

Article

Interpretation of fossil embryos requires reasonable assessment of developmental age

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Abstract.—Dinosaur embryos cause a lot of excitement in the scientific literature and are often widely reported because of the general public's interest in dinosaur biology. Well-preserved, articulated oviraptorosaur embryos in eggs are usually interpreted as representing a stage of development close to hatching because of their large size and good level of skeletal ossification. Based on this evidence, a recent report suggested that the position of the one embryo's head was reminiscent of an avian-like hatching position. Here we explore how the developmental stage of well-preserved oviraptorosaur embryos can be estimated, rather than assumed. This will help in our understanding of their developmental biology and its evolutionary consequences. Using quantitative methods and comparison with modern crocodylian embryos, we show that all articulated oviraptorosaur embryos are small relative to the egg and most likely at a stage of development equivalent to around 50%–60% of the developmental period, that is, not even close to hatching. This conclusion is supported by the fact that many elements of the crocodylian skeleton are well ossified many weeks before hatching and the position of oviraptorosaur embryos' heads was also comparable to a crocodylian embryo many days before hatching. Misunderstandings about the stage of the developmental biology of these well-preserved oviraptorosaur embryos hampers our understanding of the true nature of their reproductive biology. We urge a more conservative approach to their interpretation. This is important, because misunderstandings in the minds of the public about dinosaur biology are hard to counter once poorly evidenced ideas have been reported around the world.

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Introduction

Dinosaur embryos always attract a lot of media attention when they are reported in the scientific literature, because they capture the imagination of academics and the public alike. Spectacular fossils like that of an exceptionally well-preserved, articulated oviraptorosaur embryo in an egg from China (YLSNHM01266; Xing et al. 2022) are fascinating. Its three-dimensional (3D) level of preservation has allowed interpretation of the developmental status of this embryo. In this instance, the position of the head relative to the rest of the skeleton in this well-ossified embryo led Xing et al. (2022) to suggest that the embryo was close to hatching and that the embryo had adopted a posture comparable

to the hatching position exhibited by modern birds. There was even a suggestion that other articulated oviraptorosaur embryos in eggs exhibit similar positioning of the head. The evidence to support these assertions was the well-ossified skeleton and the position of the skeletal elements compared with micro-computed tomography scans of an ontogenetic series for the domestic fowl *Gallus gallus*. The report detailed broader implications for theropod evolution, because it purported to provide evidence that avian-like developmental features were established in non-avian theopods, rather than being a characteristic of birds themselves. However, whether this suggestion has any merit relies on the strength of the evidence.

The first embryonic dinosaurs were found in the 1980s (Horner and Weishampel 1988, 1996), and there were many reports thereafter (see Deeming [2004], but also Norell et al. [1994, 2001], Weishampel et al. [2008], Wang et al. [2016], Yang et al. [2019], and Bi et al. [2021] for oviraptorosaur embryos). The interpretation of these specimens has often relied on how the skeletons have been methodologically perceived, particularly in terms of the degree of ossification and how it relates to hatching based on modern crocodylian and avian proxies (Kundrát et al. 2008). For instance, Bi et al. (2021) reported several oviraptorosaur eggs with ossified embryonic bones that vary in size and suggested that this implied asynchronous development in a clutch. In addition, “Baby Louie” was a small, isolated, articulated, and well-ossified skeleton of a caenagnathid oviraptorosaur found in association with a clutch of *Macroelongatoolithus* eggs (Pu et al. 2017). It was considered as a perinate embryo, that is, one close to hatching, despite not being enclosed in eggshell. These fossil embryos needed to be relatively well ossified in order to be fossilized in the first instance but often many of the reported descriptions are qualitative and independent of any extant vertebrate model for development. The lack of a comparative analysis often weakens the argument for the proposed interpretation of many of these embryo specimens.

An alternative approach is more quantitative and comparative and has been used to confirm the developmental status of small ichthyosaur skeletons in association with larger adults. Deeming et al. (1993) used qualitative observations of small ichthyosaur skeletons in conjunction with quantitative data from other ichthyosaur fossils and from extant alligator embryos to suggest that these small skeletons were indeed embryos rather than cannibalistic prey items. A similar approach has been applied to pterosaur embryos, whereby four separate quantitative approaches allowed for a more precise identification of the developmental stages of skeletons *in ovo* and probable hatchlings (Unwin and Deeming 2019).

