

Hadrosauroid eggs and embryos from the Upper Cretaceous (Maastrichtian) of Jiangxi Province, China

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Abstract

Background: Dinosaur eggs containing embryos are rare, limiting our understanding of dinosaur development. Recently, a clutch of subspherical dinosaur eggs was discovered while blasting for a construction project in the Upper Cretaceous red beds (Hekou Formation) of the Ganzhou basin, Jiangxi Province, China. At least two of the eggs contain identifiable hadrosauroid embryos, described here for the first time.

Results: The eggs, attributable to Spheroolithidae indet., are thick-walled but small (~660 mL) compared to those of Lambeosaurinae. Based on the distinctive shape of the squamosal, the embryos compare favourably with *Nanningosaurus dashiensis*, otherwise known from incomplete skeletal material from Upper Cretaceous red beds elsewhere in southern China.

Conclusion: The small size of the eggs and embryos, similar to those of Hadrosaurinae, indicates that the larger eggs and hatchlings of typical Lambeosaurinae are evolutionarily derived.

Background

Dinosaur eggs are common worldwide, but embryos are rare [1]. Among the diverse duck-billed dinosaurs and their nearest relatives (Hadrosauroidea), just three identifiable species are known from perinatal material: *Hypacrosaurus stebingeri* [2], *Maiasaura peeblesorum* [3, 4], and *Saurolophus angustirostris* [5]. Accordingly, the early ontogeny of hadrosauroids is poorly understood, which hinders determination of skeletal development and allometric trends across the clade.

Recently, a construction project in the Upper Cretaceous red beds of the Ganzhou basin, Jiangxi Province, China revealed a fossilized clutch of spheroolithid eggs. In this contribution, we briefly describe two of these eggs and their embryonic contents, accessioned at the Yingliang Stone Natural History Museum (YLSNHM) in Fujian Province, China. The embryos (YLSNHM 01328 and 01373) share several features in common with hadrosauroids, but otherwise lack the more derived features present in embryonic hadrosaurids. The postorbital is distinctive and recalls that of *Nanningosaurus dashiensis* from Upper Cretaceous red beds elsewhere in southern China [6], suggesting possible affinities. We end this contribution with a consideration of the evolutionary and taphonomic implications of these eggs and their contents.

A comment on taxonomy

Hadrosauridae is traditionally split into two subfamilies, the solid-crested Hadrosaurinae and hollow-crested Lambeosaurinae [7], the former named after the eponymous *Hadrosaurus foulkii*. However, in a relatively recent phylogenetic analysis, Prieto-Marquez [8] recovered *Hadrosaurus* as the sister taxon to all other hadrosaurids, and so, abiding by the regulations of the International Code of Zoological Nomenclature, renamed the clade of solid-crested hadrosaurids Saurolophinae. Although this new name has gained some acceptance in the literature (e.g., [9-11]), not all current phylogenies recover *Hadrosaurus*

apart from the solid-crested hadrosaurids (e.g., [12, 13]). Therefore, in keeping with tradition and some recent phylogenies, we use the clade name Hadrosaurinae, which is practically synonymous with Saurolophinae, except for the inclusion of *Hadrosaurus* [14].

Geological provenance

The red beds of Ganzhou area of Jiangxi Province are divided into: (1) the Upper Cretaceous Ganzhou Group consisting of the Maodian and Zhoutian formations, and (2) the Cretaceous-Paleogene Guifeng Group, consisting of the Upper Cretaceous Hekou and Tangbian formations and the Cretaceous-Paleogene Lianhe Formation [15]. Paleomagnetic studies have dated the Guifeng Group to 71.4–65.0 Ma [16, 17]. The eggs and embryos reported here come from the Hekou Formation of the Guifeng Group in Ganzhou area (Figure 1).

The red beds of the Ganzhou area are possibly correlated to the Nanxiong Group of the Nanxiong Basin, Guangdong Province [18]. Within Guangdong Province, the Nanxiong Group is divided from bottom to top into the Cretaceous Changba, Yuanfu, Zhutian and Zhenshui formations [18]. There is little consistency between studies concerning the correlation of the Hekou Formation with the Cretaceous formations of the Nanxiong Group [18, 19]. Most recently, the Hekou Formation has been correlated to the Dafeng and Yuanpu formations of the Lower Nanxiong Group in the study of Zhang et al. [20].

