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Chicken-sized oviraptorid dinosaurs from central China and their ontogenetic implications

Junchang Lü · Philip J. Currie · Li Xu · Xingliao Zhang · Hanyong Pu · Songhai Jia

Abstract Oviraptorids are a group of specialized non-avian theropod dinosaurs that were generally one to 8 m in body length. New specimens of baby oviraptorids from the Late Cretaceous of Henan Province are some of the smallest individuals known. They include diagnostic characters such as the relative position of the antorbital fenestra and the external naris, distinct opening in the premaxilla anteroventral to the external naris, antorbital fossa partly bordered by premaxilla posterodorsally, lacrimal process of premaxilla does not contact the anterodorsal process of the lacrimal, parietal almost as long as frontal; in dorsal view, posterior margin forms a straight line between the postzygapophyses in each of the fourth and fifth cervicals; femur longer than ilium. They also elucidate the ontogenetic processes of oviraptorids, including fusion of cranial elements and changes in relative body proportions. Hind limb proportions are constant in oviraptorids, regardless of absolute body size or ontogenetic stage. This suggests a sedentary lifestyle that did not involve the pursuit of similar-sized prey. The functional implications for bite force and therefore dietary preferences are better understood through the study of such small animals. The comparison of the measurements of 115 skeletons indicates that oviraptorids maintain their hind limb proportions regardless of ontogenetic stage or absolute size, which is a pattern seen more commonly in herbivores than in carnivores. This may weakly support the hypothesis that oviraptorids are herbivores rather than active carnivores.

Keywords Baby oviraptorid · *Yulong* · Late Cretaceous · Henan Province

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Introduction

Oviraptorid dinosaurs are specialized, non-avian theropod dinosaurs (Barsbold 1976; Osmólska et al. 2004). They are characterized by short, deep skulls with toothless jaws (teeth are present in primitive forms such as *Incisivosaurus*, Xu et al. 2002 and *Caudipteryx*, Ji et al. 1998), pneumatized caudal vertebrae, anteriorly concave pubic shafts, and posteriorly curved ischia (Barsbold et al. 1990; Makovicky and Sues 1998; Barsbold et al. 2000). They are recovered primarily from Mongolia (Osborn 1924; Barsbold 1976; Osmólska et al. 2004; Osmólska 1976; Norell et al. 1994,1995; Clark et al. 1999, 2001, 2002; Lü et al. 2004, 2005) and China (Osmólska et al. 2004; Lü 2002, 2005; Lü and Zhang 2005; Xu et al. 2007; Lü et al. 2009; Longrich et al. 2010; Xu and Han 2010), although the closely related caenagnathids are best known from North America (Osmólska et al. 2004; Sternberg 1940; Cracraft 1971; Currie and Russell 1988; Currie et al. 1993; Sues 1997). With the exception of one embryo from Mongolia (Norell et al. 1994), all oviraptorids found so far are more than 1 m long, and one may have been as much as 8 m in body length (Xu et al. 2007). Baby oviraptorids from the Late Cretaceous of Henan Province (central China) are the smallest complete individuals that have been found, and elucidate the ontogenetic processes of oviraptorids.

Materials and methods

To evaluate the systematic position of *Yulong* within the Oviraptosauria, 182 characters were scored for 19 taxa (See electronic supplementary information for details). This included one new character (#182).

Phylogenetic analysis was performed using the branch-and-bound search algorithm of PAUP* 4.0b10 (Swofford 2002) (see electronic supplementary information for details). Running the whole data matrix of 19 taxa (including *Archaeopteryx*, *Herrerasaurus*, and *Velociraptor* as outgroups, plus all known oviraptorosaurs) and 182 characters produced two most parsimonious trees, each with a length of 362 under a branch and bound search (consistency index of 0.60 and retention index of 0.70).

The phylogenetic analysis suggests that *Yulong* is placed between *Gigantoraptor* and other oviraptorids (tree length: 362, CI=0.60; RI=0.70; Fig. 4). It possesses the oviraptorid autapomorphies: 25 (lacrimal recesses: absent); 29 (sagittal crest along interparietal contact: absent); 50 (occiput position in relation to ventral margin of jugal–quadratojugal bar: approximately perpendicular); 80 (ratio of length of external mandibular fenestra to total mandibular length: 0.15–0.20); 147 (pubic foot: cranial and posterior processes about equally long); 149 (greater trochanter of femur: weakly separated, or not separated, from femoral head); 151 (dorsal extremity of anterior trochanter: well below greater trochanter); 166 (an arched convexity in the ventral margin of the jaw between the anteroventral margin (chin) and the posteroventral process of the dentary: present); 170 (dentary contribution to external mandibular fenestra exceeds 50 % length of dentary) and 173 (unguals of manual digits II and III: weakly curved). One needs to be cautious about the results, however, in that immature specimens, like those of *Yulong*, usually lack derived character states that only appear at sexual maturity.

Systematic paleontology

Oviraptorosauria Barsbold 1976
Oviraptoridae Barsbold 1976
*Yulong mini* gen. et sp. nov. (Figs. 1, 2 and 3)

Etymology

Generic name derived from "Yu", the abbreviated name for Henan Province, and "long" from Chinese, meaning dragon. The specific name refers to the small size of known specimens.

Holotype

Henan Geological Museum HGM 41HIII-0107, an exceptionally well-preserved skeleton with a skull and lower jaws.

