell, 2012; Wei et al., 2022). A strongly compressed distal end of ulna is also present in caenagnathids (Makovicky and Sues, 1998; Lamanna et al., 2014). Though the carpals are badly preserved in most known caenagnathids, the well preserved carpal of *Hagryphus* possess many features similar to those of the oviraptorids, including the radiale angle larger than 40 degrees and a strongly convex semilunate carpal, indicating that a development wrist abduction should be a body plan of Caenagnathoidea rather than Oviraptoridae.

Among oviraptorids, the morphology of the wrist of caudipterids, which are regarded as the basal oviraptorosaurs in the phylogenetic result (Fig. 4), do not suggest a great capacity for wrist abduction as in avians. Although some caudipterids possesses a large radiale angle (Sullivan et al., 2010), the semilunate carpal of caudipterids is not strongly convex, and the distal end of ulna and radius of caudipterids share a similar height as in other theropods. In addition, the radiale and semilunate carpal of caudipterids are relatively small, with the combined width of these two bones being smaller than the craniocaudally height of the distal end of either ulna or radius. So, the distance between the manus and the forearm of caudipterids is so small that there is no enough space for a large wrist abduction. The smallest angle between the manus and the ulna is estimated to be larger than 120°.The combination with the morphology of the wrist and the phylogenetic result of oviraptorosaurs indicates a functional convergence in the wrist of oviraptorids and extant birds.

Conclusions

The wrist of *Heyuannia huangi* has been described in detail and its phylogenetic position has been confirmed by the modified oviraptorosaurian phylogenetic matrix. *Heyuannia huangi* and other oviraptorids possess a specialized wrist, with the semilunate carpal being strongly convex and the distal ulna being strongly dorsoventrally expanded to be plate-like. The phylogenetic result indicates that a strongly dorsoventrally compressed distal ulna and a larger radiale angle are the synapomorphies of Caenagnathoidea, and a strongly convex semilunate could only be found in caenagnathoids among oviraptorosaurs. The morphology of its wrist indicates though the center of rotation of the wrist is located at the joint of the ulna and radius on the lateromedial axis, the flat distal ulna would not prevent the rotation of the manus as in other no-avian pennaraptorans. The smallest angle between the manus and the ulna could be smaller than 90°, similar to the extant birds rather than the most non-avian theropods. The combination with the morphology of the wrist of oviraptorosaurs and the phylogenetic result indicates a functional convergence in the wrist of oviraptorids and extant birds.

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Figure 1

Holotype block of *Heyuannia huangi*. The yellow box indicates the forelimb in Figure 2.