The Hekou Formation varies in thickness between 200 and 1600 m, depending on where it is exposed. It consists of channelized, fining-upward conglomerates, sieve deposits, and alternating sandstone and mudstone beds. The depositional setting is interpreted as primarily fluviially-derived within a proximal alluvial fan system. Mudcracks and caliche deposits are common, and the prevailing palaeoclimate is interpreted as subhumid [21].

The age of the Hekou Formation is debated. Radiometric dating suggests an age range from the Coniacian to Santonian [21]. In contrast, the arguably penecontemporaneous red beds of the nearby Nanxiong Group have been assigned a Maastrichtian age [22]. Indeed, the preserved theropod assemblage, including alioramine tyrannosaurids and oviraptorosaurs [23, 24], agrees well with the dinosaur assemblage of the Nemegt Formation in Mongolia, which is often considered Maastrichtian in age [25]. For this reason, and in keeping with other recent interpretations (e.g., [26, 27]), we accept a correlation with the Nemegt Formation for the Hekou Formation. The formation has thus far yielded fossil algae, plants, dinosaur bones, and trackways, few of which have been formally described [15, 26-30]. Dinosaur eggs assigned to *Oolithes* sp., *Oolithes spheroides* [31], "*Spheroolithus minor*", *Ovaloolithus* sp., *Paraspheroolithus* sp., *Macroolithus rugustus*, Coelurosauria fam. et gen.indet. [28], and Elongatoolithidae [27] are also known from the Hekou Formation.

Methods

Eggshell histology

A piece of eggshell was removed from YLSNHM 01373 with an Engraving Pen AT-310. The shell was embedded in Araldite 2020, cut with a STX-202A diamond wire cutting machine, and then polished with P400 to P4000 abrasive paper to approximately 30 µm thick for microscopic observation under normal and cross-polarized light with a Zeiss Primotech microscope.

Results

Description of Eggs

Each embryo described here is preserved within its respective egg, both of which came from the same egg clutch. Field records note the presence of at least 13 eggs in the clutch at the time of excavation, but the original number may have been higher (S Miao, pers. comm. to LX, 2008).

The better-preserved egg of YLSNHM 01373 has the shape of a prolate spheroid, comparable to the spherical-sub spherical eggs assigned to the oofamily Spheroolithidae [32], which has been reported previously from the Hekou Formation as "*Spheroolithus minor*" [28], a nomen nudum. Given the cross-sectional dimensions of the egg, we estimate a total egg volume of approximately 600 mL. Viewed in cross-section, the embryo fills approximately 40% of the egg by area.

The eggshell of YLSNHM 01373 is poorly preserved and thus hinders our detailed description and further assignment to an oogenus. While hadrosaurids have long been associated with spheroolithid eggs based on their embryonic contents [2, 4, 33, 34], the association remains questionable due to the poor preservation and previous undetailed reports of the eggshells. The YLSNHM 01373 egg reveals an indistinct boundary between the mammillary and continuous layers (Figure 2), indicating its two-layered structure—a common microscopic feature for dinosaurian eggs. The organic cores (nucleation site for the acicular radial crystal growth in the lower part) are absent, probably due to severe embryo-induced erosion or poor preservation (or both). The radial crystals merge into a tabular structure in the external quarter of the eggshell. In comparison with previously reported spheroolithid eggs (see [35]), the eggshell of YLSNHM 01373 ranges from 3.2–4.2 mm thick, which is so far the thickest for the oofamily.