Undoubtedly, the recent description of the oviraptorosaur embryo YLSNHM01266 (Xing et al. 2022) is impressive, but to what extent

did the report’s authors offer evidence to support their proposal that the specimen was about to hatch? Did the evidence support the authors’ broader interpretation of theropod–bird evolutionary biology? We feel that the report of YLSNHM01266 is descriptive and only uses a limited comparative approach to support its interpretation. Here, we explore the key assumptions made by many paleontologists, including Xing et al. (2022), when interpreting embryos *in ovo*; namely: (1) the degree of ossification and (2) the size of the specimen accurately indicate ontogenetic status. Many other interpretations of well-ossified embryos of oviraptorosaurs (Norell et al. 1994, 2001; Weishampel et al. 2008; Wang et al. 2016; Pu et al. 2017) were underpinned by these assumptions, but here we explore the extent to which the assumptions are accurate for oviraptorosaur embryos like that reported by Xing et al. (2022).

We explore the oviraptorosaur embryo YLSNHM01266 in a 3D comparative analysis relative to crocodylian development to assess whether it is possible to provide a reasonable assessment of the ontogenetic status of the specimen. Ideally, it would be better to use avian models in this context, but while modern birds have a basic theropod body plan of a relatively small head on a long neck attached to a robust body with well-developed pelvic limbs, they lack an extended tail seen in extinct non-avian theropods. Crocodylians have the tail, but the neck is relatively short, but given that they are, like theropods, archosaurs, they are not an unreasonable model from the extant fauna.

Materials and Methods

Embryos of *Crocodylus niloticus* were obtained from La Ferme aux Crocodiles (Pierrelatte, France). Permission to collect the *C. niloticus* at the farm was granted by two directors: Luc Fougeirol and Samuel Martin. Clutches were collected from nesting areas and incubated at 28°C–31°C in a mixture of vermiculite and sand. The killing procedure was done under the veterinary supervision of Samuel Martin and consisted of two steps: (1) eggs containing embryos were transferred from incubator to room temperature conditions (~20°C) for 30 minutes and then moved into a refrigerator

(4°C–8°C) for an hour to gradually decrease circulatory activity and prevent any further movement of embryos. Subsequently, the cold eggs containing embryos were injected with formalin and then submerged in formalin completely. This procedure was chosen to preserve the original position of crocodylian embryos inside the eggs. Later, the eggs were refixed with 95% ethanol. Crocodile egg specimens were individually placed in plastic tubes filled with 95% ethanol. Each tube was then imaged with propagation phase contrast X-ray synchrotron microtomography on the beamline ID 19 of the European Synchrotron Radiation Facility (ESRF) using a polychromatic beam with an isotropic voxel size of 28 µm. The reconstruction was performed using a single distance phase retrieval process (Paganin et al. 2002). The volumes were then reconstructed using a filtered back-projection algorithm. After reconstruction, residual ring artifacts were corrected on the slices using an algorithm developed at the ESRF (Lyckegaard et al. 2011). The segmentation of the data and 3D modeling was performed with Volume Studio Max 2.1 (Heidelberg, Germany).

Details of the hatching sequence of alligators (*Alligator mississippiensis*) and various species of domesticated and wild birds are from personal observations by D.C.D. over several years. Embryos of *A. mississippiensis* investigated here were represented in photographs taken in 1988 and 1989 and are the same embryos incubated at 30°C as those reported by Deeming and Ferguson (1989) with an average egg length of 72 mm (Deeming and Ferguson 1990).

Measurements of all crocodylian embryos were taken from digital images using ImageJ (<https://imagej.nih.gov/ij/>; Schneider et al. 2012) after calibration using the relevant linear scales.

The scanned data of the critical developmental (55, 67, and 87 day) stages of the Nile crocodile have been made publicly available on the ESRF paleontology online database at <http://paleo.esrf.eu>.

Results and Discussion

Assessment of the Ontogenetic Stage of the Oviraptorosaur Embryo.—Interpretation of any fossil

embryo is reliant on a good understanding of the developmental stage of the specimen, which relies on the degree of ontogenetic maturity and interpretation of its size. The oviraptorosaur embryo YLSNHM01266 is certainly well ossified, the skeleton is articulated and relatively large, but is this sufficient to assume that it is close to hatching?