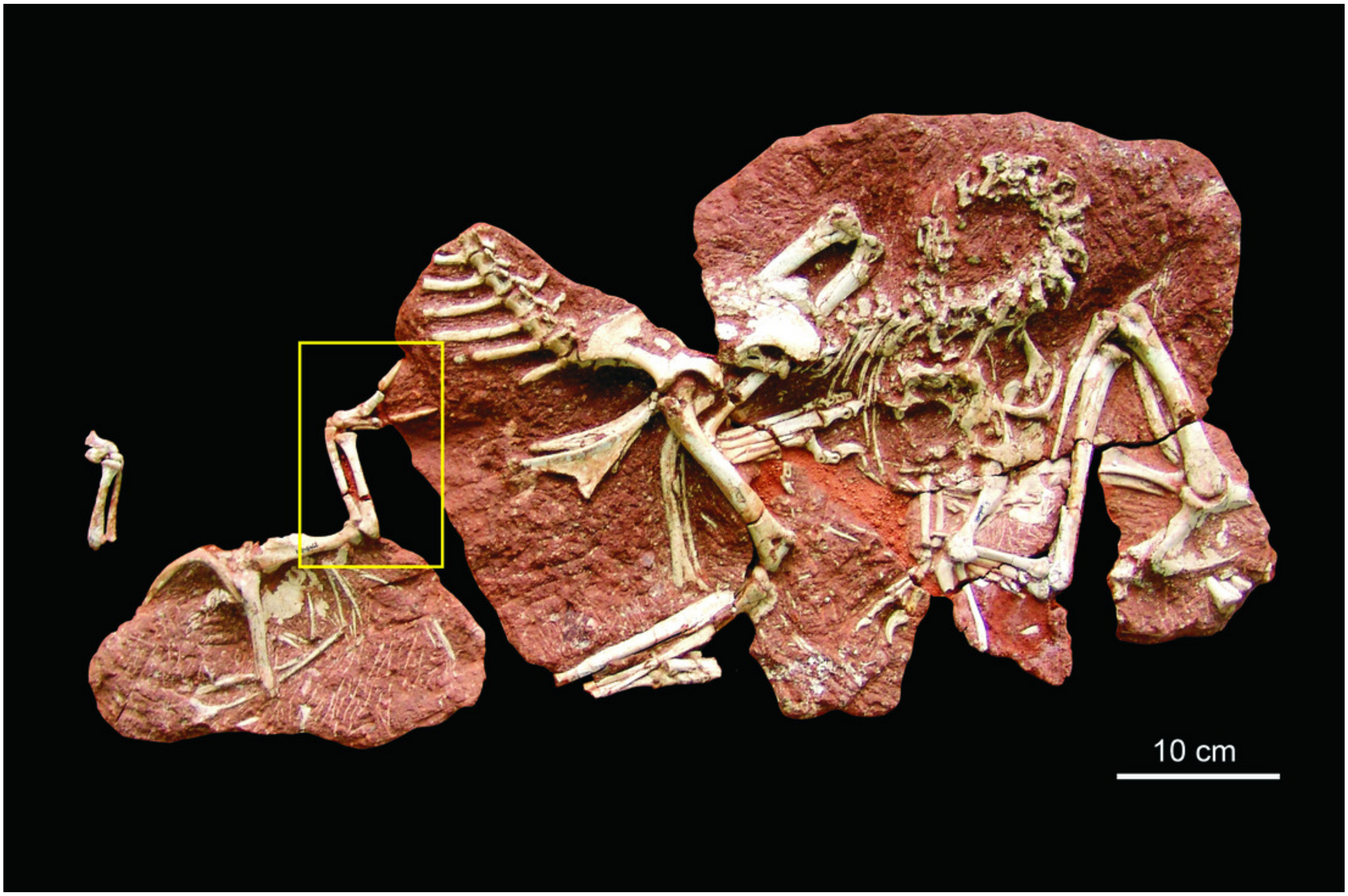

Figure 2

Photograph (A) and line drawing (B) of the right forelimb of *Heyuannia huangi* (HYMV 1-2) in the lateral view, and the measurements of the semilunate carpal (C).

Abbreviations: de, distal expansion of radius; Lap, anteroposterior length of the semilunate carpal; Llm, lateromedial length of the semilunate carpal; mcI, metacarpal I; mcII, metacarpal II; mcIII, metacarpal III; r, radius; rd, radiale; se, semilunate carpal; u, ulna.