Fig. 1 **a** Photograph and **b** line drawings of *Yulong mini* (HGM 41HIII-0107). *cv* cervical vertebrae, *d* dentary, *fe* femur, *fi* fibula, *h* humerus, *il* ilium, *mt* metatarsals, *o* orbital, *po* postorbital, *rd* radius, *ul* ulna, *ti* tibia
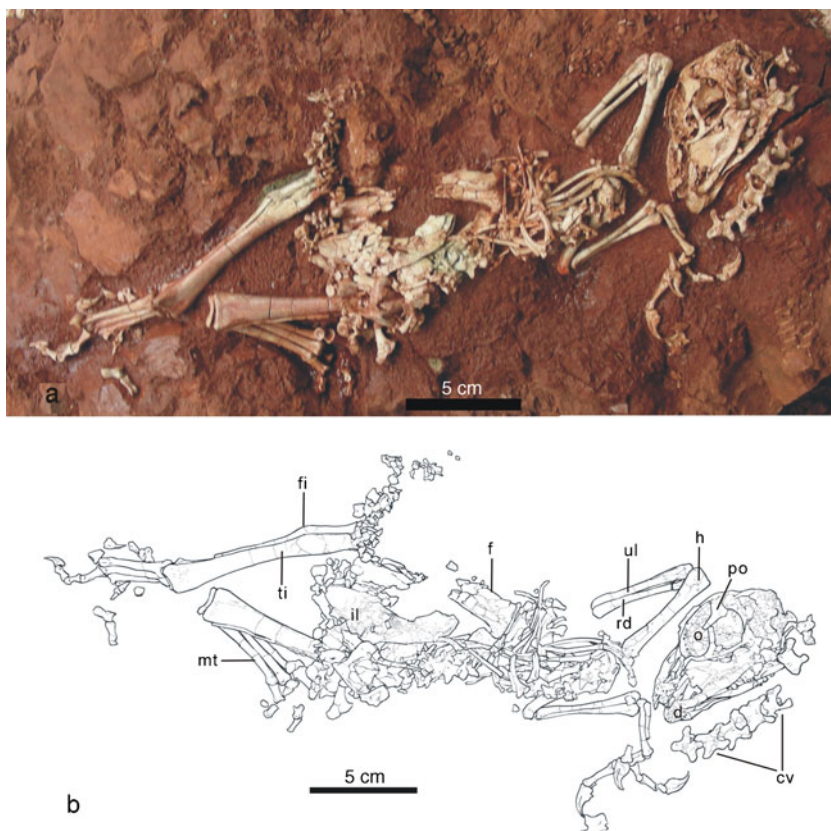
Fig. 2 Skull reconstruction of *Yulong mini* in lateral (**a**) and dorsal (**b**) views. *aofe* antorbital fenestra, *d* dentary, *emf* external mandibular fenestra, *f* frontal, *j* jugal, *mx* maxilla, *l* lacrimal, *ltf* lower temporal fenestra, *n* nasal, *no* nasal opening, *o* orbit, *p* parietal, *po* postorbital, *q* quadrate, *qj* quadratojugal, *stf* supertemporal fenestra, *sq* squamosal, *tp* tooth-like process
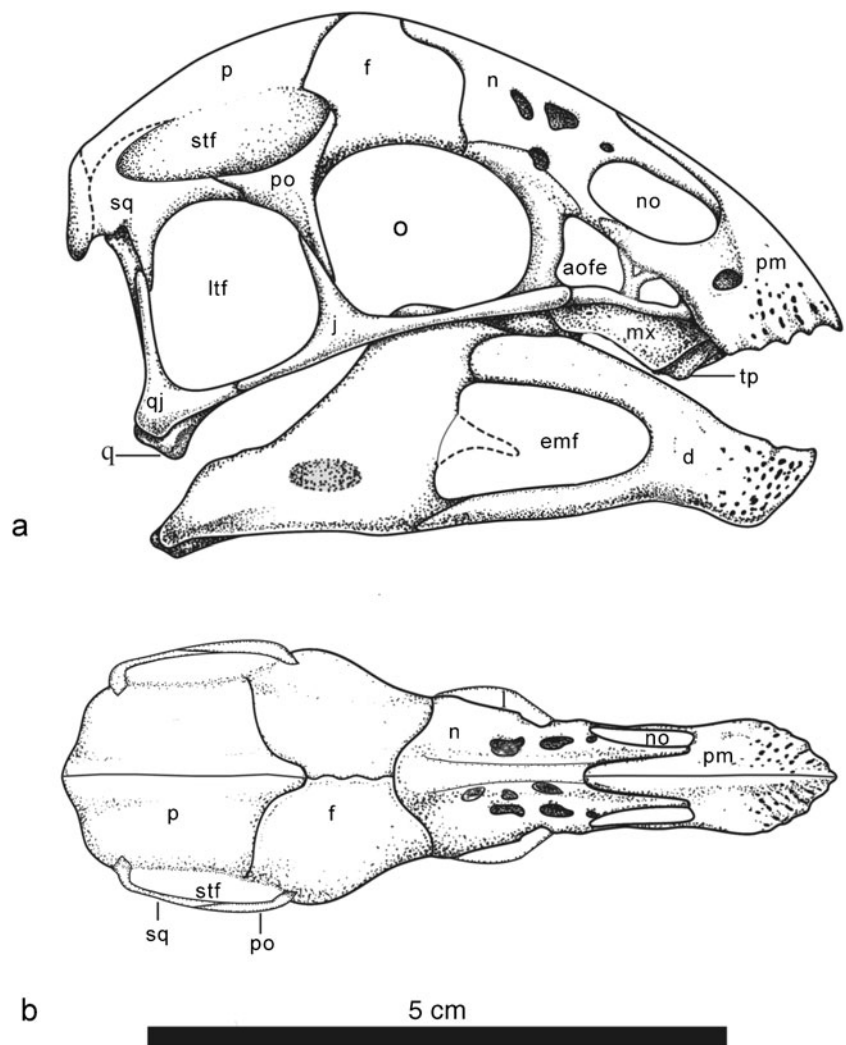
Referred specimens

