Research Focus

An old controversy solved: bird embryos have five fingers

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New studies by Larsson and Wager, and by Feduccia and Nowicki of the embryogenesis of birds undisputedly show Anlagen for five fingers. This has important implications. First, the early presence of digit I, and its later disappearance, indicate that the evolutionary reduction of digits occurred via developmental arrest followed by degeneration. Second, it shows that the digits in the wings of birds develop from Anlagen II–IV. This suggests that the hypothesized descent of birds from theropods might be problematic, because theropods are assumed to have digits I–III.

The developmental origin of digits in the wings of birds has been hotly debated for more than a century. Several researchers have claimed that early during digit development, the Anlagen of five digits can be observed, after which the Anlagen of I and V regress. Therefore, the digits in adult wings are II–IV, rather than I–III [1,2] (digit V is sometimes still rudimentarily present). The early presence of digit I was disputed, however, by some researchers, especially by those who claimed that digits I–III develop fully and digits IV and V have become reduced (for discussion see Ref. [2,3]). The presence or absence of digit I has implications for two controversial issues in evolution: (1) the evolutionary mechanism of digit reduction; and (2) the descent of birds from theropods.

A new study by Larsson and Wagner now shows unequivocally that five digits are present during the early development of chickens [4] (Fig. 1). The earliest stage of digits is a condensation of mesenchymal cells and digit I is, thus, transiently present during development. This establishes that digits in the wings of birds develop from Anlagen II–IV. The early condensation stage is brief and, therefore, easily missed. Hinchliffe [3] for instance, concluded that there is no digit I in chickens; however, this is because he stained for chondrification (cartilage formation).

Interestingly, in another new study, Feduccia and Nowicki demonstrate the transient presence of digit I by staining for cartilage in ostriches [5], in which the arrested development of digit I appears to occur at a more advanced stage than in chickens [5,6]. These findings also agree with the embryonic pattern of vascularization in the wing, which indicates a mesenchymal Anlage of digit I in both chickens and ostriches [6,7]. The early development of chicken and ostrich digits therefore provides support for the hypothesis that evolutionary digit reduction in bird wings has occurred by arrested development of digit I followed by degeneration, rather than by a repatterning of the initial embryonal Anlage followed by the development of the digits that are present later on [8,9].

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Implications for the bird–theropod link

The finding of a digit I Anlage has implications for the descent of birds from theropods. Most scientists agree that birds are descended from theropod dinosaurs, because of their impressive skeletal similarity. However, the new embryological data indicate that wing digits are II–IV, but theropod dinosaurs are assumed to have had digits I–III. Feduccia [5] claims that for this reason, a descent of birds from theropods is impossible and that instead, birds are descended from archosaurs other than dinosaurs. Certainly, Feduccia is right that the present fossil evidence for digit reduction does not favour a descent from theropods. However, it is improbable that the multitude of shared characters between theropods and birds are the result of convergence. Therefore, two hypotheses that enable birds to descend from theropods deserve attention: (1) theropod ancestors of birds initially had digits I–III and, before the origin of birds, a homeotic identity shift occurred such that digits II–IV developed with identities I–III (frame shift hypothesis, FSH of Wagner and Gauthier [10]); and, (2),

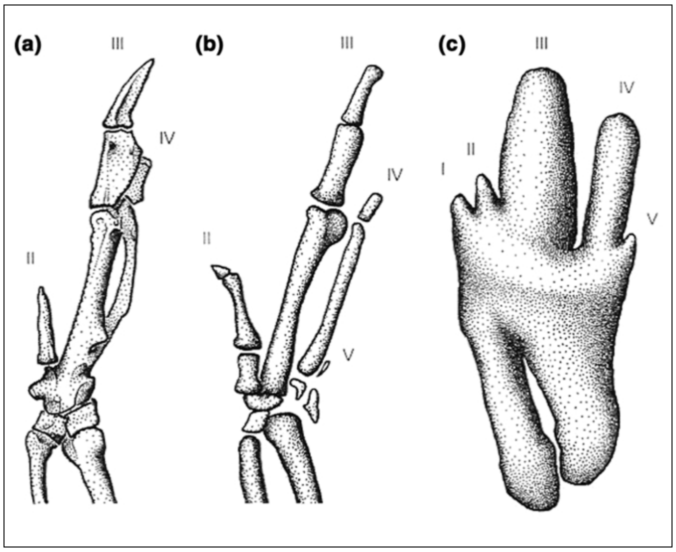

Fig. 1. Developmental stages of chick wings in dorsal view. (a) Adult wing with three ossified digits. (b) Stage 35 embryo with four chondrified digits. (c) Stage 29 embryo with five mesenchymal digit Anlagen. Reproduced, with permission, from Ref. [4].