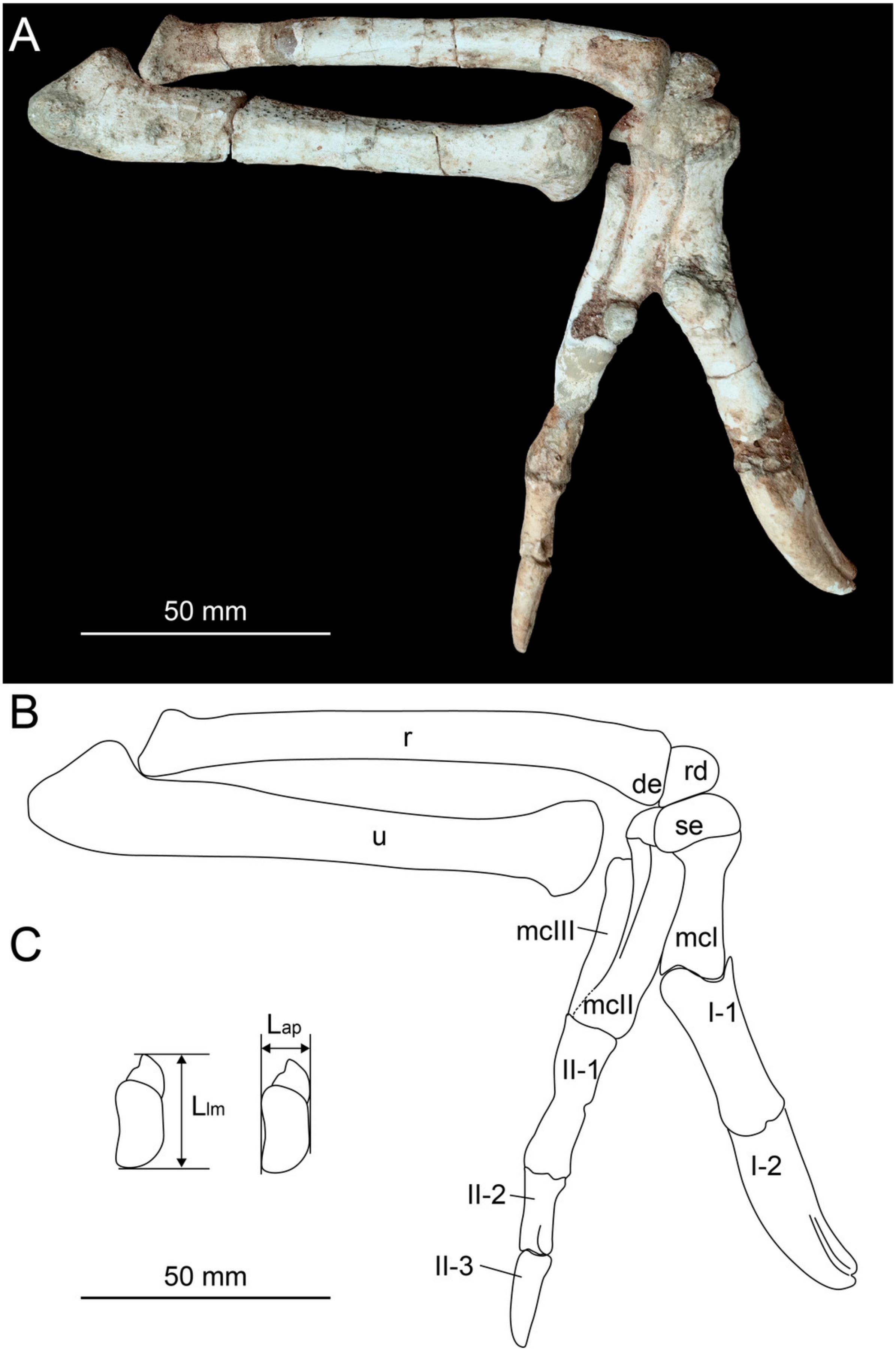
A
50 mm
B
r
de
rd
u
se
mcIII
mcI
C
mcII
I-1
Lap
II-1
Llm
I-2
II-2
II-3
50 mm

Figure 3

Photograph of the ulna of *Heyuannia huangi* (HYMV 2-8) in lateral view (A), ventral view (B) and dorsal view (C).

Figure 4

Major changes of the range of motion of the left wrist during oviraptorosaur evolution.

The significant changes of the wrist are shown, including the maximum abduction of the wrist, the shape of the distal ulna and radius, the shape of the semilunate carpal and the radiale angle. The number below the semilunate carpal is the product of multiplying the ratio of the anteroposterior length to the lateromedial length of the semilunate carpal by the ratio of the combined widths of the proximal articular surfaces of the first and second metacarpals to the lateromedial length of the semilunate carpal. The number below the radiale is the radiale angle. The wrist of *Xingtianosaurus* is redrawn from Qiu et al. (2019). The wrist of *Caudipteryx* is redrawn from Zhou et al. (2000). The wrist of *Hagryphus* is redrawn from Zanno and Sampson (2005). The distal forearm of *Anzu* is redrawn from *Lamanna* et al. (2014). The wrist of *Khaan* is redrawn from Botelho et al. (2014). The wrist of *Oksoko* is redrawn from Funston et al. (2020). The wrist of *Heyuannia yanshini* is redrawn from Easter (2013). The line drawings are not to scale. The purple lines show the smallest angle of abduction between the manus and the ulna.

