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Ovarian follicles shed new light on dinosaur reproduction during the transition towards birds

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The reproductive systems of living archosaurs, crocodilians and birds are very different; the derived features present in birds are inferred to have evolved within the derived archosaur group, Dinosauria, which includes Aves (the common ancestor of *Archaeopteryx* + living birds) as a member of the derived theropod clade, Maniraptora. Compared to Aves, crocodilians have two ovaries, prolonged folliculogenesis (maturation of ovarian follicles), large clutches and small eggs [1]. Living birds, on the other hand, nearly all have a single functional ovary and oviduct (all other amniotes have two) and rapid folliculogenesis [2]. Living birds are the most diverse Linnean class of tetrapods on the planet and within this diversity there exists a spectrum of clutch sizes and egg sizes (relative to body size) [2]. However, egg size is greater than that in crocodilians, and clutches are typically much smaller [2]. The derived reproductive system present in living birds was acquired gradually during the evolution of dinosaurs and basal birds (Fig. 1), but the timing of these changes is poorly known given the preservational constraints of the fossil record. However, the recent report of the exceptional preservation of ovarian follicles in one specimen of the basal bird *Jeholornis* and two enantiornithines from the Early Cretaceous Jehol Biota helps elucidate important stages in the evolution of the modern avian reproductive system as it occurred among derived paravian dinosaurs [3]. Although the extraordinary preservation of such structures has been met with some skepticism [4], neither strong counter arguments nor plausible alternative interpretations for the preserved structures have arisen [5]. Interpretations of the structures as seeds in the stomach are inconsistent with their position (caudodorsal to the stomachs and isolated to the left side of the body) and morphology (circular and lacking ornamentation). Furthermore, the recently described specimens from the Jehol Biota were in fact not the first fossils to preserve ovarian follicles—the type specimen of *Compsognathus longipes*, a nonavian Jurassic coelurosaur theropod dinosaur (resolved as sister taxon to Maniraptoriformes), also preserves round structures interpreted as immature eggs [6,7]. Their number, morphology and distribution are consistent with the interpretation that the circular structures represent maturing ovarian follicles. In addition, five new enantiornithine specimens preserving follicles have been identified at the Shandong Tianyu Museum of Nature (STM10–4, 10–12, 11–80, 11–121, 11–212) (Fig. 2), contributing to our understanding of theropod reproduction.