The degree of ossification of embryonic bones has often been used to assign certain characteristics to the specimens. For example, Chapelle et al. (2020) used tomographic data of *Centrochelys sulcata*, *Gallus gallus*, and *Crocodylus niloticus* embryos to help interpret well-preserved embryos of the early-branching sauropodomorph dinosaur *Massospondylus carinatus*. Unwin and Deeming (2019) used descriptions of ossification in *Alligator* and the quail *Coturnix coturnix* to interpret pterosaur embryos. By contrast, Horner and Weishampel (1988, 1996) used a more qualitative approach to interpret the poorly ossified terminal ends of small limb bones of *Maiasaura* as representing altricial development. However, as is seen in birds, only the shafts of the embryonic limb bones are ossified, and the terminal ends remain as cartilage in order to facilitate rapid growth posthatching (Starck 1996, 1998). Moreover, the degree of ossification of hatchlings does not qualitatively differ between precocial and altricial species (Starck 1996, 1998). Growth and development of bones take place over a protracted period of the developmental period in birds and crocodylians, and bones become ossified relatively early in development (Romanoff 1960; Rieppel 1993). In galliform birds, ossification starts around midway through development (Maxwell 2008). In the Nile crocodile (*C. niloticus*), a range of poorly developed elements of the skeleton are already showing substantial amounts of ossification in embryos at 39 days of development at 30°C, which is only 45% of the way through development (Fig. 1). As the embryos grow, the degree of ossification keeps pace, and embryos with well-ossified skeletons are observed some 30 or 20 days before hatching (Fig. 1). In addition, the terminal ends of the long bones are not ossified, even in hatchling birds and crocodylians (Kundrát et al. 2008: fig. 8; Maxwell 2008: fig. 1). Therefore, a well-ossified skeleton is not

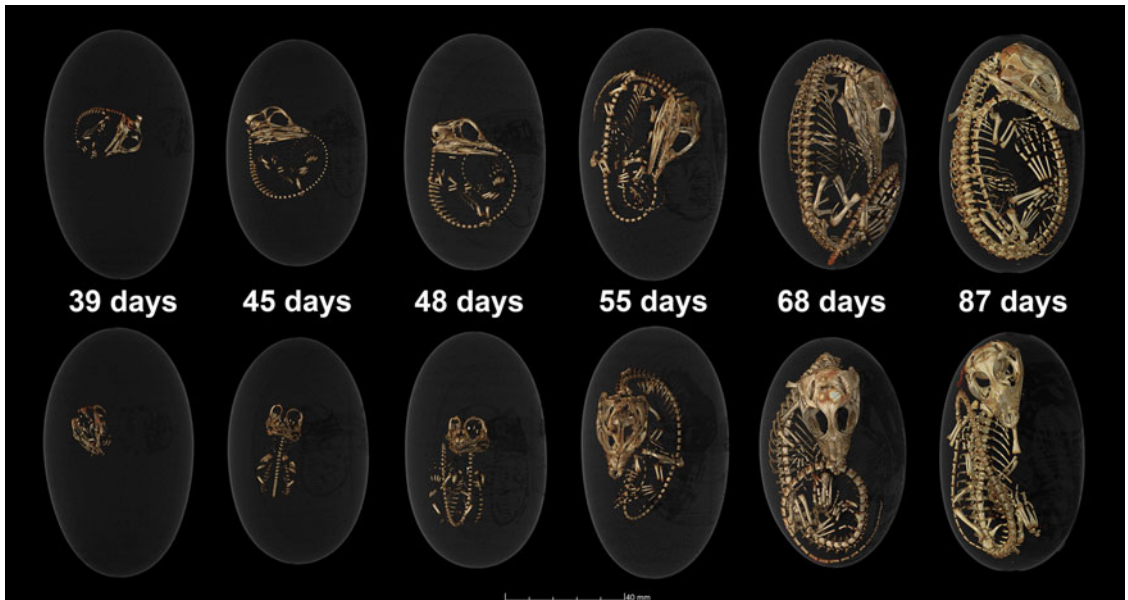


FIGURE 1. Three-dimensional mapping of real consecutive positioning and developmental geometry of cranial and post-cranial elements in *Crocodylus niloticus* embryos. The incubation period is around 90 days. Note the position of the skull inside the egg, overall curling patterns, and *in ovo* space left unoccupied by 55- and 68-day-old embryos.

evidence in itself to allow for interpretation of the developmental stage of the embryo.

The size of a specimen *in ovo* is often deemed to “fill” the egg (Xing et al. 2022), which is seen as another piece of evidence that the embryo was close to hatching. Rarely (Deeming et al. 1993; Unwin and Deeming 2019) do reports of fossilized embryos offer any quantitative assessment of age in terms of development. Therefore, how reasonable is it to assume that specimens like YLSNHM01266 (Xing et al. 2022) and other oviraptorosaur embryos (Norrell et al. 1994, 2001; Weishampel et al. 2008; Wang et al. 2016; Pu et al. 2017) are of a size that is “close to hatching”? Is it possible to gauge the stage of development of an embryo from its size? First we consider the physical characteristics of crocodylians and birds immediately leading up to and through hatching before considering how to interpret absolute size for embryos *in ovo*.