HGM 41HIII-0108, nearly complete skull with lower jaws; HGM 41HIII-0109, well-preserved skull, lower jaws and partial postcranial skeleton; HGM 41HIII-0110, partial skull, lower jaws and a few cervical centra; HGM 41HIII-0111, one complete left ilium.

Type locality and horizon

Qiupa Town, Luanchuan County, Henan Province; Upper Cretaceous, Qiupa Formation (Bureau of Geology and Mineral Resources of Henan Province 1989; Lü et al. 2007).

Diagnosis

Oviraptorid with the following characters: posterodorsal corner of the antorbital fenestra and the anteroventral corner of the external naris at the same level (similar conditions in *Citipati osmolskae* [MPC-D 100/978] and *Citipati* sp.

[MPC-D 100/42]); distinct opening in the premaxilla anteroventral to the external naris; antorbital fossa partly bordered by premaxilla anterodorsally; lacrimal process of premaxilla does not contact the anterodorsal process of the lacrimal; parietal almost as long as frontal; in dorsal view, posterior margin forms a straight line between the postzygapophyses in each of the fourth and fifth cervicals; femur longer than ilium.

Description

HGM 41HIII-0107 is almost complete and only lacks the posterior cervical, anterior dorsal and distal caudal vertebrae (Fig. 1). The specimen was in close association with another individual (HGM 41HIII-0108) that is approximately the same size. All measurable elements are smaller than their equivalents in a reported oviraptorid embryo (MPC-D 100/971). The best indication of the immaturity of the specimen is the degree of ossification in the skeleton. In the skull,

Fig. 3 Skulls of *Yulong mini*. **a** HGM 41HIII-0107; **b** HGM 41HIII-0108; **c** HGM 41HIII-0109; **d** HGM 41HIII-0110. **a–c** Right lateral views, **d** left lateral view
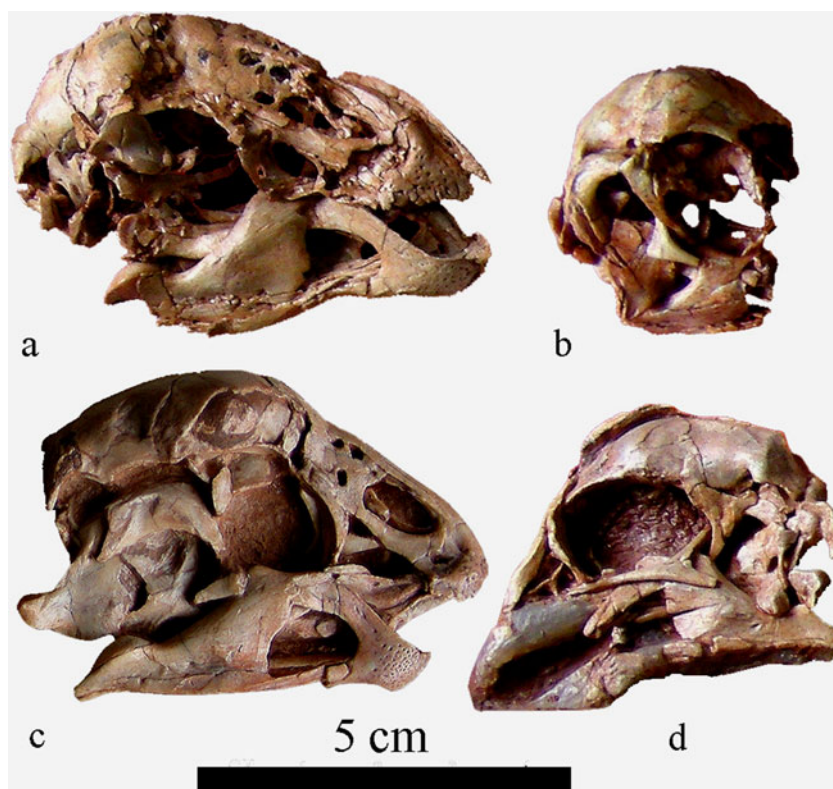
pairs of bones (including premaxillae, frontals, and parietals) that normally coossified at early ontogenetic stages in oviraptorids are separate. There is no fusion between any of the braincase bones, the exoccipitals have separated from the basioccipital, and the basisphenoid is free from the basioccipital and laterosphenoid. None of the neurocentral sutures are fused in the vertebrae. However, the nasals in HGM 41HIII-0107 and HGM 41HIII-0109 are fused, which suggests that the fusion of the nasals occurs earlier than in other elements of the skull.