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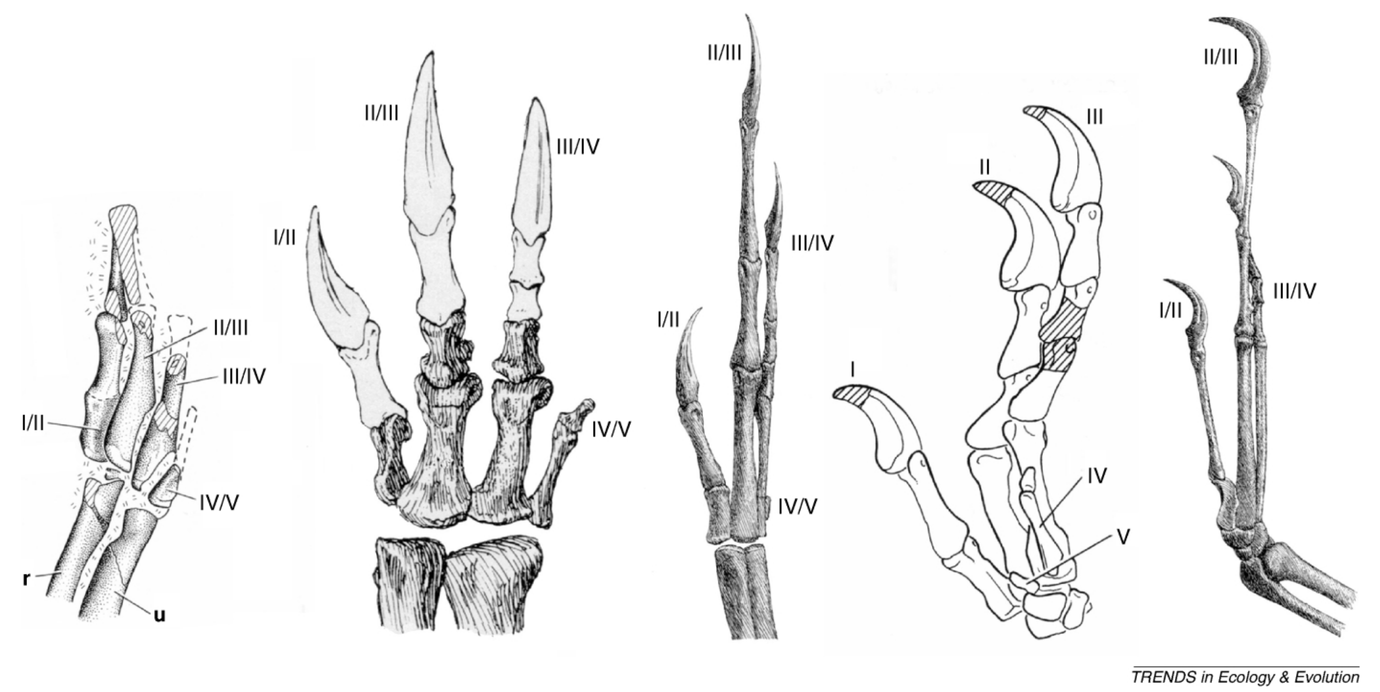

Fig. 2. A comparison of the hands of saurischians (a) *Procompsognathus*, digits are II–V or I–IV, depending on whether digit I or V was reduced earlier; (b) *Ceratosaurus*; (c) *Ornitholestes*; (d) *Herrerasaurus*, digits IV and V are markedly reduced; (e) *Archaeopteryx*. Reproduced from Ref. [19] (a), Ref. [20] (b,c,e) and Ref. [18] (d).

theropod ancestors of birds had digits II–IV, as in present-day birds [3].

Is the frame shift hypothesis plausible?