Comparison between Crocodylian and Avian Egg Immediately before Hatching.—Both crocodylian and avian embryos occupy much of the volume of the egg immediately before hatching (Grigg and Kirshner 2015). In both taxa, the embryo has absorbed the residual yolk into its abdominal

cavity and the embryo remains surrounded by the extra-embryonic membranes. In crocodylians, the allantoic sac is still full of fluid, which at 5 g is around 8% of an alligator egg of 64 cm³ (Deeming and Ferguson 1989). Within hours of hatching, air is present within the amniotic cavity (Fig. 2), which allows the perinatal alligator to vocalize, despite the allantoic fluid remaining in the egg (Andrews 2004). By contrast, in avian eggs, all of the allantoic and amniotic fluids have been resorbed by the embryo, and 15% of the egg’s volume is occupied by the air space (Ar 1991). Vocalization is only possible after the perinatal bird has internally pipped and is breathing through its beak, which is pushed into the air space (Romanoff 1960).

Hatching has been reported in crocodylians (see Ferguson 1985; Grigg and Kirshner 2015), and the following account includes additional personal observations by D.C.D. Despite reports to the contrary (Grigg and Kirshner 2015), there is no internal air space in crocodylian eggs incubated under normal conditions (D.C.D. personal observations), and this prevents internal pipping, as is seen in birds (Romanoff 1960). Hatching proceeds by the perinatal embryo externally pipping the



FIGURE 2. A full-term embryo of *Alligator mississippiensis* in situ within its egg. The top half of the eggshell with associated chorioallantoic membrane has been removed, and the allantoic fluid drained away. The embryo's head is to the left and is pointing to the top. Note the embryo occupies most of the egg, and its tail is wrapped around the abdomen and legs. (Photograph by D.C.D.)

eggshell and pushing the distal end of its rostrum and its nostrils into the air. This releases allantoic fluid that leaks from the egg. After a variable period of time (usually only a few minutes) of air-breathing, the head is simply extended through the hole, and in seconds the hatchling pushes its way out of the egg. The head of the perinatal crocodylian does not adopt a particular position before external pipping (D.C.D. personal observations).

In birds, the hatching process requires internal pipping by the beak being pushed into the air space (Romanoff 1960). This leads to the perinatal embryo adopting a position where it tucks its head under the right wing so that the beak can be pushed through the chorioallantois and inner shell membrane. Once internal pipping occurs, the air in the air space is transferred into the perinatal respiratory system, where it inflates the air sacs and the lungs. After a period of 24 hours, the perinatal embryo makes an initial external pip hole in the egg shell, which it proceeds to enlarge by rotating within the eggshell while repeatedly hitting the eggshell to form a fracture line. After a species-specific degree of rotation, the end cap of the eggshell is pushed off, and the hatchling kicks its way out of the egg (Bond et al. 1986, 1988).

Quantitative Assessment of Ontogenetic Status.—Deeming et al. (1993) used morphometrics of ichthyosaur fossils and quantitative

patterns of alligator development to demonstrate that small ichthyosaur skeletons associated with adults were embryos that were born tail first. An effective growth series is not reported for theropods, and embryos *in ovo* remain relatively rare (Kundrát et al. 2008), so how can developmental age be assessed? The YLSNHM01266 specimen is helpful, in that the surrounding eggshell is nearly intact and uncrushed, so egg length was reliably measured at 167 mm. Xing et al. (2022) also reported that the embryo specimen was ~235 mm in length and seemed to fill the egg. However, as shown earlier, both avian and crocodylian hatchlings occupy most of the egg's volume but, as Xing et al. (2022) acknowledged, YLSNHM01266 clearly has space around it. In fact, the tail never extends/projects from the embryonic body of modern crocodyles, as Xing et al. (2022) illustrated in highlights of their paper, and it bends from its base toward and around the body.

With a total length of 235 mm, the YLSNHM01266 specimen was 1.4 times the length of the egg, so how does this compare with the length of extant crocodylians at hatching? *Alligator mississippiensis* hatchlings averaged 260–300 mm in length and hatched from eggs that are 75 mm in length (Deeming and Ferguson 1989), making them 3.4–4 times the length of the egg. The *C. niloticus* hatchling in Figure 1 had a total body length of 264.9 mm from an egg measuring 101.3 mm in length, a ratio of 3.3:1. Figure 3 shows data collected from the images of *C. niloticus* in Figure 1 and from digitized photographs of *A. mississippiensis* embryos collected during development as proportions of egg length. As development proceeds, crocodylian embryos get progressively longer and average around 3.4 times the length of the egg at hatching. Figure 3 also shows the ratio of head length to egg length for the same embryos; hatchlings have heads that are around 0.5 of the egg length. Equivalent data are not available for birds, but an ostrich hatchling was 2.7 times the length of its 150 mm egg (D.C.D., personal observation); adding a tail would only increase this ratio.