Like all other oviraptorid skulls, many of the cranial bones (including premaxillae, nasals, and frontals) have a frothy appearance. The elongate external naris is bordered posteriorly and posterodorsally by the nasal, and anterodorsally and ventrally by the premaxilla. The anteroventral–posterodorsal axis of the external naris is not vertical as it is in larger specimens of oviraptorids (Fig. 2a, b). The relatively small antorbital fenestra is bordered by the lacrimal posteriorly. The posterodorsal process of the premaxilla does not contact the anterodorsal process of the lacrimal (Fig. 2a). This is different from the conditions in *C. osmolskae*, *Citipati* n. sp. (MPC-D 100/42, sometimes referred to as the unnamed Zamyn Khondt oviraptorine), and *Conchoraptor gracilis*, where the lacrimal processes of the premaxillae contact the anterodorsal processes of the lacrimals (Osmólska et al. 2004). The premaxilla forms part of the anterodorsal margin of the antorbital fenestra, similar to

that of *Rinchenia mongoliensis* (Osmólska et al. 2004). The posterodorsal corner of the antorbital fenestra and the anteroventral corner of the external naris are at the same level, just as in *C. osmolskae* (MPC-D 100/978; see Lü 2005, Plate VI) and *Citipati* n. sp. (MPC-D 100/42). There are several openings in the right maxilla of HGM 41HIII-0107 anterior to the antorbital fenestra.

The orbit is large (more than a third of the skull length) and round. The ventral margin of the lateral temporal opening is relatively long anteroposteriorly, and is slightly smaller than the orbit. The upper temporal fenestra is relatively small, and has an area of less than a quarter that of the lateral temporal fenestra (HGM 41HIII-0108). It is surrounded by frontal, parietal, postorbital and squamosal as in almost all theropods, but the supratemporal fossa does not extend up onto the dorsal surfaces of the frontal and parietal.

In addition to these cranial openings, which are found in almost all theropods, there are numerous additional openings, most of which are pneumatic in origin. The most remarkable is a relatively large opening in the premaxilla anteroventral to the external naris (Fig. 2a).

There is a deep pit medial to the orbital margin on the dorsal surface of the skull. It is lateral to the anterolateral prong of the nasal that contacts the posterior end of the subnarial process of the premaxilla. An opening in its floor penetrates the part of the orbital rim that is formed by the lacrimal. A similar opening is present in at least one

uncatalogued specimen of *Conchoraptor* (Currie, personal observations, 2011; specimen stored in the Paleontological Center of the Mongolian Academy of Sciences, Ulaan Baatar, Mongolia).

As in other oviraptorids, there are irregular-sized openings at the front of the nasal on either side of the midline that are probably pneumatic in origin (Figs. 2 and 3a, c). In HGM 41HIII-0107, there are four openings on the right side of the midline, and six on the left.

The premaxillae are not fused. Like all of the more derived oviraptorids, the premaxilla is toothless, but has a crenulated tomial edge (Osmólska et al. 2004). The subnarial body is dorsoventrally deep, although it is only marginally deeper than the anteroposterior length of the tomial margin. Furthermore, the subnarial body is inclined somewhat posterodorsally, whereas it tends to be nearly vertical in most oviraptorids. This does not appear to be an age-related character as a *Conchoraptor* skull (uncatalogued PIN specimen) from Khulsan (Mongolia), which is only slightly bigger than HGM 41HIII-0107, has a vertical subnarial body. The lateral surfaces of the premaxillae are covered with small pits. The paired medial nasal processes of the premaxillae extend posterodorsally to wedge between the anterior prongs of the nasals. The subnarial process is a relatively deep, laterally convex ramus that extends more posteriorly than dorsally to contact the nasal and exclude the maxilla from the border of the external naris. It forms part of the dorsal margin of the antorbital fenestra. In most oviraptorid specimens where this region can be seen, the maxilla usually contacts the lacrimal and excludes the premaxilla from the margin of the antorbital fenestra. The lack of contact between maxilla and lacrimal in this specimen may be due to immaturity and incomplete ossification, although this seems unlikely given that both are dermal bones. As in other derived oviraptorids, distinct tooth-like processes are present on the ventromedial surface of maxilla in HGM 41HIII-0109 (tp; Fig. 2a).

In contrast with the lack of fusion among most cranial bones of both the holotype and referred specimen, the nasals are fused and form a distinct midline ridge. Although the nasals extend back between the orbits, they are excluded from the orbital margins by the lacrimals.

The frontal is a thin, domed bone that is convex in lateral view. The fused nasals overlap the anterior ends of the paired frontals on the midline and cover the interfrontal suture posteriorly to the mid-orbital region. The frontal forms most of the arched dorsal rim of the orbit. The postorbital overlaps the frontal for a short distance behind the orbit. Posteriorly, the frontals are separated on the midline by the paired parietals. The dorsal exposure of the frontal is marginally shorter than that of the parietal as in *Nemegtomaia* and other oviraptorids (Lü et al. 2004, 2005;

Osmólska et al. 2004). In most theropods, the frontals are longer than the parietals in mature individuals.

The relatively thin parietals join anteriorly to separate the frontals on the midline. A thin anterolateral process of the parietal contacts the postorbital on the left side of HGM 41HIII-0107. Posterolaterally, the parietal extends along the dorsal surface of the paroccipital process to contact the squamosal. There is neither a sagittal crest nor a conspicuous nuchal crest, and the dorsal surface curves smoothly onto the occipital surface without a well-defined inflection.

As in other oviraptorids, the lacrimal projects beyond the lateral surface of the orbital region and the snout on the right side of HGM 41HIII-0107. It forms a plate-like surface behind the antorbital fossa in anterior view, but is thin and blade-like in lateral aspect. Pneumatopores pierce the lacrimal in the posterodorsal corner of the antorbital fossa.

