

Dinosaurs and Chicken Fingers

Are birds really the descendants of dinosaurs? Although Thomas Huxley (1868, 1870) proposed in the late nineteenth century that the birds descended from dinosaurs, it was J. H. Ostrom's 1969 description of the dinosaur *Deinonychus antirrhopus* and its similarities to the fossils of the first known bird *Archaeopteryx* that was critical in making the dinosaur-to-bird hypothesis acceptable. Ostrom listed 22 similarities between *Deinonychus* and *Archaeopteryx*, similarities found in no other groups and linking birds and dinosaurs.

Without its feathers, *Archaeopteryx* looks exactly like a small coelurosaur (such as Jurassic Park's *Velociraptor*). Indeed, one specimen of *Archaeopteryx* was misidentified as a coelurosaur for over 100 years until its feathers were noticed by Peter Wellnhofer (1993). Gauthier's cladistic work in the mid-1980s (see Gauthier 1986) provided systematic support for the theory that birds are the descendants of coelurosaurian dinosaurs. He listed 17 anatomical features shared between dinosaurs and birds and no other group, including a shifted pubic bone in the pelvis, clawed hands, large eye openings, a flexible wrist with a particularly shaped wrist bone, a strap-like scapula, clavicles fused to form a furcula (wishbone), air sacs, and even feathers and a skull (Ji et al. 2001; Sereno et al. 1999, 2008; Xu et al. 2003; Bhullar et al. 2012). Unlike any other reptiles, both birds and theropod dinosaurs (of which the coelurosaurs are a group) have a three-fingered grasping hand and a four-toed foot supported by three main toes. Thus, Padian and Chiappe (1998a) conclude that "in fact, living birds are nothing less than small, feathered, short-tailed theropod dinosaurs." And paleontologist Jack Horner (2009) has been collaborating with developmental biologists to make a dinosaur from a chick embryo. A paleontologist says: "Why not mess with a chicken embryo so that it grows into a nonavian dinosaur? It can't be that hard. After all, they are both dinosaurs."

However, whereas paleontologists were nearly unanimous in their appraisal that birds are the direct descendants of dinosaurs, some developmental biologists harbored serious doubts. Fossil evidence unambiguously identified the theropod-like birds as having wing digits 1, 2, and 3 (Padian and Chiappe 1998b)*, but embryological evidence suggested that the wing digits of current birds are 2, 3, and 4. For instance, Burke and Feduccia (1997) found that digit primordia in the fingers of early and present-day birds correspond to the index, middle and ring fingers (2-3-4). Moreover, the arrangement of cartilaginous condensations is the one expected for the 2-3-4 pattern, not the 1-2-3 pattern. This would mean that the similarity of dinosaur and bird digits is based on independent selection for three digits (convergent evolution) and is not based on shared ancestry. This developmental critique of the bird-dinosaur link has been made by other scientists studying chick limb development (Galis 2005; Welten et al. 2005). They point out that bird feet have reversed toes used for perching on branches (something dinosaurs never developed), and that theropods had a characteristic joint in their lower jaws for grasping prey (something never found in birds). Moreover, studies by Towers et al. (2011) interpret their ZPA mapping results as being consistent with the notion that birds came from theropods with digits 1, 2, and 3, rather than from dinosaurian theropods with digits 2, 3, and 4. Alan Feduccia has called the notion that birds arose directly from dinosaurs a "delusional fantasy by which one can vicariously study dinosaurs at the backyard bird feeder" (Feduccia 1997).

Thus, the discrepancy is whether avian fingers represent digits 1–3, as predicted by the fossil record, or digits 2–4 as suggested by the placement of mesenchymal condensations in the embryonic digits.

But a study by Vargas and Fallon (2005a,b) suggests that embryologists have been wrong in their assessment of bird digits. Although the condensations of the digits *look* like those expected for digits 2, 3, and 4, the Hox gene expression patterns suggest that the actual digits are indeed 1, 2, and 3, just as in the theropod dinosaurs. Fallon and Vargas claim that digit 1 (thumb/hallux) is uniquely characterized (at least in the chicken hindlimb and the mouse forelimb and hindlimb) by *Hoxd13* expression in the absence of *Hoxd12* expression. All other digit primordia express both *Hoxd12* and *Hoxd13*. Thus, Vargas and Fallon proposed that the wing digits of chickens are actually 1-2-3, and that avian digit arrangement is further proof rather than a rebuttal of the idea that birds are the descendants of dinosaurs.

Recent studies are showing some support for this “frameshift” model. The Hox expression of alligator digits (Vargas et al. 2008) also suggests that in the bird wing, digits 1, 2, and 3 develop from the embryological positions expected of digits 2, 3, and 4. Furthermore, Vargas and Wagner (2009) showed that if cyclopamine were used to inhibit sonic hedgehog signaling in chick limbs, the digit morphologies that usually develop from positions 2 and 3 shifted such that they developed from positions 3 and 4. This linked the developmental analysis of limb development to paleontological studies (Wagner and Gauthier 1999) hypothesizing that when digit 4 was lost in birds, a “homeotic frameshift” occurred, causing digits 1, 2, and 3 to develop from the embryological positions formerly giving rise to digits 2, 3, and 4. However, reconciling this with the fossil record means that the homeotic switch might have had to have occurred much earlier than expected (Bever et al. 2011).

The evolution of the bird forelimb digits remains a “bone of contention,” and tracing the evolution of these bones probably requires more fossils and more types of embryos (Xu and Mackem 2013.) Developmental biologist Richard Hinchliffe (1994, 1997) sees the argument in a larger context. While virtually all evolutionary biologists agree that birds and dinosaurs evolved from the same class of prehistoric creatures, he says, “the only question we are arguing about is whether [birds] derived very late in time from a specific group of theropod dinosaurs, the so-called raptors, or are they derived from a common-stem ancestor with dinosaurs.”

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