With a total length to egg length ratio of 1.4, the YLSNHM01266 specimen was seemingly around 55% of its way through development

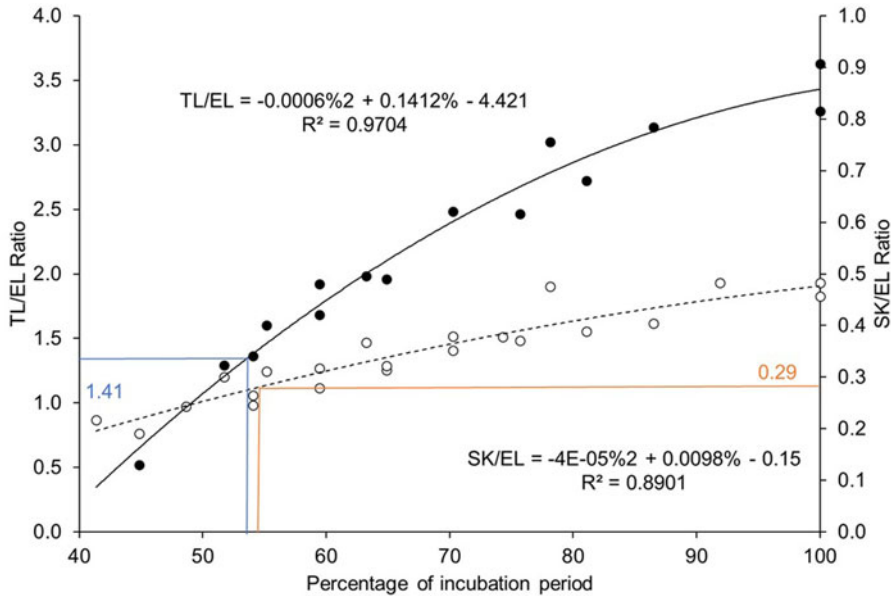


FIGURE 3. Relationships between total body length as a proportion of egg length (TL/EL, filled circles) and head length as a proportion of egg length (SL/EL, open circles) plotted against percentage of the incubation period for embryos of *Alligator mississippiensis* and *Crocodylus niloticus*. Blue number indicates TL/EL, and the orange number indicates HL/EL, for the oviraptorosaur embryo YLSNHM01266 (Xing et al. 2022). Lines indicate extrapolation of these values onto crocodylian relationships.

(Fig. 3). The skull length to egg length ratio is 0.29 for this oviraptorosaur, which also suggests a similar stage of development of ~55% of the developmental period. Juvenile specimens of oviraptorosaurs reported by Lü et al. (2013) were larger than embryos *in ovo*, but despite the availability of data from a variety of oviraptorosaurs (Lü et al. 2013), there is no consistent series of oviraptorosaur embryos and juvenile stages to allow a more direct comparison with the embryo. This makes it hard to realistically compare embryos with juvenile or adult animals.

Every oviraptorosaur embryo reported to date is well ossified and has been described as being close to hatching (Norell et al. 1994, 2001; Weishampel et al. 2008; Wang et al. 2016; Pu et al. 2017). However, these specimens were all relatively small compared with the egg length. For example, skull length of IVPP 100/971 is only 40 mm (Norell et al. 1994), whereas oviraptorosaur eggs found in nests in the same location were 180 mm in length (Clark et al. 1999). *Beibeilong sinensis* (HGM 41HIII1219; Pu et al. 2017) was an articulated, well-ossified

skeleton found associated with the largest known eggs for dinosaurs (oogenus *Macroelangoolithus*). This specimen was described as a perinate despite not being found inside an eggshell, because it was interpreted as having been expelled from one of the crushed macroelangoolithid eggs. The curled skeleton, which is missing a tail, is only 230 mm long compared with an associated egg measuring 400–450 mm in length; adding a tail of 170 mm means that the total length of 400 mm would still not exceed the length of the egg. It is clearly visible in Pu et al. (2017) that the specimen was too small in length to fill the total inner space of any associated macroelangoolithid egg. Furthermore, the embryo's head was about 66 mm long (Pu et al. 2017). Assuming an egg length of 450 mm, the total body length of 400 mm was only 0.88 of the egg length, and the skull length to egg length ratio was only 0.14. Both of these values suggest that HGM 41HIII1219 was much less than 50% of its way through development (see Fig. 1). Compared with crocodylian embryos, the positioning of the head in the *Beibeilong* holotype is also in