The jugal has three branches, one (ascending branch) extending dorsally and contacting the ventral process of the postorbital, one extending anteriorly to contact the maxilla and lacrimal, and the other extending posteriorly to contact the quadratojugal. The anterior branch is thin and rod-like, similar to those of other oviraptorids. The ascending branch is almost perpendicular to the anterior and posterior branches.

The quadratojugal is a Y-shaped bone. The dorsal branch is longer than the anterior branch that overlaps the posterior extension of the jugal. The sutural area of the quadratojugal for the quadrate is concave. The quadrate and quadratojugal are not fused, and some movement was possible at the contact as in *Nemegtomaia* (Lü et al. 2002, 2004, 2005). The quadratojugal forms the lateral margin of the quadratic foramen.

The pterygoid process of the quadrate is well developed, and is half as long anteroposteriorly as the bone is tall. HGM 41HIII-0107 preserves the medial edge of the quadratic foramen, which appears to have been 3 mm high. The dorsal cotyle plugged into a socket in the squamosal. The ventral articulation for the lower jaw has the characteristic oviraptorid shape in which the lateral and medial condyles are separated by only a shallow longitudinal concavity. There is a distinct depression posterior to the medial condyle that may lead into a small pneumatopore.

The basioccipital is a low, relatively flat bone that forms most of the occipital condyle. The posterior surface of the condyle has a shallow depression representing the remnants of a notochordal pit. When viewed posteriorly, the same flat appearance of the basioccipital has been previously noted in juvenile troodontids (Carpenter 1982; Currie 1985). The exoccipital sutures extend along each side of the basioccipital for most of the length and height of the bone. A foramen ventral to the exoccipital suture and immediately anterior to the basal tubera does not pass through the bone, but appears to be a pneumatopore entering the interior of the

basioccipital as in carcharodontosaurids, troodontids, and tyrannosaurids (Coria and Currie 2006). The ventral surface of the basioccipital is shallowly concave between the basal tubera.

The exoccipital, even at the early stage of development that is represented in these specimens, is indistinguishably fused with the opisthotic to form the paroccipital process. The paroccipital process is relatively short, and in the holotype extends laterally only 9.8 mm from the lateral edge of the foramen magnum. Its distal end, which is slightly expanded, is downturned to reach about the same level as the occipital condyle. Above the foramen magnum, the dorsomedial surface of the exoccipital has a distinct facet, presumably for its short contact with the supraoccipital. A line of three foramina pierce the base plate lateral to the occipital condyle but dorsal to the basioccipital suture. Each passes more or less directly through the bone from an opening on the inside surface. The basioccipital suture is continuous from the exoccipital contribution to the occipital condyle and faces ventrally and slightly medially.

The tapering cultriform process of the basisphenoid–parasphenoid complex extends forward to the level of the anterior orbital margin. It is thin but has a longitudinal midline trough on the dorsal surface.

The mandibles have all of the characteristics expected of an oviraptorid, such as a more highly arched dentary and a more distinct coronoid process than seen in other theropod dinosaurs, and even the dentaries were sutured tightly together (but not fused) at the symphysis by the time of death. Like other oviraptorids, the symphysis was inclined to form a rudimentary symphysial shelf that is quite different from the extended shelf seen in caenagnathids (Currie et al. 1993). The posteroventral process of the dentary extends beyond the back of the external mandibular fenestra. The jaws are deep, with their maximum heights being about one third of the total lengths. The external mandibular fenestra is characteristic of oviraptorids in its relatively large size (20 % of the jaw length) and in that its borders are formed mostly by the dentary. The height of the fenestra is about three quarters of its length. A characteristic, prominent prong inserts into the back of the opening from the surangular, and is well preserved on the left mandible of the holotype. The surangular and articular were apparently not coossified into a single unit in HGM 41HIII-0107, presumably because of the immaturity of the specimen. The articular formed a single, relatively wide, dorsally convex, ridge-like articulation for the quadrate as in all other oviraptorids and caenagnathids.

The intercentrum and neurapophysis of the atlas are slightly disassociated, whereas the axial intercentrum, axial centrum and odontoid are still articulated in the holotype. The length of atlantal intercentrum is about a quarter of the combined length of the centrum and intercentrum of the axis. The crescentic neurapophysis extends 1.4 mm between extremities. There is a notochordal pit in the back of the axial centrum, whereas the side of the centrum is pierced by a pneumatopore at mid-length.

One cervical centrum lacks a facet for an intercentrum, and therefore must be the third or a more posterior cervical. It has a single large pleurocoel (1.7 mm long, almost 30 % the length of the centrum) close to the anterior intercentral articulation.

All of the cervical neural arches are about the same size, roughly 11 mm across between the pre- or postzygapophyses, and 12 mm from the anterior tip of the prezygapophysis to the posterior tip of the postzygapophysis. The cervical neural spines are low, and the top of each spine is only 2.6 mm above the roof of the neural canal. In dorsal view, the posterior edge between the postzygapophyses forms a straight line in each of the fourth and fifth cervicals, but becomes progressively more emarginated in subsequent vertebrae. The epipophyses are low mounds set back from the posterior edges of the postzygapophyses. The neural canal is large relative to the centrum. The centrum of the fifth cervical is relatively low and flat, and has a pleurocoel on each side posterodorsal to the parapophysis.

The dorsal vertebrae of the holotype were disarticulated before burial and are scattered among the dorsal ribs. Most of the lateral surface of any dorsal vertebra is excavated in its anterior half by a large pneumatic depression, which has a pleurocoel with a diameter of about 1 mm.