How plausible is the first hypothesis, a homeotic shift in identity of three consecutive digits? The identity of digits is determined early during digit development, before the articulations between phalanges become visible [11]. Evolutionary changes during early limb development are highly constrained [12,13], but this is less so at the time when digit identity, rather than digit number is determined. Homeotic shifts of one digit appear to have occurred several times independently in reptiles, birds and mammals, always in association with an adaptive shift. Tree-dwelling birds, for instance, often have feet with two backward-pointing toes instead of one. Either digit IV (e.g. woodpeckers) or digit II (e.g. trogons) has been partially transformed into the identity of digit I, to obtain a better grasp on branches [14] (but see Ref. [15]). In swifts and pelicaniformes, digit I has been partially transformed into the identity of digits II, III or IV, leading to a foot with an extra toe included in the paddle, presumably for greater strength. The developmental basis of these transformations is not clear, but it seems probable that parts of the developmental pathways have been co-opted by different digits; that is the developmental pathway of digit I by either digit II or IV in tree-dwelling birds, which would make these truly homeotic transformations. Experimental results also indicate that homeotic shifts of digit identity can be induced during development [11]. The most serious challenge to this hypothesis comes from the absence thus far of a plausible selective scenario. A homeotic shift of digits I–III into digits II–IV in theropods without further anatomical changes does not appear to lead to an adaptive advantage. The absence of an adaptive advantage in combination with the constraint on changes of early digit development is a problem for the plausibility of this hypothesis.

Could birds have had theropod ancestors with digits II–IV?

The second hypothesis assumes that theropod ancestors of birds had digits II–IV rather than I–III. This hypothesis is not considered in the modern literature, which is surprising given that the reduction from five to four fingers in theropods or their ancestors during the Triassic is poorly documented in fossil records and does not exclude this possibility. The transition in theropods from four to three fingers forms less of a problem. There are many fossils of Triassic and Early Jurassic ceratosaurs with four fingers in the hand of which the most posterior finger is reduced (IV or V, Fig. 2a,b). In addition, there are indications that the maniraptoriform theropod *Ornitholestes* had a tiny remnant of a finger posterior to its three functional fingers (Fig. 2c). It is thus, probable that the transition from four to three fingers in bird ancestors occurred by the reduction of the most posterior digit.

The transition from five to four digits is impossible to deduce from the currently known fossil records. It is usually assumed that bird ancestors are descended from either theropods or saurischians with hands with reduction of digits IV and V, because this is the situation in the five-fingered *Eoraptor* and *Herrerasaurus* [10] (Fig. 2d). However, the phylogenetic position of *Herrerasaurus* and *Eoraptor*, relative to four-fingered theropods, is not as yet well resolved. It not clear whether they are basal theropods or basal saurischians. If they are theropods, they are considered to be incertae sedis ('of uncertain position', [16–18]).

Given the uncertainty about the phylogenetic position of *Herrerasaurus* and *Eoraptor* and the incomplete fossil record on digit reduction, there is no firm evidence to conclude that digit V was the first digit to be reduced in the theropod ancestors of birds. In addition, there are several ceratosaurs with the most posterior of their four digits (digit IV or V) less reduced than digit IV of *Herrerasaurus* (Fig. 2). Given the apparent irreversibility of digit reduction [12,13], this does not support a descent of ceratosaurs from *Herrerasaurus*, or other saurischians with a similarly more reduced digit IV and digit V still present. This indicates a considerable period of nondocumented independent digit reduction in *Herrerasaurus* and ceratosaurs. As ceratosaurs and the tetanuran ancestors of birds presumably have a common ancestry (based on characters other than reduction of the digits), this independence also holds true for birds.

We are therefore left with several scenarios: (1) birds descending from archosaurs other than dinosaurs, which cannot satisfactorily explain the many similarities between birds and theropods; (2) the FSH, for which there is as yet no adaptive significance that would overcome the evolutionary constraint; and (3) birds descending from theropods with digits II–IV, which is the most parsimonious evolutionary transition scenario but for which there is as yet no fossil evidence. More fossils from bird ancestors in the Triassic and Jurassic are, therefore, eagerly awaited to solve this vexing mystery. Reanalysis of incomplete four- (and possibly five-) fingered theropod fossils given the knowledge that perhaps digits I and V have become reduced in theropods might also be helpful. Furthermore, more studies of the developmental mechanisms of homeotic digit shifts are necessary to evaluate the FSH. Important progress has, however, been made. The new studies have convincingly shown that in bird wings, the digits develop from Anlagen II–IV and that digit reduction has occurred by developmental arrest.

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