agreement with the ratios presented earlier, despite being partly disarticulated. Ironically, Pu et al. (2017) suggested in figure 4 of their supplementary materials that, based on skeletal orientation, the “perinate” specimen had probably died several months before hatching. It is interesting that Chapelle et al. (2020) used observations of the osteology of extant vertebrates to conclude that embryos of the basal sauropodomorph dinosaur *M. carinatus* were only ~60% through their incubation period and so were also younger than previously hypothesized.

Implications of an Early-Stage Ossified Embryo.—The quantitative evidence presented here suggests that, despite being well ossified, the YLSNHM01266 embryo (Xing et al. 2022) was not close to hatching. This means that the positioning of the head relative to the body cannot bear any relationship to hatching position in this animal. The space at the blunt of the egg cannot be interpreted as an air space (Xing et al. 2022), because the embryo did not occupy most of the volume of the egg. The positioning of the head in the YLSNHM01266 specimen is more reminiscent of a stage of development equivalent to between 55- and 68-day-old crocodile embryos illustrated in Figure 1, which is far from hatching. If this is the case, then the scenario proposed by Xing et al. (2022) to suggest an avian-like prehatching posture, and the associated coordinated embryonic movements, has no supporting evidence.

Although not universally accepted, most evidence suggests that oviraptorosaur eggs were buried (Deeming 2002, 2006). In addition, there is strong evidence that the developmental periods of dinosaurs were long and comparable to those exhibited by extant reptiles (Ruxton et al. 2014; Erickson et al. 2017; Varricchio et al. 2018). Long periods of incubation are associated with precocial development in both birds and crocodylians and allow for a prolonged period of ossification and growth during the second half of incubation (Deeming and Ferguson 1989; Ricklefs and Starck 1998). Embryos of therizinosaurid theropods (Kundrát et al. 2008) and *Troodon* (Varricchio et al. 2002) have been interpreted as being precocial based on their degree of ossification of the skull and postcranial skeleton. Whether the

fossil record of oviraptorosaur embryos illustrates the same pattern is also questionable because of variable eggshell microstructure, substrate moisture, and nesting strategy in these groups (Varricchio et al. 1997, 2018; Deeming 2002, 2006; Weishampel et al. 2008; Hogan and Varricchio 2021; Kundrát and Cruickshank 2021). Resolution of these issues will depend on more specimens of oviraptorosaur embryos in eggs being uncovered.

In conclusion, while it is possible that oviraptorosaur embryos did exhibit a particular hatching position, we do not accept that specimen YLSNHM01266 (Xing et al. 2022) or any other oviraptorosaur embryo identified to date supports a view that the position was directly comparable to that of modern birds. It is unclear how unfounded speculation is supposed to further our understanding of theropod development or reproductive biology. Rather, this approach is in danger of establishing an erroneous view that could cloud our interpretation of future discoveries. While Xing et al. (2022) do accept limitations of their study, the title and tone of the report do seem to reinforce an idea that is not supported by any real evidence. More crucially, such an approach may prevent recognition of the significance of differences between extant and extinct birds and their theropod ancestors, which will be to the detriment of our understanding of the evolutionary history and paleobiology of both groups. Unfounded speculation about fossils has other consequences. Widespread reporting of such ideas by the global media can establish an idea in the public consciousness that is subsequently hard to dispel. We urge more caution in the interpretation of future discoveries of fossil embryos.