About 20 semi-articulated caudal vertebrae are present, and all seem to be from the anterior part of the tail. It is not possible to know how many additional caudals there may have been, but the difference in dimensions from the largest to the smallest (which has less than half the width) suggests that the tail was tapering rapidly and could not have been much longer. Distinct pleurocoels are present in the centra of at least the first 15 caudals, which is another clear indication that this is a derived oviraptorosaurid (Osmólska et al. 2004; Barsbold et al. 2000; Benson et al. 2011). The platycoelous centra are almost as broad as they are long, but are only about 60 percent as high as they are wide. These proportions are similar to those found in other oviraptorosaurids (Barsbold et al. 2000).

The scapular shaft is elongate and slightly curved medially. The proximal end is broad, and the coracoid suture is open. Most of the scapular part of the glenoid is present, and was oriented posteroventrally. The distal end of the scapula is no broader than the shaft. The furcula is U-shaped and shows no sign of fusion between left and right sides. Both branches are anteroposteriorly flattened.

The humerus is subequal in length with the ulna, and two-thirds the length of the femur. The shaft is slightly

twisted. Its deltopectoral crest is positioned proximally, and is not as well developed as in other derived oviraptorids. The apex of the deltopectoral crest is approximately a quarter of the way down the shaft. There is an internal tuberosity that expands slightly longitudinally. The ulna is straight like that of *Ingenia* (Osmólska et al. 2004), whereas the radius is slightly curved. The diameter of the ulnar shaft is slightly larger than that of the radius. The ulna has a poorly developed olecranon, as in other oviraptorids (Osmólska et al. 2004).

The first metacarpal is only slightly more robust than the second. The second metacarpal is the longest and the third metacarpal is more slender than the second metacarpal. The third finger is slightly shorter than the second finger, which is similar to that of MPC-D 100/42 (Osmólska et al. 2004) that was identified as *Citipati* sp. (Clark et al. 2002). The proximodorsal lip of the ungual is low, the flexor tuber is weakly developed, and the shaft of the ungual is only slightly curved.

The overall shape of the ilium is similar to that of *Ingenia* (Barsbold et al. 1990; Lü and Zhang 2005). The dorsal margin of the ilium is convex in lateral view. The anterior part of the preacetabular process is only moderately expanded anteroventrally and has a rounded anteroventral margin. The end of the postacetabular process is truncated. The anterior blade is deeper than the posterior blade.

The femur is longer than the ilium, unlike other oviraptorids, in which the femora are approximately as long as the ilia (Osmólska et al. 2004). The ratios of femoral to iliac lengths vary with age in most theropods (Currie 2003a), however, and these bones may be subequal in size in mature animals. The femoral head is large with a distinct neck in proximal view. The ratio of femoral to tibial length is 0.81.

The proximal ends of the tibia and fibula are covered by matrix. The distal end of the tibia expands lateromedially. The fibula is tightly appressed to the tibia and contacts both proximal tarsals.

The ascending process of the astragalus extended at least 23.5 mm up the anterior face of the tibia, and its lateral edge was in contact with the fibula for that entire distance. There is a well-defined facet for the calcaneum, which shows that a small lateral process of the astragalus extended above the calcaneum to reach the margin of the tarsus as in *Nomingia* and *Heyuannia* (Barsbold et al. 2000; Lü 2005).

The first metatarsal and its associated digit are as small as they are in most other theropods. The second metatarsal is shorter than the fourth metatarsal and the third is the longest, as the case in *Heyuannia* (Lü 2005) and other oviraptorids. The pedal unguals are slightly larger than the manual unguals.

Comparison and discussion

Yulong is a derived oviraptorid, based on the high, narrow and short skull with toothless jaws, the long parietal, the distinctive shape of the medial process of the articular, pneumatized proximal caudals, and the relatively short tail (Osmólska et al. 2004; Barsbold et al. 2000). Primitive oviraptorosaurs, such as *Incisivosaurus* and *Caudipteryx*, bear teeth. Furthermore, the anterior caudal vertebrae of *Caudipteryx* are not pneumatized.

At present, 19 genera of oviraptorosaurs have been described from Asia. Among them, 10 are from Mongolia (*Avimimus*, *Citipati*, *Conchoraptor*, *Elmisaurus*, *Ingenia*, *Khaan*, *Nemegtomaia*, *Nomingia*, *Oviraptor*, *Rinchenia*) and nine are from China (*Banji, Caudipteryx, Gigantoraptor, Heyuannia, Incisivosaurus, Luoyanggia, Machairasaurus, Shixinggia, Similicaudipteryx* (Xu et al. 2007; Lü et al. 2009; Xu and Han 2010; Lü 2002, 2005; He et al. 2008). *Yulong* is clearly distinct from the primitive forms, such as *Incisivosaurus* and *Caudipteryx*, which both have teeth; in the latter at least, the anterior caudal vertebrae are apneumatic. The relative positions of the antorbital fenestrae and external nares in *Yulong* are similar to *Citipati* and *Oviraptor*, indicating that *Yulong* may have a close relationship with them rather than with other derived oviraptorids.

At least five individuals of *Yulong* were found in the Qiupa Area, but they are from different quarries up to 4 km apart. The geological survey indicates that these different quarries belong to the same age. Because four or more of the skulls have the same length, it is possible they came from the same nest, or that they hatched at the same time, and died at the same ontogenetic stage for perhaps the same reasons. Either of these suppositions is impossible to prove, however, and it is likely that they are the same size because they were coincidentally the same ages when they perished.

