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Preservation of ovarian follicles reveals early evolution of avian reproductive behaviour

Xiaoting Zheng[1,2], Jingmai O'Connor[3], Fritz Huchzermeyer[4], Xiaoli Wang[1], Yan Wang[1], Min Wang[3] & Zhonghe Zhou[3]

The two groups of archosaurs, crocodilians and birds, form an extant phylogenetic bracket for understanding the reproductive behaviour of dinosaurs. This behaviour is inferred from preserved nests and eggs, and even gravid individuals[1]. Data indicate that many 'avian' traits were already present in Paraves—the clade that includes birds and their close relatives—and that the early evolution of the modern avian form of reproduction was already well on its way[2,3]. Like living neornithine birds, non-avian maniraptorans had daily oviposition and asymmetrical eggs with complex shell microstructure, and were known to protect their clutches[4–6]. However, like crocodilians, non-avian maniraptorans had two active oviducts (one present in living birds), relatively smaller eggs, and may not have turned their eggs in the way that living birds do[1,6]. Here we report on the first discovery of fossilized mature or nearly mature ovarian follicles, revealing a previously undocumented stage in dinosaur reproduction: reproductively active females near ovulation. Preserved in a specimen of the long bony-tailed *Jeholornis* and two enantiornithine birds from the Early Cretaceous period lacustrine Jehol Biota in northeastern China, these discoveries indicate that basal birds only had one functional ovary, but retained primitive morphologies as a result of their lower metabolic rate relative to living birds. They also indicate that basal birds reached sexual maturity before skeletal maturity, as in crocodiles and paravian dinosaurs. Differences in follicular morphology between *Jeholornis* and the enantiornithines are interpreted as forming an evolutionary gradient from the reproductive condition in paravian dinosaurs towards neornithine birds. Furthermore, differences between the two enantiornithines indicate that this lineage might also have evolved advanced reproductive traits in parallel to the neornithine lineage.

Three specimens of Mesozoic birds from the Tianyu Natural History Museum, Shandong, China (STM), have been found to contain mature ovarian follicles (a follicle being the primary oocyte and the sac in which it is contained[7]) preserved in their body cavity. The largest specimen (STM2-51 slab and counterslab; Fig. 1 and Supplementary Fig. 1) is referable to *Jeholornis* sp., a basal bird with a bony tail longer than that of *Archaeopteryx* (see Supplementary Information). The specimen, in dorsoventral view, preserves approximately 20 follicles ventral to the vertebral column and cranial to the pelvic girdle, overlapped by thoracic ribs. The follicles are all round and subequal in size, ranging from approximately 7.1 to 8.8 mm in diameter (Fig. 1c, d, Supplementary Fig. 2 and Supplementary Table 1); the total number of follicles may have been higher than that observed in all specimens, obscured by overlap. In STM2-51, the follicles are distributed in rows between the caudal end of the sternum and the pelvis; the number of follicles in each row decreases caudally (three to four proximally, one to two distally); however, this pattern may be exaggerated by a crack that laterally borders the preserved follicles. In the main slab, the follicles are preserved permineralized by a dark macrocrystalline mineral (too thick to be eggshell; Fig. 1d). In the counterslab, the follicles are preserved as pale pink impressions, although some small crystals of the black mineral are also present (Fig. 1c).

The two smaller specimens (STM29-8 and STM10-45; Fig. 2 and Supplementary Figs 3–7) are referable to Enantiornithes (see Supplementary Information); this large clade forms the sister group to Ornithuromorpha, the clade that includes living birds (Neornithes), and represents the first major avian radiation[8,9]. The two specimens vary in proportions of the humerus/ulna and femur/tibiotarsus and the shape of the coracoid, indicating that they represent different taxa, although poor preservation prevents identifying either specimen at the species level (see Supplementary Information). Both specimens preserve mature ovarian follicles in their body cavity visible in dorsoventral (slab and counterslab) view.

Enantiornithes indeterminate (indet.) STM29-8 (Fig. 2c and Supplementary Fig. 5) preserves at least 12 follicles *in situ* along the left side of the vertebral column next to the synsacrum. Two additional follicles are recognized displaced proximally near the left wing. All the follicles are nearly circular, with slight variation in size, ranging from 5.8 to 8.8 mm in diameter (Supplementary Table 1). The follicles are preserved as black carbonization in the slab (Fig. 2a, c) and as impressions in the counterslab (Supplementary Fig. 4). The surfaces of the follicles preserve an uneven lattice structure of fibres, which may potentially be imprints of the blood vessels from the highly vascularized perifollicular membrane[7].

