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EVOLUTION

How birds became birds

Sustained size reduction was essential for the origin of birds and avian flight

By Michael J. Benton

Birds evolved from dinosaurs, but how long did this evolutionary transition take? Twenty years ago, it was widely assumed that the first bird—*Archaeopteryx*, which lived in the Late Jurassic (see the photo)—evolved its feathers, wings, and ability to fly within just 10 million years or so. Since then, it has become clear that most of the 30 or more characteristics that distinguished the small, flying *Archaeopteryx* from ground-dwelling, carnivorous dinosaurs (theropods) emerged much earlier. On page 562 of this issue, Lee et al. (1) provide evidence for sustained miniaturization for 50 million years before *Archaeopteryx* evolved (see the graph).

The story of this revolution begins in 1994, when paleontologists from China brought photographs of amazing new fossils to the Annual Meeting of the Society of Vertebrate Paleontology in New York. The photos showed a small dinosaur without wings or other bird characters, but covered with a fuzz of feathers. This was the beginning of a flood of Chinese theropod fossils with feathers of all kinds, from simple bristles through branched down feathers to fully elaborated flight-type feathers (2, 3). Some theropod dinosaurs even had extended forearms and quill-like feathers arranged as wings. The dromaeosaurid *Microraptor* also had distinct wings on its legs, resurrecting the old “tetrapteryx,” a supposed four-winged precursor of modern two-winged birds (4). The fossils showed that from about 170 to 120 million years ago, all these dinosaurs—the Paraves—were experimenting with flight in various modes, including parachuting, gliding, and leaping from tree to tree. One clade, represented by *Archaeopteryx*, made the crucial leap to powered flight, and so birds were born.

Feathers are so typically avian today that they are often seen as the key character of birds. However, feathers arose at least 50 million years before *Archaeopteryx*, and perhaps much earlier (5). They presumably arose first for insulation and display, as witnessed by the colorful, patterned feathers of dinosaurs (6, 7), and were then co-opted in expanded gliding surfaces and increasingly in substantial, aerodynamic wing structures among Paraves (8).

So, what makes a bird a bird and not a flying dinosaur? As Lee et al. show, the key seems to be miniaturization. The trend to miniaturization in Paraves had already been noted in size comparisons across all theropods (9). Macroevolutionary analysis has confirmed that this size reduction happened at evolutionary rates 150 times faster than normal (10). Lee et al. now show that miniaturization was a long-term trend over 50 million years (see the graph). The study is based on analysis of an enormous data set and uses sophisticated analytical tools. The authors looked at 120 species of theropod dinosaurs and early birds, coded for 1549 skeletal characters (a data matrix comprising 185,880 cells), and calculated the best-fitting phylogenetic tree while also exploring evolutionary rates.

Until recently, paleontologists relied on qualitative approaches to establish narratives of change through geologic time. They used cladistic methods to discover

best-fitting or most likely phylogenetic trees; evolutionary change was then mapped loosely over the tree. Now, phylogenetic comparative methods (11) make it possible to calculate ancestral states of any character, and to establish points of unusually fast or slow rates of change. Such “diversification shifts” help in determining the most likely evolutionary models for a tree or part of a tree.

Earlier studies (9, 10) used three steps: build the tree, date the branching points, and then map the characters. Lee et al. ran all three calculations simultaneously, working with phylogenetic information, geologic dates for branching points, and character state reconstructions at the same time. All methods are well established, and it is not clear which approach is most reliable. They all give similar results in this case.

The authors find that theropod body size decreased 12 times, from an initial mean mass of 163 kg to 0.8 kg in *Archaeopteryx*. How could such a long-term trend be maintained? Lee et al. note that miniaturization brought numerous changes, because it shortened normal developmental patterns. For example, bird heads can be seen as dinosaur heads that retain juvenile features in the adult (pedomorphic) (12), with short snouts, large brains, and large eyes (see the figure). Smaller size might also have been facilitated by co-option of feathers for insulation. In addition, birds have decoupled hindlimbs and forelimbs (13), allowing each limb set to function independently, unlike in most other tetrapods (see the figure). What might have triggered these changes?

The crucial driver may have been a move to the trees, perhaps to escape from predation or to exploit new food resources. Tree living requires small bodies, and reduced body size enables other characteristics that enhance success in the trees, such as enlarged eyes for three-dimensional vision (so avoiding collisions when leaping from branch to branch); enlarged brains to cope with diverse arboreal habitats; insulating feathers to enable nocturnal activity (many insects are nocturnal to evade cold-blooded predators); and elongated forelimbs, distinct from the hindlimbs in their function, and with expanded flight surfaces to enable ever more daring leaps from tree to tree. The physical changes are reminiscent of those that later occurred in our own clade, the Primates, also interpreted as driven by tree living. ■