Yulong shows the early developmental stages of skull ossification in oviraptorids. This includes the sequence of fusion, which shows that the nasals fuse together earlier than other parts of the skull. Fusion of the nasals at an early stage is interesting, because nasal fusion is only found in a limited number of theropod clades (including abelisaurids and tyrannosaurids; Currie 2003a) and has functional implications for bite force and therefore diet (Snively et al. 2006). It has been suggested that oviraptorids ate eggs, clams, nuts and other hard foods (Osmólska et al. 2004), which may have required a strong bite, even in juveniles, although they were also considered as possible herbivorous theropods (Smith 1992). The coronoid process plays an important role in the jaw mechanics. Except for the size of coronoid processes, the power also depends on how strong the muscles attaching to the process and their orientation, such as in hadrosaurian dinosaurs (Ostrom 1961). In ceratopsian

dinosaurs, the increased height of the coronoid process effects the increased depression of the jaw articulation, which increases the jaw power (Ostrom 1964, 1966). In ornithopod dinosaurs, the coronoid process is often considered to be related to the bite force in that the taller the coronoid process, the greater the force produced by the adductor muscle mass (Wu and Russell 1997). The lower jaw of *Yulong* has a prominent coronoid process, suggesting it was capable of producing a powerful bite force.

Oviraptorids were relatively conservative in their anatomy, even between the two subfamilies (Oviraptorinae, Ingeniinae). This also seems to be true for their body proportions; mature individuals seem to vary only among proportions of the front limbs. The measurements of 115 skeletons of oviraptorids (see electronic supporting information, Table S2 and Table S3) were compared to see what can be learned about oviraptorid scaling patterns caused by either growth or by interspecific differences in mature body sizes. Although intraspecific and interspecific allometric coefficients can be quite different (Currie 1978), this approach was considered useful for at least looking at the trends of proportional changes related to size differences. There are relatively few juvenile oviraptorosaurs known, so there is unquestionably a problem separating proportional differences that are related to ontogeny from those that are simply a byproduct of the absolute sizes of the individuals being compared. As in a study on allometric growth in tyrannosaurids (Currie 2003b), femur length was used as the standard of against which all other measurements are compared. In theropods and many other animals, this is one of the least variable lengths in the body (Russell 1970; Wood 1979; Currie and Zhao 1993; Holtz 1994; Rosenberg and Dodson 1996; Currie 2003a) when it is compared with a wide suite of measurements. Femoral length is also highly correlated with body mass among extant mammals (Christiansen 1999) and other animals (Farlow et al. 2005). Although the femoral circumference is regarded as a more reliable indicator (Campione and Evans 2012), the measurement of femoral circumference is not possible in this case. Several bivariate comparisons with expected results were done as a control to check that femoral length was behaving as expected in most animals. These included ilium length and femur shaft circumference, where growth is expected to be isometric and in fact turned out to be that way. Furthermore, comparisons were done with the primitive oviraptorosaur *Caudipteryx* as a separate series and second control, again to ensure that the results were consistent with what is known about that animal. *Caudipteryx* was specifically selected because of its relationship to oviraptorids, and because it is represented by numerous specimens. Because all of the *Caudipteryx* specimens are preserved as articulated specimens in slabs of

sediment, it was not possible to take measurements of certain dimensions such as femur circumference. In this case, the non-oviraptorid oviraptorosaur used was *Avimimus*. Again, as expected, the bivariate measurements for *Avimimus* all fell on the regression line for oviraptorids.

Two subfamilies are generally recognized for Oviraptoridae, and are distinguished on the basis of hand proportions. Consequently, comparative manus measurements for members of the Ingeniinae (*Conchoraptor*, *Heyuannia*, *Ingenia*, *Nemegtomaia*) were analyzed separately from those of the rest of the Oviraptoridae (our phylogenetic analysis produced a paraphyletic "Oviraptorinae"). The humerus, radius and ulna were not found to be significantly different in relative lengths in the two subfamilies. However, *Yulong* sorted with non-Ingeniine oviraptorids when the second metacarpal was compared with the femur.

Twenty-five bivariate comparisons were made (ESM, Table S3). Measurements were transformed logarithmically to normalize the distribution of the dependent variable, and regressions were calculated using the least squares method. Each regression line is therefore defined as $\log(y)=b+k \log(x)$, which is the logarithmic expression of the simple power equation ($y=bxk$). The sum of the error terms was not included in the calculation. Confidence limits (95 % level) were calculated for each of the allometric coefficients (k) to determine whether or not increases in size were likely to have been isometric in comparison with a standard unit (femur length in most cases). The comparisons include all specimens of all oviraptorid genera, regardless of their ontogenetic stage. Size increases are considered to have been isometric when $k=1.0$; negative allometry is suggested when k is significantly less than 1.0, and positive allometry is likely when k is significantly more than 1.0. In most cases, the comparisons produced the expected results with skull length, orbit size, occipital condyle width, dentary length and total mandibular length showing strong negative allometry with increases in femur length. No other measurements deviated significantly from an isometric growth pattern when compared with femoral length. This included the comparison of the size increases of tibiae to femora, and metatarsals to femora between *Yulong* (41H III-0301) and other oviraptorosaurids. For the tibiae, the bivariate comparison was done first with all specimens of all taxa ($n=26$, $k=0.9362$, $r^2=0.9957$), and was then redone for each taxon where a growth series (multiple specimens of different sizes) is known (*Chirostenotes*, *Citipati*, *Conchoraptor*, and *Ingenia*). In all four genera, the relative growth of the femur and tibia is statistically isometric ($2<n<5$, $0.9311<k<1.1492$). The comparison was then done with only the measurements of femora and tibiae of apparent adult oviraptorosaurs (*Avimimus*, *Caudipteryx*, *Chirostenotes*, *Citipati*, *Conchoraptor*, *Ingenia*, *Gigantoraptor*, *Heyuannia*, *Khaan*, *Nomingia*),