Enantiornithes indet. STM10-45 (Fig. 2b, d) preserves fewer follicles (at least five), subequal in size (ranging from 6.7 to 8.8 mm in diameter; Supplementary Table 1). The follicles are located on the left of the vertebral column distal to the sternum but cranial to the pelvis; a few disarticulated rib elements overlap the follicles. Four well-preserved follicles are associated together (possibly obscuring more follicles); an additional follicle(s) is caudally displaced slightly from the others (estimated total of five to seven preserved). The surfaces of the follicles are marked by small, black circular spots of mineralization; the roundness of these structures suggests that preservation of the follicles in STM10-45 may have been bacterially mediated.

The circular structures interpreted as follicles are clearly located in the body cavity of these fossil birds; in both the slab and counterslab they are preserved overlapping with bone. The structures are not considered to be seeds preserved in the stomach on the basis of their morphology and position (E. M. Friis, personal communication), as well as comparison with other types of seeds observed in Jehol fossils. In *Jeholornis prima* IVPP (Institute of Vertebrate Palaeontology and Paleoanthropology, Beijing) V13274, which preserves seeds in its stomach[10], the seeds are more numerous, larger (about 10 mm in diameter), differ in shape (tapered at one end, not circular) and the surface is ornamented. The seeds are distributed more ventrally whereas the follicles in *Jeholornis* STM2-51 are dorsally located along the vertebral column and just cranial to the pelvis, consistent with the position of the ovaries in living archosaurs. Seeds are also preserved in the crop of some Jehol birds (*Sapeornis*, *Hongshanornis*)[11]; in these

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[1]Institute of Geology and Paleontology, Linyi University, Linyi, Shandong 276000, China. [2]Tianyu Natural History Museum of Shandong, Pingyi, Shandong 273300, China. [3]Key Laboratory of Vertebrate Evolution and Human Origin of the Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China. [4]Department of Paraclinical Sciences, Faculty of Veterinary Science, University of Pretoria, Private Bag X 04, Onderstepoort 0110, South Africa.