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Literature Cited

- Andrews, R. M. 2004. Patterns of embryonic development. Pp. 75–102 in D. C. Deeming, ed. *Reptilian incubation, environment, evolution and behaviour*. Nottingham University Press, Nottingham, U.K.
- Ar, A. 1991. Egg water movements during incubation. Pp. 157–173 in S. G. Tullett, ed. *Avian incubation*. Butterworth-Heinemann, London.
- Bi, S., R. Amiot, C. Peyre de Fabrègues, M. Pittman, M. C. Lamanna, Y. Yu, C. Yu, T. Yang, S. Zhang, Q. Zhao, and X. Xu. 2021. An oviraptorid preserved atop an embryo-bearing egg clutch sheds light on the reproductive biology of non-avian theropod dinosaurs. *Science Bulletin* 66:947–954.
- Bond, G. M., V. D. Scott, and R. G. Board. 1986. Correlation of mechanical properties of avian eggshells with hatching strategies. *Journal of Zoology* 209:225–237.
- Bond, G. M., R. G. Board, and V. D. Scott. 1988. An account of the hatching strategies of birds. *Biological Reviews* 63:395–415.
- Chapelle, K. E. J., V. Fernandez, and J. N. Choiniere. 2020. Conserved in-ovo cranial ossification sequences of extant saurians allow estimation of embryonic dinosaur developmental stages. *Scientific Reports* 10:4224.
- Clark, J. M., M. A. Norell, and L. M. Chiappe. 1999. An oviraptorid skeleton from the Late Cretaceous of Ukhaa Tolgod, Mongolia, preserved in an avianlike brooding position over an oviraptorid nest. *American Museum Novitates* 3265:1–36.
- Deeming, D. C. 2002. Importance and evolution of incubation in avian reproduction. Pp. 1–7 in D. C. Deeming ed. *Avian incubation: behaviour, environment and evolution*. Oxford University Press, Oxford.
- Deeming, D. C. 2004. Reptilian incubation: evolution and the fossil record. Pp. 1–14 in D. C. Deeming, ed. *Reptilian incubation, environment, evolution and behaviour*. Nottingham University Press, Nottingham, U.K.
- Deeming, D. C. 2006. Ultrastructural and functional morphology of eggshells supports the idea that dinosaur eggs were incubated buried in a substrate. *Palaentology* 49:171–185.
- Deeming, D. C., and M. W. J. Ferguson. 1989. Effects of incubation temperature on the growth and development of embryos of *Alligator mississippiensis*. *Journal of Comparative Physiology* 159B:183–193.
- Deeming, D. C., and M. W. J. Ferguson. 1990. Methods for the determination of the physical characteristics of eggs of *Alligator mississippiensis*: a comparison with other crocodilian and avian eggs. *Herpetological Journal* 1:456–462.
- Deeming, D. C., L. B. Halstead, M. Manabe, and D. M. Unwin. 1993. An ichthyosaur embryo from the Lower Lias (Jurassic: Hettingan) of Somerset, England, with comments on the reproductive biology of ichthyosaurs. *Modern Geology* 18:423–442.
- Erickson, G. M., D. K. Zelenitsky, D. I. Kaya, and M. A. Norell. 2017. Dinosaur incubation periods directly determined from growth-line counts in embryonic teeth show reptilian-grade development. *Proceedings of the National Academy of Sciences USA* 114:540–545.
- Ferguson, M. W. J. 1985. The reproductive biology and embryology of crocodilians. Pp. 329–491 in C. Gans, F. Billet, and P. F. A. Maderson, eds. *Biology of the Reptilia*, Vol. 14. Wiley, New York.
- Grigg, G., and D. Kirshner. 2015. *Biology and evolution of the crocodylians*. CSIRO Publishing, Clayton, Australia.
- Hogan, J. D., and D. J. Varricchio. 2021. Do paleontologists dream of electric dinosaurs? Investigating the presumed inefficiency of dinosaurs contact incubating partially buried eggs. *Paleobiology* 47:101–114.
- Horner, J. R., and D. B. Weishampel. 1988. A comparative embryological study of two ornithischian dinosaurs. *Nature* 332:256–257.
- Horner, J. R., and D. B. Weishampel. 1996. A comparative embryological study of two ornithischian dinosaurs—a correction. *Nature* 383:103.
- Kundrát, M., and A. R. I. Cruickshank. 2021. New information on multispherulitic dinosaur eggs: Faveololithidae and Dendrolithidae. *Historical Biology* 34:1072–1084.
- Kundrát, M., A. R. I. Cruickshank, T. W. Manning, and J. Nudds. 2008. Embryos of therizinosauroid theropods from the Upper Cretaceous of China: diagnosis and analysis of ossification patterns. *Acta Zoologica* 89:231–251.
- Lü, J., P. J. Currie, L. Xu, X. Zhang, H. Pu, and S. Jia. 2013. Chicken-sized oviraptorid dinosaurs from central China and their ontogenetic implications. *Naturwissenschaften* 100:165–175.
- Lyckegeard A., G. Johnson, and P. Tafforeau. 2011. Correction of ring artifacts in x-ray tomographic images. *International Journal of Tomography and Statistics* 18:1–9.
- Maxwell, E. E. 2008. Comparative embryonic development of the skeleton of the domestic turkey (*Meleagris gallopavo*) and other galliform birds. *Zoology* 111:242–257.
- Norell, M. A., J. M. Clark, D. Demberelyin, B. Rhinchen, L. M. Chiappe, A. R. Davidson, M. C. McKenna, P. Altangerel, and M. J. Novacek. 1994. A theropod dinosaur embryo and the affinities of the Flaming Cliffs dinosaur eggs. *Science* 266:779–782.
- Norell, M. A., J. M. Clark, and L. M. Chiappe. 2001. An embryonic oviraptorid (Dinosauria: Theropoda) from the upper Cretaceous of Mongolia. *American Museum Novitates* 2001:1–20.
- Paganin, D., S. C. Mayo, T. E. Gureyev, P. R. Miller, and S. W. Wilkins. 2002. Simultaneous phase and amplitude extraction from a single defocused image of a homogeneous object. *Journal of Microscopy* 206:33–40.
- Pu, H., D. K. Zelenitsky, J.-C. Lü, P. J. Currie, K. Carpenter, L. Xu, E. Koppelhus, S. Jia, L. Xiao, H. Chuang, T. Li, M. Kundrát, and C. Shen. 2017. Perinate and eggs of a giant caenagnathid dinosaur from the Late Cretaceous of central China. *Nature Communications* 8:14952.
- Ricklefs, R. E., and J. M. Starck. 1998. Embryonic growth and development. Pp. 31–58 in J. M. Starck and R. E. Ricklefs, eds. *Avian growth and development: evolution within the altricial-precocial spectrum*. Oxford University Press, Oxford.
- Rieppel, O. 1993. Studies on skeleton formation in reptiles. V. *Patterns of ossification in the skeleton of Alligator mississippiensis Daudin (Reptilia, Crocodylia)*. *Zoological Journal of the Linnean Society* 109:301–325.
- Romanoff, A. L. 1960. *The avian embryo*. MacMillan, London.
- Ruxton, G. D., G. F. Birchard, and D. C. Deeming. 2014. Incubation time as an important influence on egg production and distribution into clutches for sauropod dinosaurs. *Paleobiology* 40:323–330.
- Schneider, C. A., W. S. Rasband, and K. W. Eliceiri. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* 9:671–675.
- Starck, J. M. 1996. Comparative morphology and cytokinetics of skeletal growth in hatchlings of altricial and precocial birds. *Zoologischer Anzeiger* 235:53–75.
- Starck, J. M. 1998. Structural variants and invariants in avian embryonic and postnatal development. Pp. 59–88 in J. M. Starck, and R. E. Ricklefs eds. *Avian growth and development: evolution within the altricial-precocial spectrum*. Oxford University Press, Oxford.
- Unwin, D. M., and D. C. Deeming. 2019. Pre-natal developmental patterns and their implications for super-precocial flight ability in pterosaurs. *Proceedings of the Royal Society of London B* 286:20190409.
- Varricchio, D. J., F. D. Jackson, J. J. Borkowski, and J. R. Horner. 1997. Nest and egg clutches of the dinosaur *Troodon formosus* and the evolution of avian reproductive traits. *Nature* 385:247–250.