Fig. 4 A cladogram representing a strict consensus of two most parsimonious trees showing the phylogenetic position of *Yulong* in the Oviraptorosauria. For detailed information, see Electronic Supplementary Information
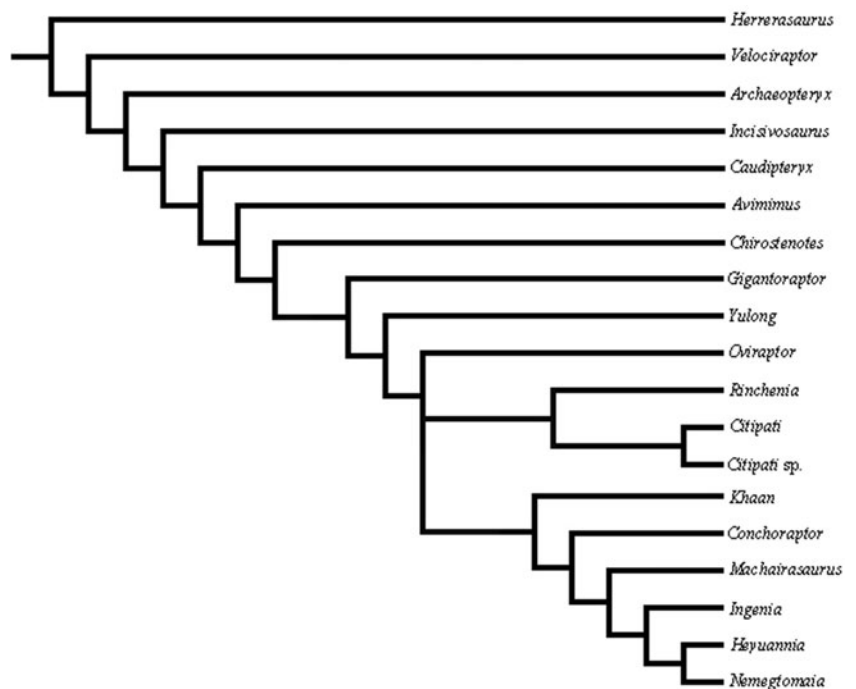
which shows that in interspecific size comparisons, the tibia increases in size isometrically with femoral size increases ($n=10$, $k=0.9364$, $r^2=0.9931$). The sample size was smaller (and therefore less significant) for comparing the femur with the length of the third metatarsal, but the results are generally similar. One noteworthy difference is that the points for taxa with arctometatarsalian feet (*Avimimus* PIN 3907/1, *Chirostenotes* TMP 1979.20.1, and eight specimens of *Caudipteryx* and *Similicaudipteryx*) fall above and outside the general trendline for non-arctometatarsalian oviraptorosaurs, although the separation between the arctometatarsalian and non-arctometatarsalian lines is not statistically significant because of the small sample size. Overall, the isometric increases (both ontogenetic and interspecific) in relative proportions of femora, tibiae and third metatarsi is unusual considering that most other theropods where growth series are known show strong negative allometry in tibial and metatarsal lengths with size increase (Currie 2003b). The significance of this is that oviraptorids (but not necessarily non-oviraptorid oviraptorosaurs) maintain their hind limb proportions regardless of ontogenetic stage or absolute size, which is a pattern seen more commonly in herbivores than in carnivores (a femur to tibia length comparison in 20 species of hadrosaurs, for example produces an allometric coefficient [k] of 0.9592, $r^2=0.9915$; the same comparison for 25 specimens of psittacosaurids and "protoceratopians" has $k=0.9417$, $r^2=0.9738$). This may weakly support the hypothesis that oviraptorids are herbivores (Smith 1992) rather than active carnivores.

A cross-section of the rib of HGM 41HIII-0107 (Fig. 5) has no growth lines, which indicates that this animal was less than 1 year old when it died. In spite of its young age, the ends of the limb bones are well developed. The lack of adult skeletons associated with babies from different localities suggests that there may have been no parental association after birth. Similarly well-developed limb bones were reported in ornithischian embryos (Horner and Makela 1979), and it was suggested that they indicate precocial development of young.
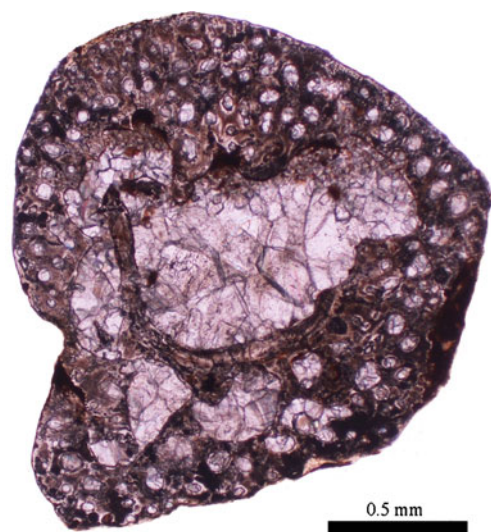
Fig. 5 Thin section of the rib of *Yulong*, showing no growth line present

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