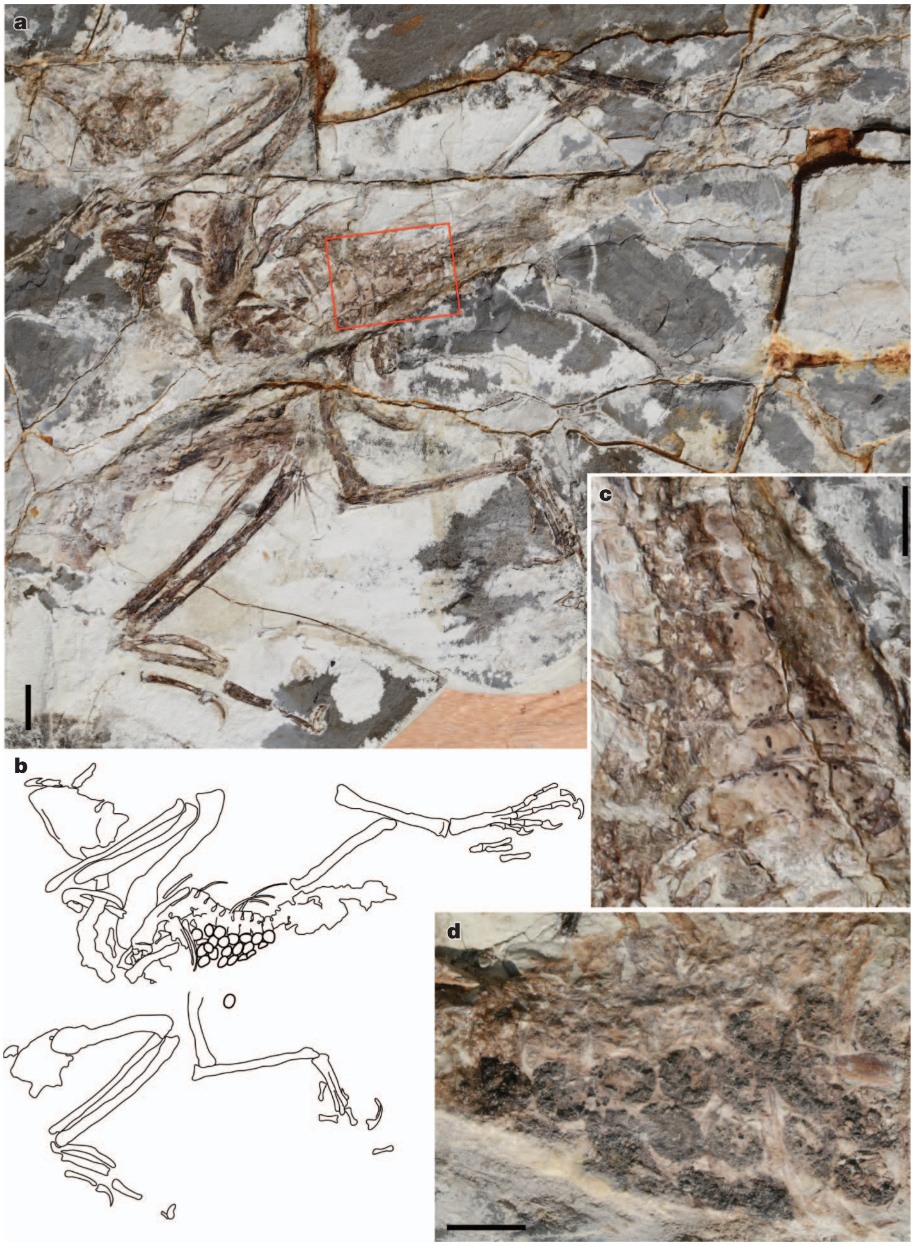

Figure 1 | *Jeholornis* sp. STM2-51 preserving mature ovarian follicles. **a**, Photograph of the main slab in dorsal view. Scale bar, 2 cm. **b**, Interpretative drawing of the slab. **c**, Close-up of the follicles indicated by the red square in the main slab photograph. Scale bar, 1 cm. **d**, Close-up of the follicles in the counterslab. Scale bar, 1 cm.

specimens, the crop is found cranial to the sternum and the seeds differ from the follicles in that they are uneven in size and morphology (less round). These structures are clearly not gastroliths, which are commonly preserved in a large number of Jehol ornithuromorph birds[11]; these stones are always preserved nearly as in life: three-dimensional, numerous, varying in shape, size and mineral composition, with polished surfaces. Furthermore, gastroliths are proportionately much smaller than the soft-tissue structures preserved here. The circular shape of the preserved structures is consistent with two-dimensional preservation of a spherical structure, such as the mature follicles of the ovary (single enlarged cells). The absence of any preserved eggshell and their clumped association, with no caudally located *in situ* follicles, indicates that the follicles had not entered the oviducts.

Living archosaurs—crocodilians and birds—differ greatly in their reproductive habits in terms of clutch size, nesting behaviour, degree of parental care and developmental strategy of young, posing the evolutionary questions of when, how and why derived avian reproductive traits evolved within Dinosauria. The evidence indicates that although the non-avian theropod reproductive system retained some primitive archosaurian traits (that is, two functional oviducts, hyper-ellipsoidal eggs, precocial offspring), derived bird-like characteristics were also present (one egg per oviduct per day deposited, larger eggs relative to body size, complex eggshell microstructures, asymmetrical eggs, parental care)[1,5,6,12]. However, information on the soft-tissue anatomy of reproductive organs and the sequence and timing of changes in reproduction strategy within the Aves class itself remains poorly understood. These new specimens provide the first glimpse into how basal birds reproduced. They also record a fairly wide bracket within the Mesozoic bird phylogenetic tree (Fig. 3), thus revealing different stages of evolution.