Description of embryos

YLSNHM 01328

This partial, articulated skeleton consists of the posterior cranium (missing most of the snout), complete cervical series, and the anterior-most dorsal vertebrae and associated ribs (Figure 3). The bridge of the rostrum has buckled; its original profile is obscured. The elongate, paired nasals are unfused and broken anteriorly where they reach their greatest transverse breadth. In lateral profile, the nasal is subtly bowed dorsally above the naris. The squamosal is notable in having a swollen process (Figure 4) that projects anteroventrally to both buttress the descending process of the postorbital and constrict the laterotemporal fenestra dorsally. The anterior third of the left maxilla is missing, whereas the preserved portion measures 14 mm long. Whether a palatal process of the maxilla (sensu [36])^¾whose absence is

diagnostic of Lambeosaurinae³ originally existed cannot be determined. The jugal facet of the maxilla faces laterally, and its long axis is horizontal as in the perinates of *Maiasaura peeblesorum*, whereas the same facet is distinctly angled in those of *Hypacrosaurus stebingeri* [2]. The partial maxilla has eight teeth *in situ* (there is a total 12 maxillary teeth in embryonic *H. stebingeri*; [2]). Each has a straight primary (median) ridge and lacks both subsidiary ridges and marginal denticles (Figure 5), as in the perinates of *M. peeblesorum* [37]. The occlusal surfaces of the teeth are not visible, hindering determination of whether they bear wear facets as they do in the embryos of *H. stebingeri* [2]. The quadrate (17.0 mm tall) is robust with a broadly rounded head that articulates dorsally with the squamosal in a hinge joint. The pterygoid flange is broad, and the quadratojugal notch, largely obscured by the quadratojugal, occurs in the lower half of the quadrate body. The quadrate is gently bowed anteriorly along its length; the dorsal and ventral halves form an angle of approximately 154°. The ossified braincase elements are unfused and have been displaced; the basisphenoid now rests against the skull roof and the orbitosphenoid has shifted posteriorly. The prootic is visible beneath the basisphenoid, where the single opening for c.n. V (trigeminal nerve) can be seen. The otoccipital (opisthotic + exoccipital) occurs further posteriorly. On the occiput, the well-developed paroccipital process is pendant and projects posterolaterally beneath the squamosal.

The cervical series is nearly complete and preserved in a gentle sigmoid along its length, being dorsiflexed anteriorly and ventroflexed posteriorly. The neurocentral sutures are unfused. The neural spines are low, whereas the postzygapophyses are strongly developed and hooked, both of which are common to all hadrosauroids. The postzygapophyses do not extend above the level of the neural spines as they do in adult hadrosaurids (e.g., [38, 39]). Many of the transverse processes have buckled ventrally, obscuring their corresponding centra. The few remaining cervical ribs are L-shaped, with elongate posterior processes. The transition between the cervical and anterior dorsal series is nearly indistinguishable. We tentatively identify the first dorsal as that bearing the first preserved elongate rib, which itself is broken along its length. As such, we identify 12 cervical vertebrae, although the count may have been higher by one or two vertebrae (depending on whether the first preserved long rib reached the sternum or not). For comparison, the cervical series contains 11 vertebrae in *Equijubus normani* [40], *Tethyshadros insularis* [41], and *Gobihadros mongoliensis* [42], 13 in *Parasaurolophus walkeri*, *Edmontosaurus regalis* and *Gryposaurus notabilis* [39, 43], 14 (or more) in *Lambeosaurus* spp. [44], and 18 in *Orolotitan arharensis* [45]. The neural spines increase in size and posterior inclination by the 15th presacral vertebra, but the dorsal series is not preserved beyond the 17th presacral vertebra.

YLSNHM 01373

This articulated skeleton is lacking parts of the skull, distal limb elements, and tail (Figure 6). The parietal, which is poorly visible in YLSNHM 01328, is elongate (2.7 times longer than wide), as in non-lambeosaurine hadrosauroids. The preserved cervical and dorsal vertebrae show unfused neural arches. We consider the first dorsal vertebra to be that bearing the first long rib that presumably connected with the sternum, in which case, we count 11 cervical vertebrae and 18 dorsal vertebrae. However, we can neither confirm the presence of the atlas/axis in the preserved series nor rule out the possibility that the