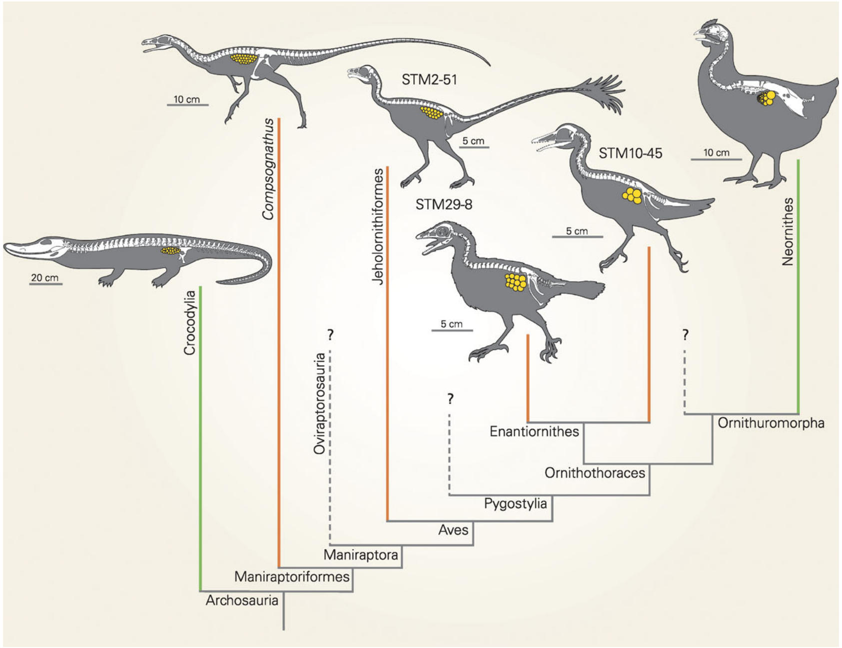

Figure 1. Preserved data regarding ovarian anatomy mapped over a simplified cladogram of Theropoda, with a focus on Maniraptora, the derived clade that includes Aves. Crocodylia are placed as the outgroup, and this clade and crown group birds define an extant phylogenetic bracket for interpreting the reproductive traits of Mesozoic birds and other extinct theropods (modified from [3]).

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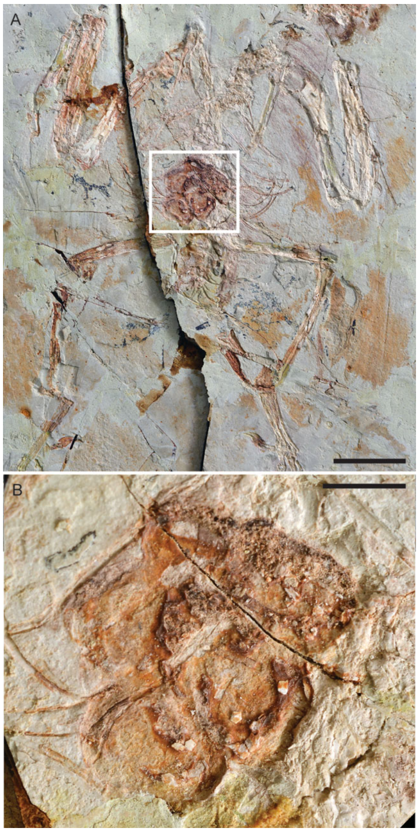

Figure 2. (A) New specimen of Enantiornithes indet (STM10–12) preserving ovarian follicles, note the specimen is preserved in dorsal view and the follicles are preserved on the left side of the body, scale bar equals 20 mm. (B) Close-up of the follicles (enlarged from white box in A), scale bar equals 5 mm.

All the avian specimens from the Jehol preserve the cluster of ovarian follicles only on the left side of the body, indicating the presence of a single functional ovary [3] (Fig. 2); unfortunately, the *Compsognathus* holotype is preserved in lateral view and the number of ovaries cannot be observed. *Jeholornis*, with its long dinosaurian boney tail, is only slightly more derived than *Archaeopteryx* [8], indicating that even the most basal birds were already modern in this aspect. One specimen of oviraptorosaurian maniraptoran theropod (NMNS-VPDINO-2002-0901) preserves two eggs between the pubes, interpreted as in the oviducts [9] indicating that in this derived maniraptoran lineage (more closely related to birds than *Compsognathus*), two functional ovaries and oviducts were still present (Fig. 1). The most widely accepted hypothesis for the presence of a single functional ovary in living birds is that the right ovary, the larger of the two in crocodilians, was lost to reduce body mass in gravid females during flight [10]. This would have been particularly important in basal birds that were probably poor flyers. *Jeholornis* together with oviraptorosaurian (NMNS-VPDINO-2002-0901) create a phylogenetic bracket for the loss of the right ovary (Fig. 1), indicating that this occurred at—or very near—the dinosaur–avian transition, supporting the hypothesis that birds lost the use of the left ovary due to the energetic pressures of flight [3].