In living archosaurs, as in all vertebrates, the female reproductive system is generally divided into two separate parts: the ovary and oviduct[13,14]. Birds are unique among amniotes in that, although the embryo has two ovaries and oviducts, only the left ovary and oviduct

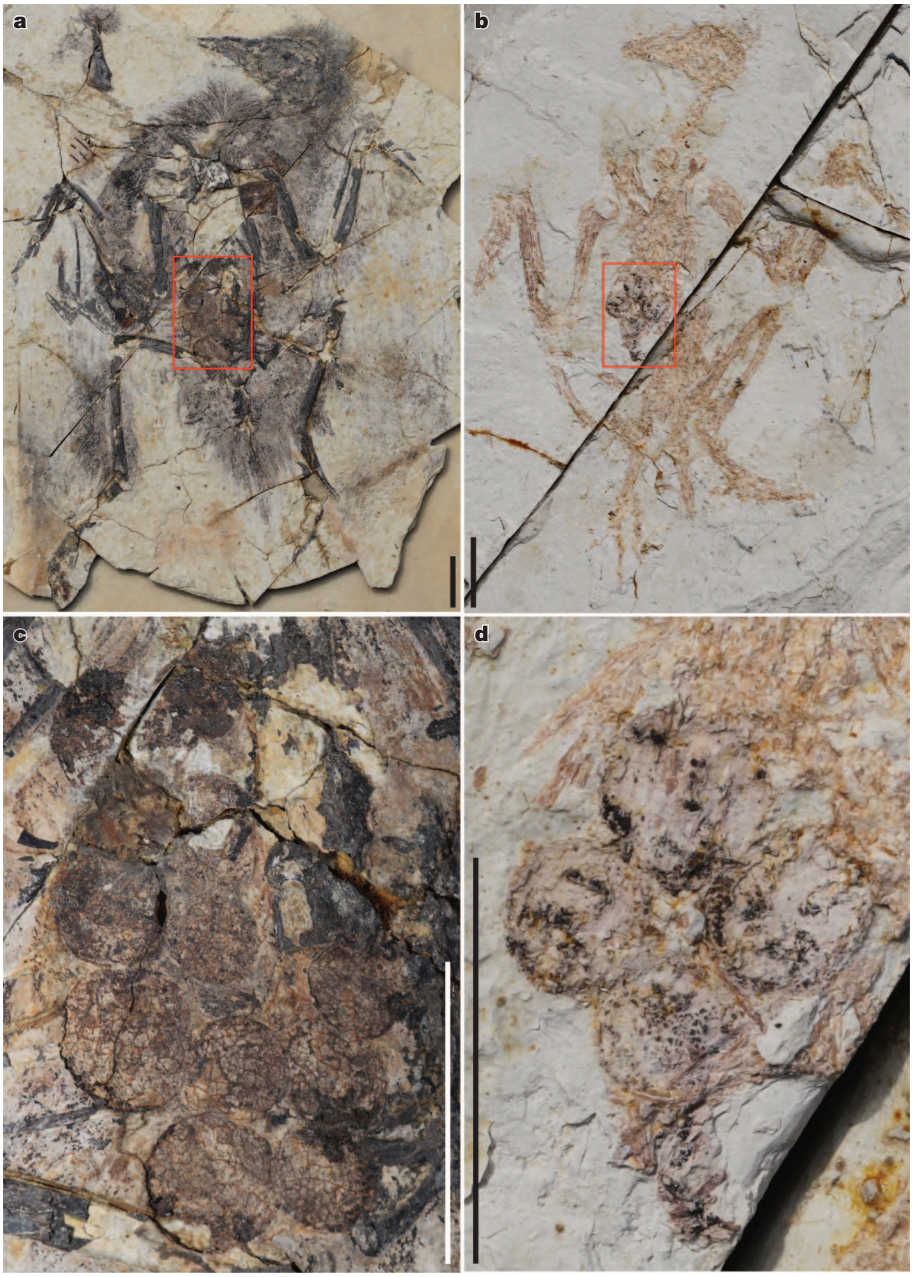

Figure 2 | Enantiornithine specimens preserving mature ovarian follicles in dorsal view. **a**, Photograph of the main slab of STM29-8. **b**, Photograph of the main slab of STM10-45. **c**, Close-up of the follicles in STM29-8 preserved in the region indicated by the red box in **a**. **d**, Close-up of the follicles in STM10-45 preserved in the region indicated by the red box in **b**. All scale bars, 2 cm.