- Varricchio, D. J., J. R. Horner, and F. D. Jackson. 2002. Embryos and eggs for the Cretaceous theropod dinosaur *Troodon formosus*. *Journal of Vertebrate Paleontology* 22:564–576.
- Varricchio, D., M. Kundrát, and J. Hogan. 2018. An intermediate incubation period and primitive brooding in a theropod dinosaur. *Science Reports* 8:12454.
- Wang, S., S. Zhang, C. Sullivan, and X. Xu. 2016. Elongatoolithid eggs containing oviraptorid (Theropoda, Oviraptorosauria) embryos from the Upper Cretaceous of southern China. *BMC Evolutionary Biology* 16:67.
- Weishampel, D. B., D.E. Fastovsky, M. Watabe, D. Varricchio, F. Jackson, K. Tsogtbaatar, and R. Barsbold. 2008. New oviraptorid embryos from Bugin-Tsav, Nemegt Formation (Upper Cretaceous), Mongolia, with insights into their habitat and growth. *Journal of Vertebrate Paleontology* 28:1110–1119.
- Xing, L., K. Niu, W. Ma, D. K. Zelenitsky, T. -R. Yang, and S. L. Brusatte. 2022. An exquisitely preserved in-ovo theropod dinosaur embryo sheds light on avian-like prehatching postures. *iScience* 15:103516.
- Yang, T. R., T. Engler, J.N. Lallensack, A. Samathi, M. Makowska, and B. Schillinger. 2019. Hatching asynchrony in oviraptorid dinosaurs sheds light on their unique nesting biology. *Integrative and Organismal Biology* 1:obz030.