posteriormost free dorsal vertebra would eventually become incorporated in the synsacrum as a dorsosacral [7]; the true cervical count could be higher. The few preserved caudal vertebrae show that the neural spines were low. The coracoid foramen is not enclosed but opens posteriorly to separate the contact surfaces for the humerus and scapula, as in *Hypacrosaurus stebingeri* perinates [2]. The scapular blade is slender and the caudal end is irregular and poorly ossified. The length of the deltopectoral crest of the humerus is moderate compared to the length of the humerus (ratio = 0.53), which contrasts with the condition of most hadrosaurids (ratio > 0.55) [7, 8]. The distal condyles of the humerus are poorly defined. The left ilium has drifted anteriorly to be preserved alongside the skull. It is low in lateral profile, with a well-developed supracetabular process and a preacetabular blade that is only weakly arched dorsally. The pubic and ischiadic penduncles are poorly defined. The femur is 26 mm long, with a well-developed greater trochanter and poorly defined distal condyles. The fourth trochanter is not visible, on account of the outward rotation of the femur. The preserved tibia and fibula are missing their extremities.

Discussion And Conclusions

The embryos described here can be confidently assigned to Hadrosauroidea based on the following derived features (from [8]): (1) large jugal contact of maxilla faces strongly laterally; (2) deltopectoral crest of humerus wide relative to minimum width of humeral shaft (ratio = 1.71). Dentary teeth having a centrally located primary ridge and lacking subsidiary ridges are also considered derived for hadrosaurids [8], and while these features are present on the teeth of the embryos described here, we are unable to confirm their occurrence specifically on the dentary teeth (the dentary tooth crowns are not visible in YLSNHM 01328, and the loose teeth of YLSNHM 01373 are not definitively from the dentary).

Derived features that would allow the embryos to be assigned to Hadrosauridae (see synapomorphies listed in [8]) are lacking. For example, in hadrosaurids (including their embryos: [2, 5, 37, 46]), the deltopectoral crest of the humerus is both proximodistally elongate and exhibits a pointed distal corner; this is not the case in YLSNHM 01373. The parietal and nasals are also long compared to the condition seen in lambeosaurines (although parietal length is negatively allometric over the course of lambeosaurine ontogeny; [8]). Many definitive hadrosaurid characters are associated with the ilium. However, these characters typically relate to the pubic and ischial peduncles that comprise the acetabular plane, which is poorly preserved in YLSNHM 01373, and so these characters cannot be properly assessed.

The presence of a swollen process of the squamosal that constricts the dorsal half of the laterotemporal fenestra is strongly reminiscent of the condition in *Nanningosaurus dashiensis* [6]. However, the poor temporal resolution of the Late Cretaceous red beds of southern China makes it difficult to know whether the embryos described here were penecontemporaneous with *N. dashiensis*, rendering such an assignment tentative at best. Accordingly, we do not wish to press the issue too far. We do note several points of disagreement between the embryonic teeth of YLSNHM 01328/01373 and the holotype of *N. dashiensis*. Whereas the embryonic teeth described here lack marginal papillae and subsidiary ridges, and the single primary ridge is straight, the dentary teeth of the holotype of *N. dashiensis* possess weak

marginal papillae and subsidiary ridges, and have a laterally offset, sinuous primary ridge. At least some of these characters are known to vary with ontogeny [2, 37], so their taxonomic significance is uncertain. If YLSNHM 01328 and 01373 are taxonomically equivalent to *N. dashiensis*, they provide evidence consistent with recent hypotheses classifying *N. dashiensis* as a non-hadrosaurid hadrosauroid [47, 48], and contrary to the original hypothesis that the species is nested within Lambeosaurinae [6].

In describing hadrosaurine and lambeosaurine eggs and embryos from Montana, Horner [4] noted that those of hadrosaurines tend to be much smaller than those of lambeosaurines. Hadrosaurine embryos (*Maiasaura peeblesorum*) have femora that vary in length between 35 and 40 mm, and their subspherical eggs were calculated to have a volume of approximately 900 mL. Lambeosaurine embryos (*Hypacrosaurus stebingeri* and an indeterminate form), by contrast, have femora that vary between 60 and 80 mm long, and are derived from eggs approaching 4000 mL [2, 4]. Horner [4] hypothesized that these differences were typical of their respective subfamilies, and further suggested that the smaller hadrosaurine hatchlings were altricial, based on their poorly ossified epiphyses [3, 49].