are functional in the adult. The kiwi differs from other birds in that both the left and right ovaries develop (and are functional), although it is only the left oviduct that develops (other exceptions occur, particularly among birds of prey)[14]. The ovary contains all of the female reproductive oocytes, the number of which diminishes during the lifespan of the individual, although the ovary itself enlarges as the bird approaches reproductive maturity. Each reproductive cycle some of the normally small oocytes mature into follicles, becoming enlarged through yolk deposition (vitellogenesis) in preparation for ovulation. In crocodiles, similar to birds, the follicles do not mature all at once, forming a hierarchy that reflects the order in which follicles will ovulate. Crocodilians have a low metabolic rate and therefore vitellogenesis lasts an extended period of time (months compared to 4–16 days in birds)[14,15]; as a result, the follicular hierarchy is much less distinct in crocodilians and mature follicles are subequal in size[15]. Living birds have a high metabolic rate and yolk deposition is rapid, resulting in strongly apparent follicular hierarchy[7] (Fig. 3). No medullary bone (a rapidly mobilized source of eggshell calcium in living birds) forms before oviposition[16,17]; instead, crocodilians access calcium from structural bone[18]. Female crocodilians will ovulate a full clutch of up to 60 eggs (average clutch size ranges from 12 to 48 among living crocodilians)[19], and store the eggs in the distal end of the oviduct for several weeks, with egg laying occurring en masse when the embryos are approximately at the 18-somite stage[18]. Although the adult guards the nest and young, eggs are passively incubated and young are not typically fed by the adult, a highly precocial developmental strategy. Living neornithine birds oviposit daily, with the exception of the paleognaths, which lay one egg every 2–6 days[14].

Non-avian maniraptoran dinosaurs are known to have two active oviducts, from the paired association of eggs in the body cavity of one specimen[5]. Why living birds lost the right ovary and oviduct is unclear, but the most common hypothesis suggests that this was related to the need to reduce weight in flight during the reproductive season, the female having to carry only a single egg inside rather than two, although loss may also have been to alleviate the demands for calcium during ovulation[20]. As the follicles are interpreted as being in the ovaries of these specimens, we cannot comment directly on the number of functioning oviducts; however, both enantiornithines, in dorsal

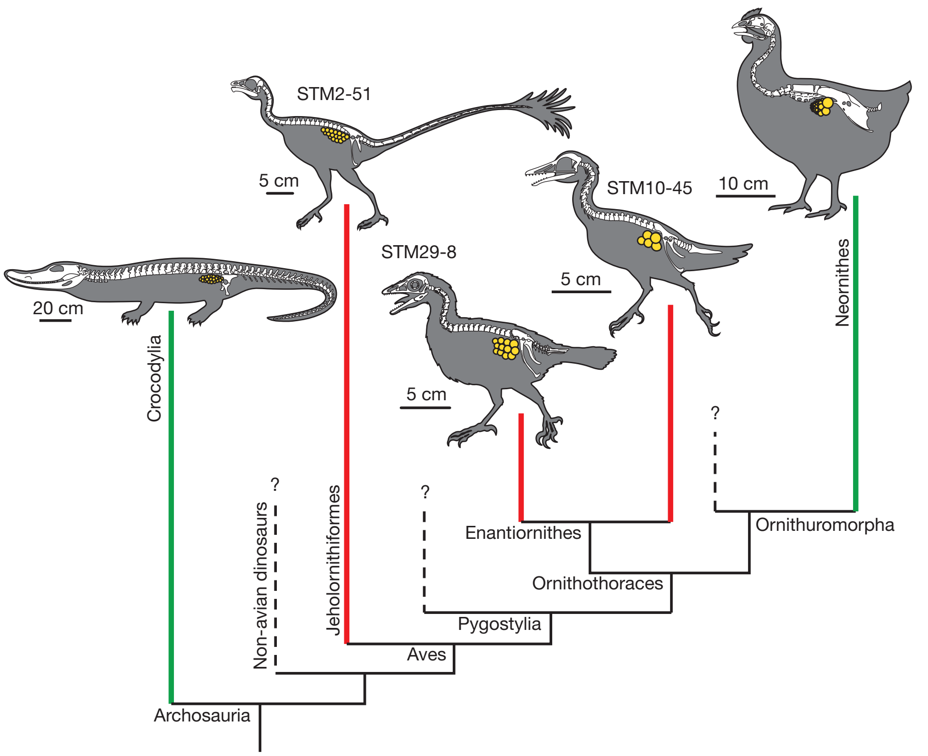

Figure 3 | Reconstructions of living archosaurs Crocodylia and Neornithes, as well as the three fossilized specimens showing relative ovary morphology mapped over a simplified cladogram of Archosaur relationships. Green lines indicate extant lineages, red lines indicate extinct lineages and dashed lines indicate lineages with no data.

