How the bird wing evolved

The wings of birds have three digits—the reduction in digit number being an adaptation that enabled the evolution of flight—and there is a long-running controversy about whether these are digits 1 2 3 or digits 2 3 4 of the ancestral pentadactyl limb plan. This issue is important for tracing the evolution of the wing from the birds' dinosaur ancestors. A group of dinosaurs known as theropods bridge the transition between a five-digit hand found in the earlier dinosaurs and the three-digit bird wing (Fig. S13.1). Paleontologists identify the three digits in theropods such as *Allosaurus* as 1 2 3, with digits 5 and then 4 being first reduced, and subsequently lost, during theropod evolution. According to fossil evidence, the three chick wing digits are 1 2 3.

The pattern of digit loss seen in theropods is unusual. In other cases of digit loss, it is the lateral digits that are lost (see Section 14.12 for the horse and other hoofed mammals). Indeed, classical morphologists comparing the order and the positions in which the digits develop in the embryonic chick wing with the embryonic forelimbs of other vertebrates—alligator and turtle—inferred that the digits are 2 3 4, and digit 1 has been lost; a cartilage condensation representing digit 5 appears transiently (Fig. S13.2). An anterior expression domain of Sox9 (the transcription factor required for cartilage differentiation) recently detected in the chick wing bud could represent the remnants of digit 1. So how can the different views be reconciled? One suggestion is that the three bird wing digits are 1 2 3, like the three digits of dinosaur hands, but that during evolution they shifted to the positions in which digits 2 3 4 normally form in tetrapod limbs—the frame-shift theory. Comparative analysis of Hox

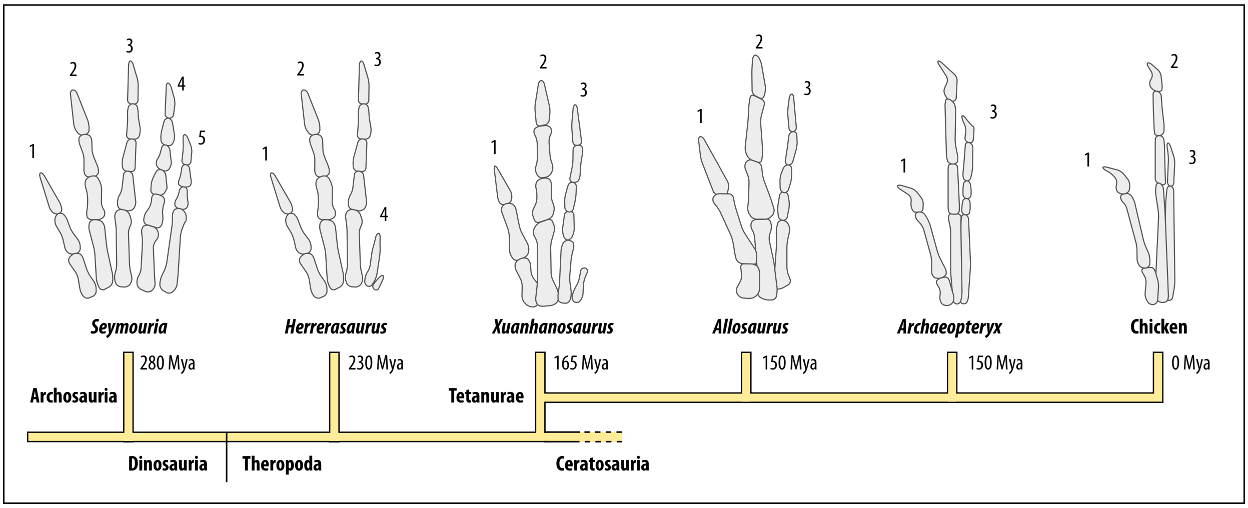

Figure S13.1 *From Wieschampel, D.B. Dodson, P., Osmolska, H. (eds)* The Dinosauria *2nd edition, University of California Press, 2004.*

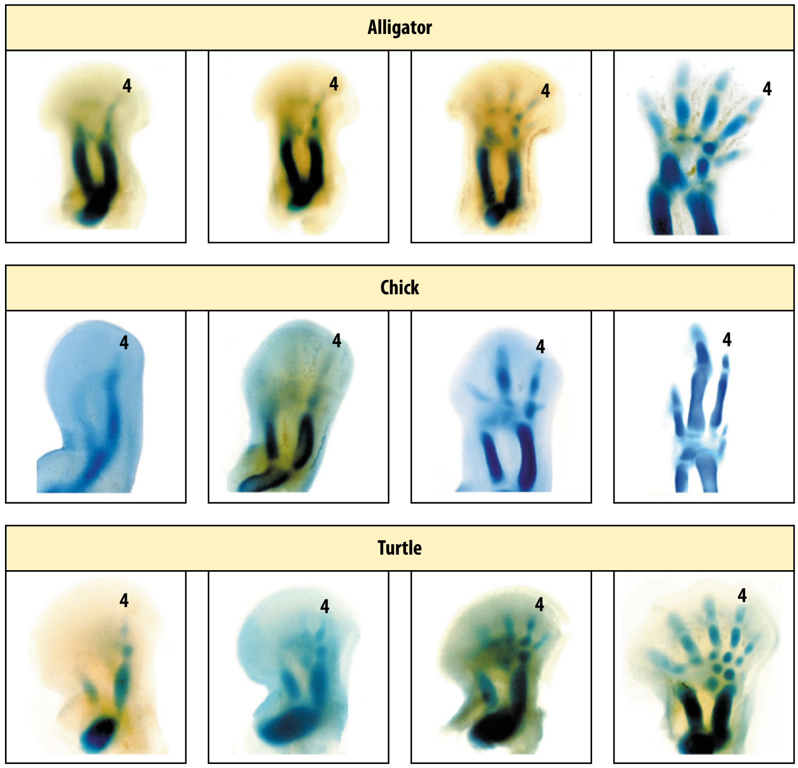

Figure S13.2 *Photos from Burke, A.C., Feduccia, A.:* ***Developmental patterns and the identification of homologies in the avian hand****.* Science *1977,* ***278****: 666-668.*

gene-expression patterns in the chick wing, chick leg, and mouse limbs supports the 1 2 3 theory and microarray analysis shows that the transcriptomes of the first chick wing digit and digit I in the chick leg are highly conserved. Fate maps made by grafting GFP-expressing tissue from transgenic chickens into chick wing and leg buds or by genetically labeling Shh-producing cells in mouse limb buds show that the origin of the chick wing digits is the same as the origin of digits 1 2 3 in the chick leg and the mouse limb.

The debate seems likely to continue: domains of Sox9 expression might not necessarily represent digits, and fate maps only give a retrospective view of evolution. This underscores the problems of integrating evidence from the fossil record with evidence from the embryology of present-day animals. By contrast, the study of recent evolutionary changes, such as the loss of pelvic fins in different forms of sticklebacks co-existing today, can uncover the basis of the evolutionary change (see Section 14.16 and Box 14D).

Further reading

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