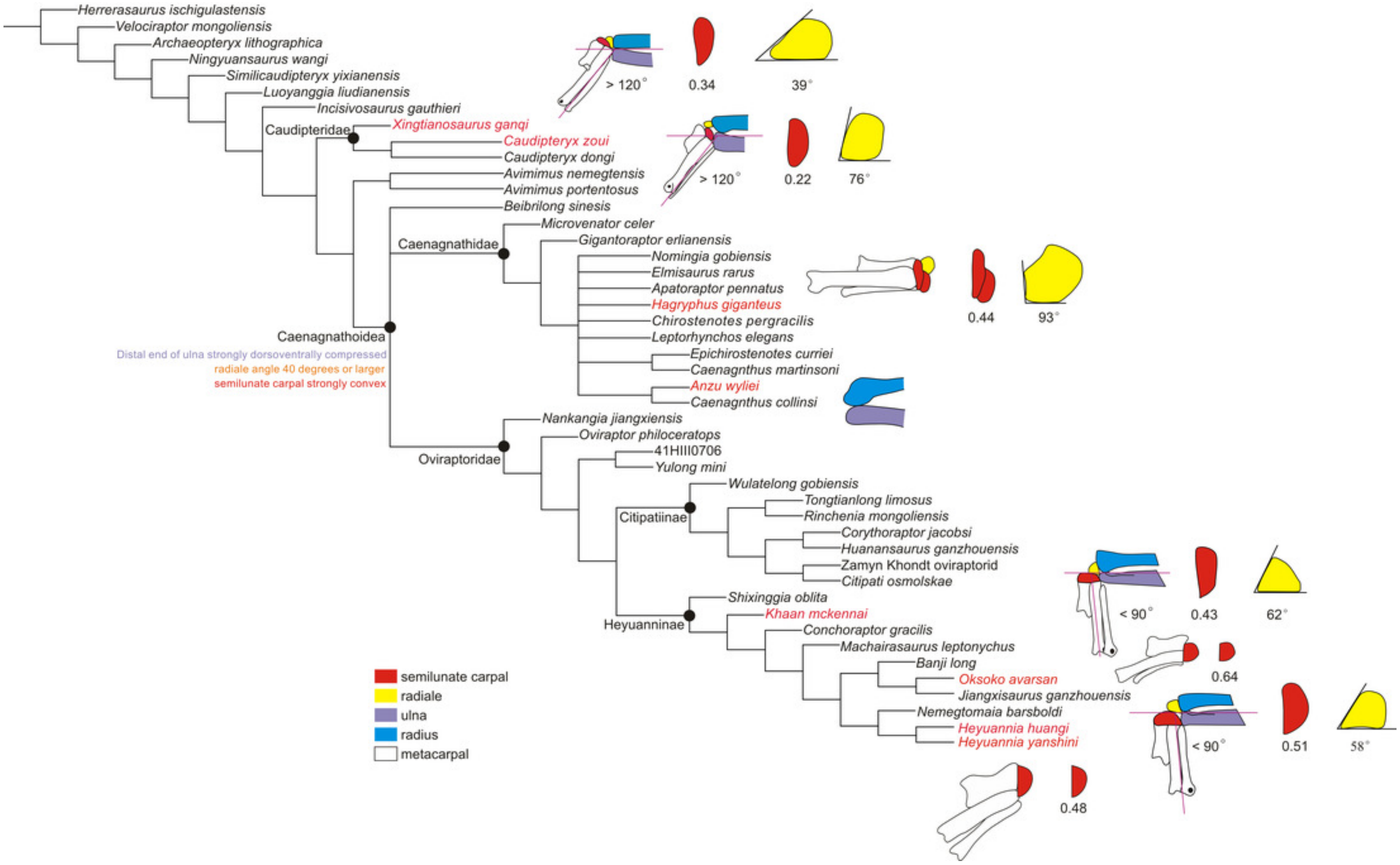
Herrerasaurus ischigulastensis
Velociraptor mongoliensis
Archaeopteryx lithographica
Ningyuansaurus wangi
Similicaudipteryx yixianensis
Luoyanggia liudianensis
Incisivosaurus gauthieri
Caudipteridae
Xingtianosaurus ganqi
Caudipteryx zoui
Caudipteryx dongi
Avimimus nemegtensis
Avimimus portentosus
Beibrilong sinesis
Caenagnathidae
Microvenator celer
Gigantoraptor erlianensis
Nomingia gobiensis
Elmisaurus rarus
Apatoraptor pennatus
Hagryphus giganteus
Chirostenotes pergracilis
Leptorhynchos elegans
Epichirostenotes curriei
Caenagnthus martinsoni
Anzu wyliei
Caenagnthus collinsi
Caenagnathoidea
Distal end of ulna strongly dorsoventrally compressed
radiale angle 40 degrees or larger
semilunate carpal strongly convex
Oviraptoridae
Nankangia jiangxiensis
Oviraptor philoceratops
41HIII0706
Yulong mini
Citipatiinae
Wulatelong gobiensis
Tongtianlong limosus
Rinchenia mongoliensis
Corythoraptor jacobsi
Huanansaurus ganzhouensis
Zamyn Khondt oviraptorid
Citipati osmolskae
Heyuanninae
Shixinggia oblita
Khaan mckennai
Conchoraptor gracilis
Machairasaurus leptonychus
Banji long
Oksoko avarsan
Jiangxisaurus ganzhouensis
Nemegtomaia barsboldi
Heyuannia huangi
Heyuannia yanshini
> 120°
0.34
39°
> 120°
0.22
76°
0.44
93°
< 90°
0.43
62°
0.64
< 90°
0.51
58°
0.48
semilunate carpal
radiale
ulna
radius
metacarpal

Figure 5

The wrist of turkey, *Meleagris gallopavo* (A), *Deinonychus antirrhopus* (B) and *Heyuannia huangi* (C).

