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Early Evolution of Avian Flight and Perching: New Evidence from the Lower Cretaceous of China

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Fossil bird skeletons discovered in Lower Cretaceous lake deposits in China shed new light on the early evolution of avian flight and perching. The 135 million-year-old sparrow-sized skeletons represent a new avian, *Sinornis santensis*, n. gen. n. sp., that preserves striking primitive features such as a flexible manus with unguals, a footed pubis, and stomach ribs (gastralia). In contrast to *Archaeopteryx*, however, *Sinornis* exhibits advanced features such as a broad sternum, wing-folding mechanism, pygostyle, and large fully reversed hallux. Modern avian flight function and perching capability, therefore, must have evolved in small-bodied birds in inland habitats not long after *Archaeopteryx*.

THE SKELETON OF THE OLDEST BIRD, *Archaeopteryx*, is characterized by elongate grasping forelimbs and a long balancing tail, and its skeleton resembles in many regards that of its nearest theropod relatives (*1*). *Archaeopteryx*, nevertheless, was clearly capable of gliding or primitive powered flight, as evidenced by flight feathers of modern avian aerodynamic design and arrangement along the forearm and manus (*2*). Late Cretaceous carinate birds such as *Ichthyornis*, in contrast, exhibit an advanced avian flight apparatus, including an expansive keeled sternum for bulky flight musculature and wing and tail modifications for aerial maneuverability (*3*). The basic components of the modern avian flight apparatus, thus, must have arisen in the Early Cretaceous, during the first third of avian history.

But the fossil record for the Early Cretaceous, thus far, has provided little documentation of this critical transformation (*4*). Recently, partial bird skeletons have been discovered in the Lower Cretaceous of Asia (*5*) and Europe (*6*) (Fig. 1) that provide important clues to the early evolution of flight, but none of these specimens is complete. We report on the discovery of sparrow-sized bird skeletons in Lower Cretaceous beds in northeastern China (*7*). The holotype skeleton (Fig. 2B) of the new bird, *Sinornis santensis*, n. gen. n. sp. (*8*), is preserved on part and counterpart slabs of fine-grained freshwater lake sediment and is associated with abundant fish (*Lycoptera*), insect, and plant remains (*9*). The associated pollen and spore assemblage suggests a Valanginian age for the bird (*10*), which, if correct, would make it second only to *Archaeopteryx* in age among birds (Fig. 1C).

The skull and skeleton exhibit a number of striking primitive features that have not been reported thus far in any bird except *Archaeopteryx*. The skull has a proportionately short, toothed snout (Fig. 2A) as in *Archaeopteryx*. The carpus and manus in the forelimb are separate, rather than fused into a unit carpometacarpus, and the manus is composed of freely articulating metacarpals, with well-formed phalanges and unguals on the first and second digits (Fig. 3C). The manual unguals are relatively small and only moderately recurved, in contrast to the slender, highly recurved unguals in *Archaeopteryx* (*11, 12*). The pelvis is remarkably primitive and closely resembles that of *Archaeopteryx* (Fig. 4B). The elements of the pelvic girdle are free rather than coossified (*6, 12*), the iliac blades are erect rather than converging toward the midline, and the ischium is blade-shaped rather than strap-shaped. The rodlike shaft of the pubis appears to be directed more ventrally than posteriorly and terminates distally in a hook-shaped foot similar to that in *Archaeopteryx* and theropod dinosaurs. As in *Archaeopteryx*, the metatarsals are separate, rather than coossified, along all but their proximal ends. Rows of slender stomach ribs (gastralia) are preserved on the ventral aspect of the trunk, passing between the hind limbs (Fig. 4B). Gastralia have been lost in all other birds except *Archaeopteryx* (*12*). These retained archaic features are not specifically involved in flight or perching and add to current evidence that favors theropod dinosaurs as the nearest avian relatives. Lack of fusion in the manus, pelvis, and hind limbs seems to document the primitive avian condition, rather than signify immaturity in the holotype skeleton, because bone surfaces are finished throughout the skeleton and the components in the dorsal vertebrae and pygostyle are completely fused (*13*).

Advanced avian characters in the skeleton of *Sinornis* are almost all directly related to flight or perching. There appear to be no more than 11 dorsal vertebrae in the trunk as in the Spanish bird (*6*), rather than 14 as occur in *Archaeopteryx* and most theropods. The tail is short with only eight free vertebrae and a large pygostyle for attachment of the rectricial fan. The short trunk and tail in *Sinornis* shift the center of mass toward the forelimbs, as in modern powered fliers, as opposed to a center of mass near the hind limbs, as in the terrestrial cursor *Archaeopteryx*. In living birds the pygostyle is closely correlated with the size of the rectricial fan

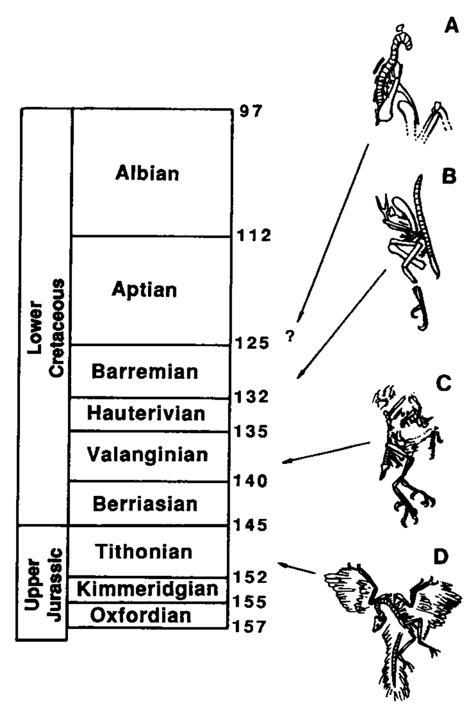

Fig. 1. Temporal position of Upper Jurassic and Lower Cretaceous fossil birds. (**A**) *Ambiortus dementjevi*, (**B**) Las Hoyas bird, (**C**) *Sinornis santensis*, and (**D**) *Archaeopteryx lithographica*.

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