

A Precocial Avian Embryo from the Lower Cretaceous of China

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An avian embryo was collected from Lower Cretaceous lacustrine shale in Liaoning, in northeast China (fig. S1). It was in the final stage of development and represents an early precocial bird.

The embryo is enclosed in an oval ~35 mm by 20 mm. No evidence of eggshell was recognized. During incubation, bird embryos shift into a tucking position shortly before hatching and occupy most of the egg. The tucked posture of the Liaoning fossil is consistent with a late-stage embryo rather than with a hatchling, in which case the head would have raised beyond the vicinity of the feet.

The skeletal elements are nearly intact in articulation, with a complete skull and nearly complete postcranial bones (Fig. 1, A and B). The skull is large, with toothed jaws and an expanded braincase. The vertebral col-

umn is strongly curved. Both hindlimbs are folded and in tight contact with the skull and other postcranial bones. The long bones have obvious striations and less ossified epiphyses. The unguals of the pedal digits are large and curved, indicating that the adult would be an arboreal bird.

Extant bird embryos have a special structure on the top of the bill, the egg tooth. This tooth is used for breaking eggs before hatching and drops off soon after hatching. Such a structure is absent in the Liaoning embryo, although true teeth are still present as in most other Mesozoic birds. The egg tooth probably represents a novel feature that arose later.

The embryo has several enantiornithine apomorphies such as a strutlike coracoid with a convex lateral margin, a V-shaped furcula,

metacarpal III extending well past metacarpal II distally, and metatarsal IV being more slender than metatarsals II or III.

Several avian embryos have been reported from the Upper Cretaceous, but none with feathers (1, 2). The Liaoning embryo has a well-ossified skeleton with well-grown feather sheets. The jaws lie below the wing as a result of the rotation of the skull. The distal elements of the wing are well ossified, suggesting that it was in the final stage of embryological development (3, 4). The embryo also preserves imprints of wing and tail feather anlagen enclosed in the feather sheets (Fig. 1, B and C). The presence of long feather sheets with no open vanes is further evidence that the fossil is an embryo.

Altricial birds are naked and helpless when they hatch, whereas precocial birds are covered with natal down and can move and feed independently. Precocial birds hatch with relatively large brains. The presence of well-developed feather sheets and the large brain indicates that the Liaoning embryo is a precocial or even a superprecocial bird. It is generally believed that precociality is ancient and altriciality is derived. All exclusively precocial bird orders have been phylogenetically arranged in the infraclass Eoaves (5) and placed at the basal node of the cladogram (3). The recognition of a Lower Cretaceous precocial avian embryo supports this phylogeny. It has been suggested that the dinosaur *Troodon* developed precocially (6), and the Late Cretaceous oviraptorid dinosaurs may also be precocial (7). Because these are close relatives of birds, the precociality of birds might represent a feature derived from their dinosaurian ancestor.

References and Notes

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Supporting Online Material

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Fig. S1

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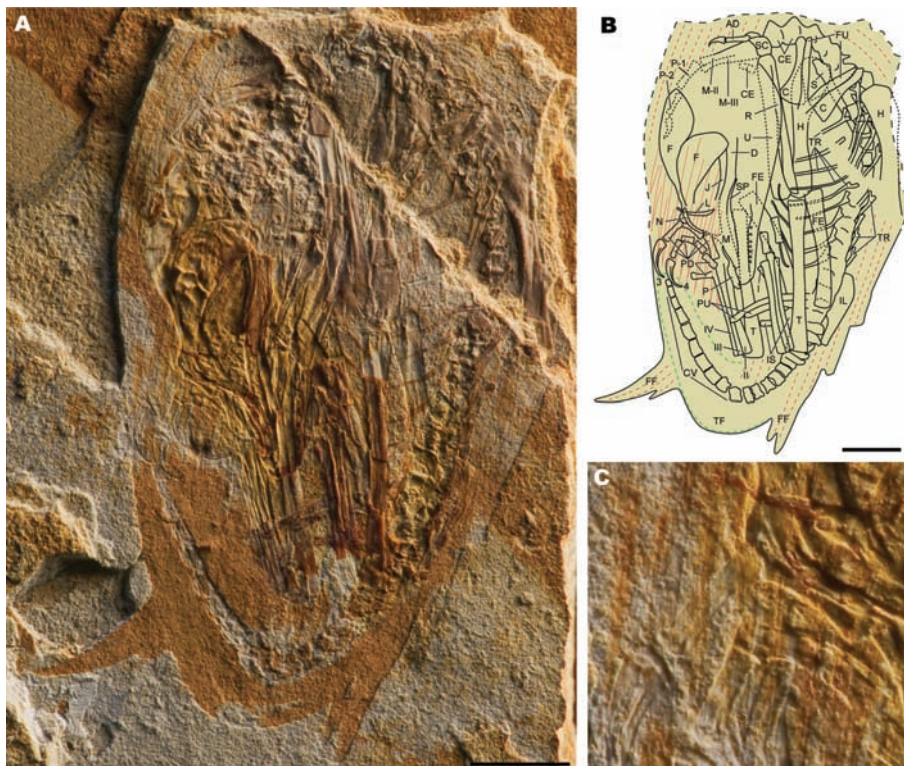


Fig. 1. (A) Photograph of a Lower Cretaceous avian embryo from Liaoning, China (Institute of Vertebrate Paleontology and Paleoanthropology no. V14238). (B) A line drawing of the fossil shown in (A). Red lines indicate wing feather sheets, and the green line shows imprints of tail feather anlagen. (C) A close-up view of long wing feather sheets near the pedal claws. Scale bars, 5 mm. AD, alular digit; C, coracoid; CE, cervical vertebra; CV, caudal vertebra; D, dentary; F, frontal; FE, femur; FF, wing feather sheets; FU, furcula; H, humerus; IL, ilium; IS, ischium; J, jugal; L, lachrymal; M, maxilla; M-II, metacarpal II; M-III, metacarpal III; N, nasal; PD, pedal digits; P, premaxilla; PU, pubis; P-1, first phalanx of the major digit; P-2, second phalanx of the major digit; R, radius; S, scapula; SC, semilunate carpal; SP, splenial; T, tibia; TF, tail feather sheets; TR, thoracic rib; U, ulna; 3 and 4, pedal digits III and IV; and I to IV, metatarsals I to IV.