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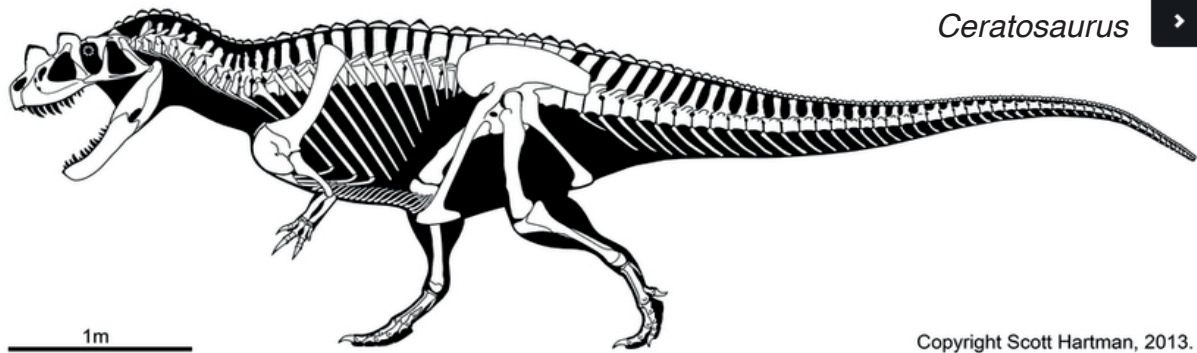
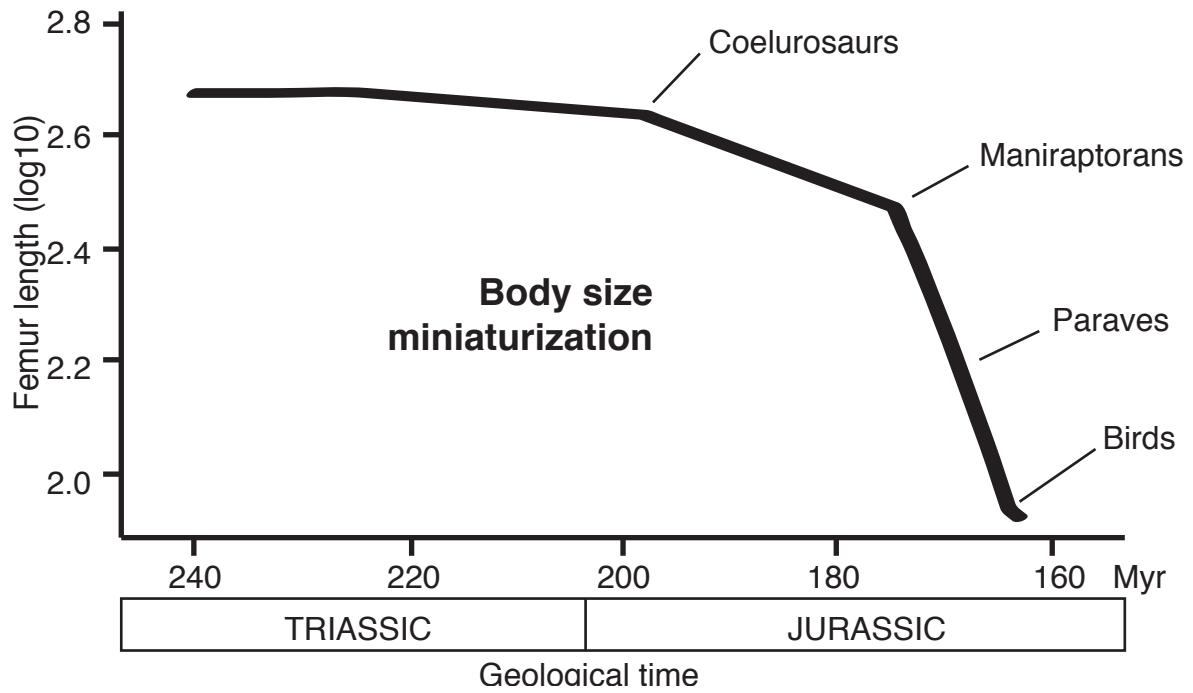
FIGURE CAPTIONS:

Early bird. Fossils of *Archaeopteryx*, which lived around 150 million years ago, provide important clues to how birds evolved from their theropod ancestors.

Making a bird from a dinosaur. Key characteristics of birds that distinguish them from their theropod ancestors include quill-like feathers, forelimbs that are decoupled from hindlimbs, a pedomorphic skull, and small size.

Getting smaller. Lee et al. show that between 210 and 160 million years ago (Ma), the ancestors of today's birds shrank at a rapid evolutionary rate, as captured by the length of the femur (thigh bone). This was crucial to enable flight.

School of Earth Sciences, University of Bristol, Bristol BS8 1RJ,
UK. E-mail: mike.benton@bristol.ac.uk



massive size reduction; feathers;
forelimb decoupled from hindlimb



Elongate forelimb, perhaps for gliding wing

Deinonychus

Pedomorphic skull (juvenilized features, including large eyes and large brain)



Forelimb forms wing for powered flight

Archaeopteryx