view, preserve the association of follicles clearly on the left side of the body. The position of the ovary is not clear in *Jeholornis* STM2-51; however, the thoracic vertebrae dorsal to the follicles are preserved in left lateral view and the follicles appear to be isolated to the left side, as in the enantiornithines, suggesting that only the left ovary was active. As the closest-related dinosaurs are known to have two functioning oviducts, the loss of function in the right ovary is believed to have occurred very close to the non-avian maniraptoran–avian transition, supporting the hypothesis that its loss is flight related. Notably, it is documented in some crocodilians that the right ovary is the larger of the two, producing a greater number of mature follicles (and thus having a greater weight)[15].

The large and even size of the follicles preserved in these specimens suggests that these female individuals were ready or near ready to ovulate; if the birds were in the early stages of vitellogenesis, follicle size would not be so large and consistent. The slightly higher variation in size among the follicles preserved in STM29-8 may suggest that vitellogenesis was incomplete. Alternatively, this may indicate that vitellogenesis occurred more rapidly and over a shorter period of time, producing a more distinct follicular hierarchy, similar to living birds. This latter hypothesis is consistent with the smaller number of follicles relative to *Jeholornis* and the more derived phylogenetic placement of enantiornithines. The ovaries are not preserved in their entirety. We infer that the immature oocytes, previtelline follicles and atretic follicles in the ovary were either not preserved or are not visible (small, obscured by overlap), or potentially a combination of both. We propose that the presence of a perivitelline layer and other protective layers (absent in immature oocytes)[7] facilitated preservation of the mature follicles (see Supplementary Information). The absence of eggs in the oviduct(s) suggests that ovulation had not yet begun; alternatively, the animal may have died in the time between laying one egg and ovulating another (typically less than 1 hour in living birds), or an egg(s) in the oviduct(s) may have been expelled from the body after death, similar to the female pterosaur reported from the Jurassic of China[21].

In the long-tailed bird *Jeholornis* STM2-51 the size of the follicles is very consistent (Fig. 1c, d), suggesting a more crocodilian style of reproduction, in which a large number of follicles reach maturity near simultaneously so that follicular hierarchy is minimal[22]. This suggests that vitellogenesis occurred more slowly, similar to crocodilians, and is consistent with the lower metabolic rate relative to extant taxa predicted for basal birds[23]. The preserved size of the follicles suggests that egg size was large relative to the body in basal birds, despite morphological restrictions such as distally contacting pubes; eggs would have been too large to store in the body and so oviposition would have to occur between ovulation, as in other maniraptorans and living birds, but unlike crocodiles[5].

In a healthy and undisturbed female, all mature follicles will ovulate and thus the number of mature follicles is a good proxy for clutch size[7,15]. Crocodilians have much larger clutches than birds, but the follicle (and complete egg) is much smaller compared to the adult body size. In *Alligator mississippiensis* the mature follicle has a width of 45 mm; the follicle/femur ratio changes with age, but averages 0.017 (refs 15, 24). Comparative data on follicle size is limited, but in *Gallus* mature follicles reach 40 mm (ref. 7) (size exaggerated through domestication), comparable to that of *A. mississippiensis* despite their vast difference in body size (follicle diameter/femur length ratio 0.51). Although the absolute size of the preserved follicles, inferred to be slightly exaggerated by compression, is similar between the three specimens, the adult body size differs considerably: *Jeholornis* STM2-51 body mass is estimated at 676 g; enantiornithine STM29-8 is estimated to be 125 g; enantiornithine STM10-45 is estimated to be 105 g (ref. 25 was used to estimate body mass; Supplementary Table 2). As a result, each specimen has a distinct egg/body size ratio. *Jeholornis* sp. STM2-51 preserves the largest number of follicles, which are proportionately the smallest compared to overall body size (follicle diameter/femur length ratio 0.087), consistent with the basal position of this taxon within Aves (only more derived than *Archaeopteryx*). The larger enantiornithine STM29-8 preserves a larger number of smaller follicles (follicle/femur ratio 0.171), whereas the smaller enantiornithine STM10-45 preserves only a few follicles nearly the same size as *Jeholornis* STM2-51, despite the disparity in their overall body size (follicle/femur ratio 0.217). These specimens show the same trade-off between egg size and clutch size observed in living birds[26]. The large clutch size in *Jeholornis* STM2-51 and Enantiornithes indet. STM29-8 is consistent with the precocial reproductive strategy inferred for basal birds[27]. The smaller clutch preserved in Enantiornithes indet. STM10-45 (although potentially an artefact of preservation) suggests that enantiornithines may also have been diverse in their reproductive strategies.