The hadrosauroid eggs and embryos reported here facilitate character polarization of egg and hatchling size among hadrosaurids. The 26 mm femur of YLSNHM 01373 is closer to *M. peeblesorum* perinates in size, and the corresponding egg (660 mL) similarly is more like those of *M. peeblesorum* than to those of any known lambeosaurine [4]. Importantly, the YLSNHM 01373 embryo is not fully developed, evidenced by the fact that the skeleton does not entirely fill the egg. This likely explains the missing ends of the tibia-fibula, which ossify from the diaphyses outward, and the absence of many of the manual and pedal elements in an otherwise mostly undisturbed skeleton; they may simply not have ossified by the time of death [50]. It is probable, therefore, that these embryos were yet several embryonic stages away from hatching. Consequently, we are unable to determine whether these young were altricial, given the incomplete development of the embryo. The small sizes of the eggs and embryos reported here, comparable to those of hadrosaurines, indicate that the lambeosaurine condition of having larger eggs and hatchlings is an evolutionarily derived trait.

Dinosaur eggs and embryos occur commonly in semi-arid, upland palaeoenvironments [1]. Palaeontologists once maintained that these were the preferred nesting grounds of dinosaurs [33, 51], but rare perinatal bones have also been found in lowland deposits (e.g., [46, 52], and it is now widely held that the wet, acidic conditions of such palaeoenvironments exerted a bias against the preservation of eggs and their contents [52]. The Hekou Formation of China, with its diversity of fossil dinosaur eggs combined with sedimentological indicators of moderately dry, well-drained conditions (e.g., caliche, mudcracks, carbonate nodules), is entirely consistent with this framework of understanding. These strata promise to reveal many more clues about early dinosaur development.

Abbreviations

atic: atlas intercentrum, ax: axis, bsp: basisphenoid, ca, caudal vertebrae, CL: continuous layer, cnV: cranial nerve V exit, co: coracoid, cv, cervical vertebrae, ?d1: first dorsal vertebra (possibly), dto: dentary

tooth, dr: dorsal rib, dv, dorsal vertebrae, f: frontal, fe: femur, fl, fibula, h: humerus, il: ilium, is: ischium, j: jugal, mt: metatarsal, ML: mammillary layer, mx: maxilla, mxto: maxillary tooth, n: nasal, oc: occipital condyle, osp: orbitosphenoid, oto: otoccipital, p: parietal, pl: palatine, po: postorbital, poc: postorbital contact, pocp: postcotyloid process, prcp: precotyloid process, prf: prefrontal, pro: prootic, pt: pterygoid, pu: pubis, q: quadrate, qj: quadratojugal, r: radius, sa: sacrum, sc: scapula, sp: swollen process of squamosal, sq: squamosal, t: tibia, to: tooth, ul: ulna, YLSNHM: Yingliang Stone Natural History Museum

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Availability of data and materials

All data generated or analysed during this study are included in this published article.

Competing interests

The authors declare that they have no competing interests.

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Authors' contributions

LX managed the project and photographed the eggs and embryos. KN obtained the specimens, conducted the geological survey, supervised specimen preparation, and contributed to discussions of morphology and taphonomy. T-RY contributed the eggshell histological analysis. TM produced the anatomical drawings in Figures 3 and 6. JCM designed the figures. LX, T-RY, DW, TM, and JCM wrote the manuscript. All authors read and approved the final manuscript.

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Figures



Figure 1

Map showing location of YLSNHM 01328 and 01373 (“fossil site”) in southern China.



Figure 2

Cross-section of the YLSNHM 01373 eggshell under the transmitted, unpolarized light. The dotted line marks the boundary between the mammillary (ML) and continuous (CL) layers. The white arrows indicate the locations of organic cores.