Consistent with their phylogenetic position, basal bird ovaries still possessed primitive traits and thus reveal patterns intermediate between living birds and crocodilians. Although one ovary has been lost, the degree of follicular hierarchy in the fossil bird ovaries is subtle, similar to crocodilians [3]. This suggests that, as in crocodilians, folliculogenesis occurred slowly [1]; and yolk deposition does not begin in all follicles simultaneously, but rather reflects the order in which follicles will ovulate. This process proceeds rapidly in living birds producing a distinct hierarchy in size between follicles with the largest follicles representing those that will ovulate first [2]. The ability to rapidly deposit yolk is a direct product of the higher basal metabolic rate of derived birds relative to other reptiles [2]. Bone histology confirms that basal birds had lower basal metabolic rates than endothermic neornithine birds; thus, the absence of a hierarchy, indicative of slow yolk deposition and a low metabolic rate, is also consistent with other information regarding basal bird biology. Given the varied preservation and even deformation of the follicles in the *Compsognathus*, the reported size range (6.4–9.4 mm) [7] most likely reflects poor preservation rather than a true follicular hierarchy.

Differences in the size and number of ovarian follicles from *Compsognathus* (Coelurosauria: Maniraptoriformes) to Enantiornithes (Maniraptora: Aves) reveal an interesting trend regarding egg and clutch sizes in derived theropods and birds. The follicles are proportionately smaller than those in *Jeholornis* and enantiornithines [3], with an average follicle to femur length (estimated 108.8 mm) ratio of 0.069, consistent with the much larger number of follicles present (30 preserved in total) [6,7]. Similarly, the basal bird *Jeholornis* preserves a larger number (estimated 20 follicles preserved) of proportionately smaller follicles (follicle:femur ratio 0.087) compared to the more derived enantiornithines [3]. Within Enantiornithes, STM29-8 preserves a large number of smaller follicles (14 follicles, follicle:femur ratio 0.171) while STM10-45 preserves a smaller number of proportionately larger follicles (five follicles, follicle:femur ratio 0.217), representing the known extremes for the clade. These differences in proportions between specimens (Table 1) parallels a similar trend in living birds, in which egg and clutch sizes are inversely related to each other [2,11], reflecting a broad trend toward more *K*-selected life history strategies (large number of young with minimal energetic investment versus smaller numbers of offspring, with increasingly greater energetic cost) [3].

Interestingly, the sizes of the follicles are similar in all specimens, despite very different follicle to body size ratios and inferred clutch sizes. These data support the hypothesis that egg/follicle size is more conservative than body size [11]. Similar trends are seen in living ratites: the extreme size of the kiwi egg is the result of evolution reducing the bird's body size around a large egg (thus egg size was conserved) [12]. Recently, the large size of the kiwi egg has been reinterpreted as a hyper *K*-selected life history strategy with the single egg equal in clutch mass to that of other ratites [13]. However, this strategy may have only evolved because of egg conservatism, through the conservation of egg size during miniaturization of the body. Dinosaurs and basal birds do not show the extremes in the egg/clutch size trade-off present in Neornithes; however, among derived theropods, there is a trend toward smaller clutches of larger eggs, which may indicate a decreasing amount of precociality relative to the nearly self-sufficient nests and offspring of crocodilians. This trend toward more *K*-selected lifestyles continues into Neornithes, in parallel to the Cretaceous radiation of enantiornithines; the larger spectrum of recognized follicle to body

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Table 1. List of specimens preserving ovarian follicles showing differences in body to egg size ratios among Mesozoic theropods. Measurements in mm.

Taxon	Specimen no.	Femur length	No. of follicles	Avg follicle diameter	Femur: follicle ratio
Compsognathus longipes	AS I 563	108.8	∼30	7.5	0.069
Jeholornis prima	STM2-51	88	20	7.7	
Enantiornithes indet	STM29-8	40.2	12	7.6	0.17
Enantiornithes indet	STM10-45	34.9	∼5	6.9	0.22
Enantiornithes indet	STM10-4	38.7	2–3	7.15	0.18
Enantiornithes indet.	STM10-12	–	5–6	7.7	–
Enantiornithes indet.	STM11-80	37.7	7–8	6.5	0.17
Enantiornithes indet.	STM11-121	37.5	5	6.8	0.18
Enantiornithes indet.	STM11-212	∼32–35	4–5	5.4	0.15–17

size ratios and clutch sizes recognized within the clade suggests that enantiornithines also utilized a range of reproductive strategies.

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