Another key difference between living archosaurs is the timing of sexual maturation. In crocodilians reproductive maturity has an early onset, before the animal reaches skeletal maturity. Modern birds grow rapidly, typically reaching skeletal maturity within 1 year, although not typically becoming sexually mature until later (2–8 years; only 6 months in the domestic chicken)[7,14]. Histological analyses of paravian dinosaurs reveal a crocodilian pattern of reaching sexual maturity before skeletal maturity[28]. Enantiornithine STM10-45 shows a clear absence of fusion in compound bones like the carpometacarpus (Supplementary Fig. 8). In Enantiornithes, compound bones are known to fuse late in ontogeny[8] and STM10-45 is regarded as a subadult, indicating that, in at least this lineage of enantiornithines, reproductive maturity was achieved before skeletal maturity, as in paravian dinosaurs and crocodilians. Histological analysis was attempted on the three specimens, but unfortunately no bone could be sampled from STM10-45. Samples from STM2-51 and STM29-8 were badly crushed and the medullary cavity was not clearly preserved, preventing the identification of medullary bone (see Supplementary Information). However, it was determined that enantiornithine STM29-8, which shows a greater degree of fusion in the compound bones (poor preservation prevents determining the exact degree of fusion), was skeletally mature and required more than 1 year to reach adult size (see Supplementary Information).

The preservation of reproductive organs such as ovarian follicles allows a rare opportunity to confidently identify the gender of these specimens and recognize sexually dimorphic traits. The elongate paired tail feathers present in some enantiornithines strongly resemble those of *Confuciusornis*, which have been interpreted as a sexually dimorphic trait present only in males; this interpretation is controversial as the feathers do not co-vary with size as expected[29]. Feathers are only preserved in STM29-8 (Fig. 2a). The feathers around the pygostyle are clearly preserved and confirm the absence of paired elongate rectrices in this reproductively mature (adult) female.

The ovarian follicles preserved in these Early Cretaceous birds, the first discovery of this kind, reveal new clues regarding basal bird reproduction. Based on the bracket placed by the fossil record, the consistent preservation of the follicles on the left side of the body in all three specimens suggests that the right functional ovary was lost at the dinosaur–avian transition. Clutch size in basal birds is inferred to be plesiomorphically large, consistent with the precocial developmental strategy inferred from embryos and juveniles, and information from closely related dinosaurs. Within Aves there is an observable trend towards smaller clutches with relatively larger eggs that extends from long bony-tailed birds closely related to *Archaeopteryx* into Neornithes, and clade-specific specializations in reproduction strategy were not limited to the crown group. Despite the presence of advanced features, the ovary in Mesozoic birds was large with minimal follicular hierarchy, and sexual maturity preceded skeletal maturation as in crocodilians, both conditions consistent with the lower metabolic rate inferred for basal birds and paravian dinosaurs compared to neornithine birds.

METHODS SUMMARY

Bone samples were taken from all three specimens; only a single sample could be retrieved from STM10-45 and it could not be used for histological analysis. Two samples were taken from each of the other specimens where the bone was already broken, as close to midshaft as preservation allowed: the ulna and femur were sampled in STM2-51 and the humerus and femur were sampled in STM29-8. The samples were taken using a micro-saw and were embedded in EXAKT Technovit 7200 one-component resin and allowed to dry for 24 h. The samples were then cut and polished until the desired optical contrast was reached. The samples were viewed under normal and polarized light using a Leica DMRX polarizing microscope.

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Supplementary Information is available in the online version of the paper.

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