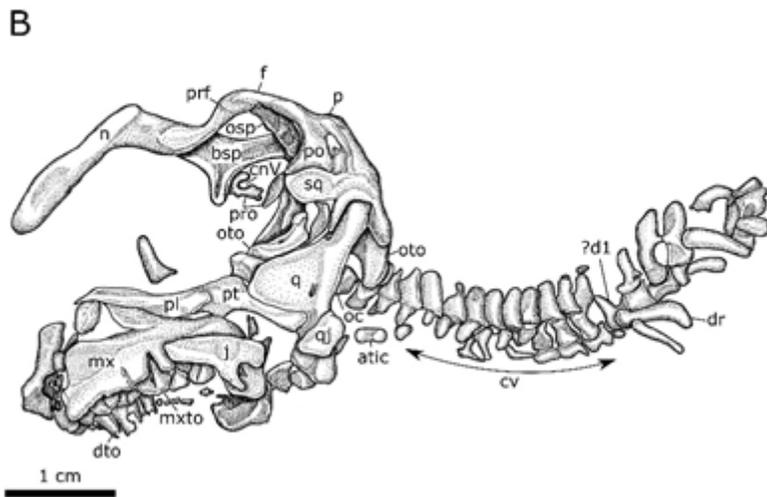


Figure 3

Hadrosauroid partial embryonic skeleton (YLSNHM 01328). A, photograph, B, interpretive drawing. See text for list of abbreviations.

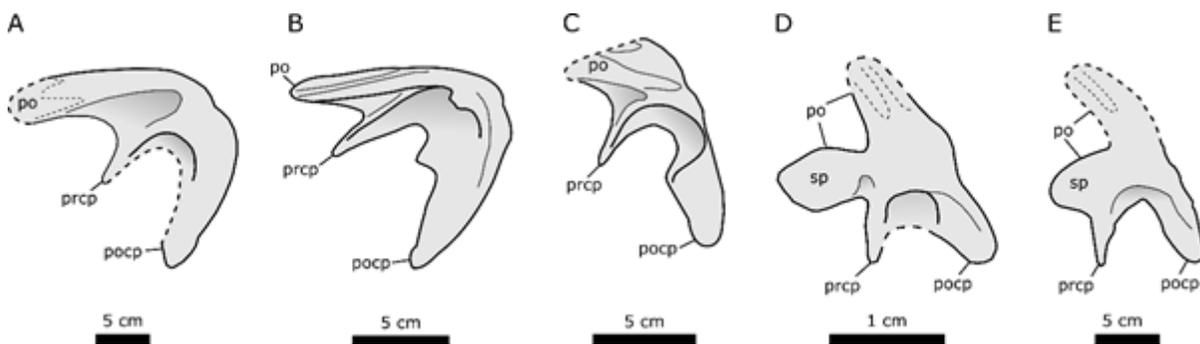


Figure 4

Hadrosauriform squamosals in left lateral view. A, *Iguanodon bernissartensis*; B, *Prosaurolophus maximus*; C, *Corythosaurus casuarius*; D, YLSNHM 01328; E, *Nanningosaurus dashiensis*. See text for list of abbreviations.

Figure 5

Occluded teeth of YLSNHM 01328. Maxillary teeth (top row) exhibit a strong primary (median) ridge and no subsidiary ridges and marginal denticles.

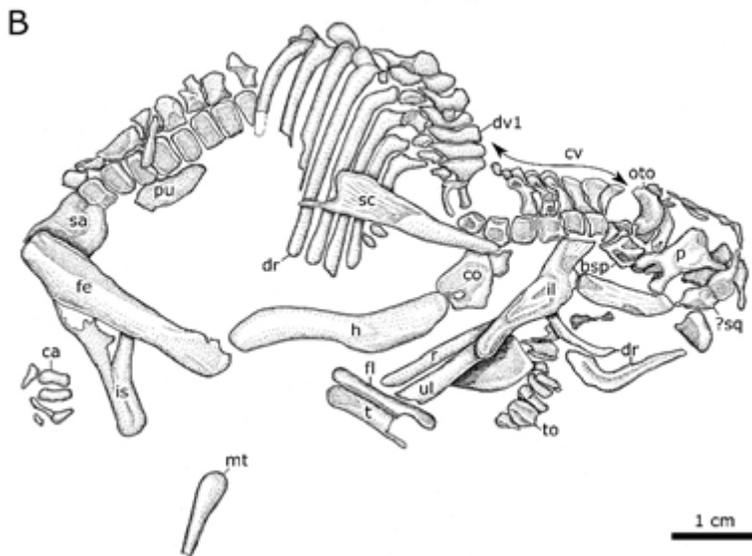


Figure 6

Hadrosauroid partial embryonic skeleton (YLSNHM 01373). A, photograph, B, interpretive drawing. See text for list of abbreviations.