The upper wrists are in the maximum adduction, and the lower wrists are in the maximum abduction. The wrist of turkey is modifed from Sullivan et al. (2010). The wrist of *Deinonychus antirrhopus* is modifed from Ostrom (1969). The line drawings are not to scale.

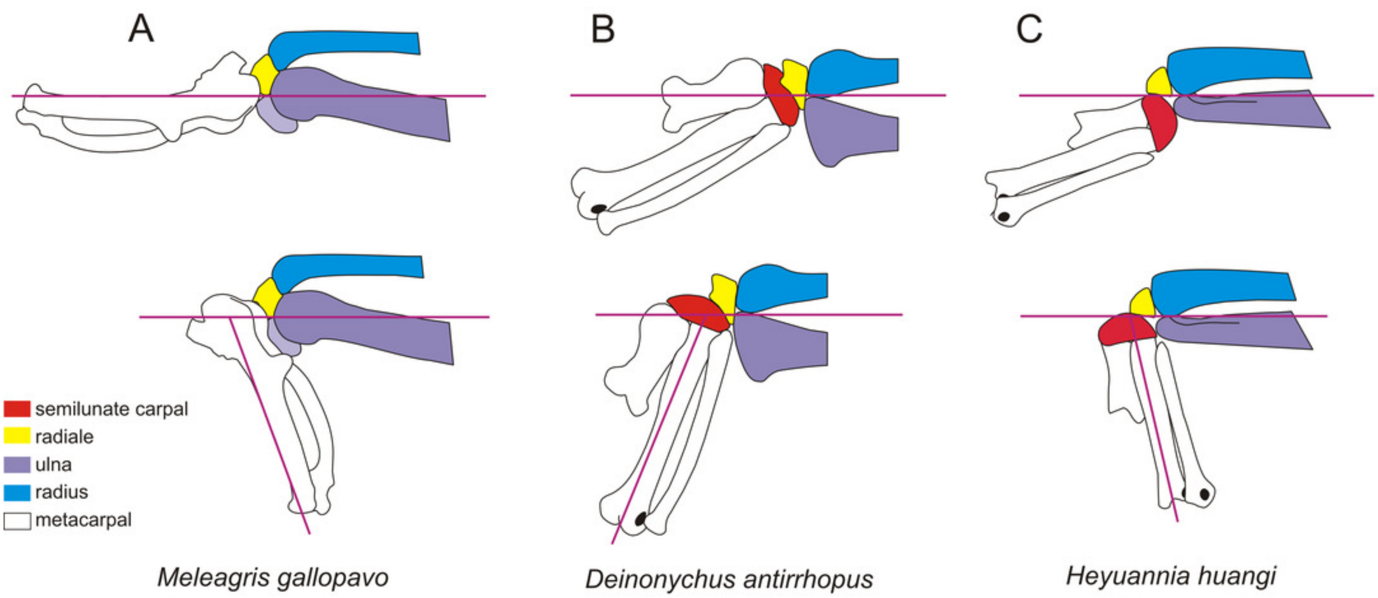

Table 1(on next page)

The parameters of the semilunate carpal.

The result multiplying the ratio of the anteroposterior length to the lateromedial length of the semilunate carpal (Rll) by the ratio of the combined width of the proximal articular surfaces of the first and second metacarpals to the lateromedial length of the semilunate carpal (Rwl) indicates whether the semilunate carpal is strongly convex. The Rll and Rwl are from measuring the high-resolution images and detailed description except *Heyuannia huangi*.

	R_{ll}	R_{wl}	R_{ll*} R_{wl}	Image or Description Reference
Herrerasaurus	0.330239	0.842458	0.278212	Xu et al., 2014
Archaeopteryx	0.648590	1	0.648590	Wellnhofer, 2009
Xingtianosaurus	0.440284	0.768116	0.338189	Qiu et al., 2019
Caudipteryx	0.422515	0.517697	0.218735	Zhou et al., 2000
Hagryphus	0.435163	1	0.435163	Zanno and Sampson, 2005
Khaan	0.425841	1	0.425841	Balanoff and Norell, 2012
Heyuannia huangi	0.512051	1	0.512051	This paper
Oksoko	0.816154	0.783495	0.639453	Funston et al., 2020
Heyuannia yanshini	0.484362	1	0.484362	Easter, 2013