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Counting the Fingers of Birds and Dinosaurs

Homologies of the three fingers in birds have been debated for more than a century. Paleontologists have traditionally identified avian digits as I-II-III largely on the basis of phalangeal counts, whereas embryologists number them II-III-IV on the basis of development in the egg. The report by Ann C. Burke and Alan Feduccia (1) is a synthesis of the embryological evidence. They observe that in most amniotes, the first digit to form in the pentadactyl manus is digit IV, which develops a "primary axis." With the use of this developmental constraint, they identified the primary axis in birds as digit IV, and the surviving digits as II-III-IV. This conclusion is incompatible with theropod (dinosaur) ancestry of birds because theropod digits are identified as I-II-III, with vestigial fourth and fifth digits apparent in the fossil record. The origin of birds from dromaeosaurid-like theropods is supported by a large suite of synapomorphies, and thus has achieved wide acceptance (2-4). Burke and Feduccia apparently regard these similarities as convergence, not homology.

The interpretation of Burke and Feduccia

is based on the "ground-plan" of the hand of living tetrapods (alligators, for example) in which digit IV always appears first during development. In the case of digital reduction, however, the correspondence between primary axis and digit IV appears to break down. For example, in salamanders, the first digit to form is digit II, not digit IV (5). Burke and Feduccia acknowledge that the loss of digit IV in theropod evolution was unusual and does not follow the general rule of hand development. Furthermore, digit IV was absent in two-fingered *Tyrannosaurus* (I-II) and one-fingered *Mononykus* (I), which reveals the shortcoming of the rule. If birds are members of theropods (3-4), the presence of digit IV in *Archaeopteryx* and adult birds is doubtful. It would be difficult to argue that later birds re-evolved digit IV, while losing digit I, regardless of the pattern of development. It is more likely that, over eons, the primary axis shifted its position in concert with the reduction of digits. Shubin (6) proposed that the primary axis in birds may actually represent digit III because of developmental acceleration, which would

favor the I-II-III hypothesis. The shift of the axis may be linked to the ossification of the distal carpal elements, which may have caused perturbation of the distal branching pattern by modification of the expression domains of the *Hox D* genes (5). That the ulnare is supposed to part of the primary axis, but is lost during avian ontogeny (7), is strong evidence for perturbation of the primary axis in birds.

Developmental biologists have used other criteria to support the II-III-IV hypothesis, such as the topographic position of the pisiform and the sequence of chondrogenesis. Hinchliffe (7) identifies five precartilaginous elements in developing chicks: the radiale, ulnare, distal carpal 3 (semilunate bone), X, and pisiform. He regards two proximal carpals as the pisiform and the radiale. He states that the true ulnare regresses during development and is replaced by a new "element X" of uncertain affinity. Because the pisiform occurs laterally and adjacent to the fifth metacarpal in primitive archosaurs, the rudimentary metacarpal in the chick's wing is identified as digit V, and the rest as digits IV, III, and II.

It appears that in Hinchliffe's interpretation great weight is given to the pisiform's position for identifying digits. In a

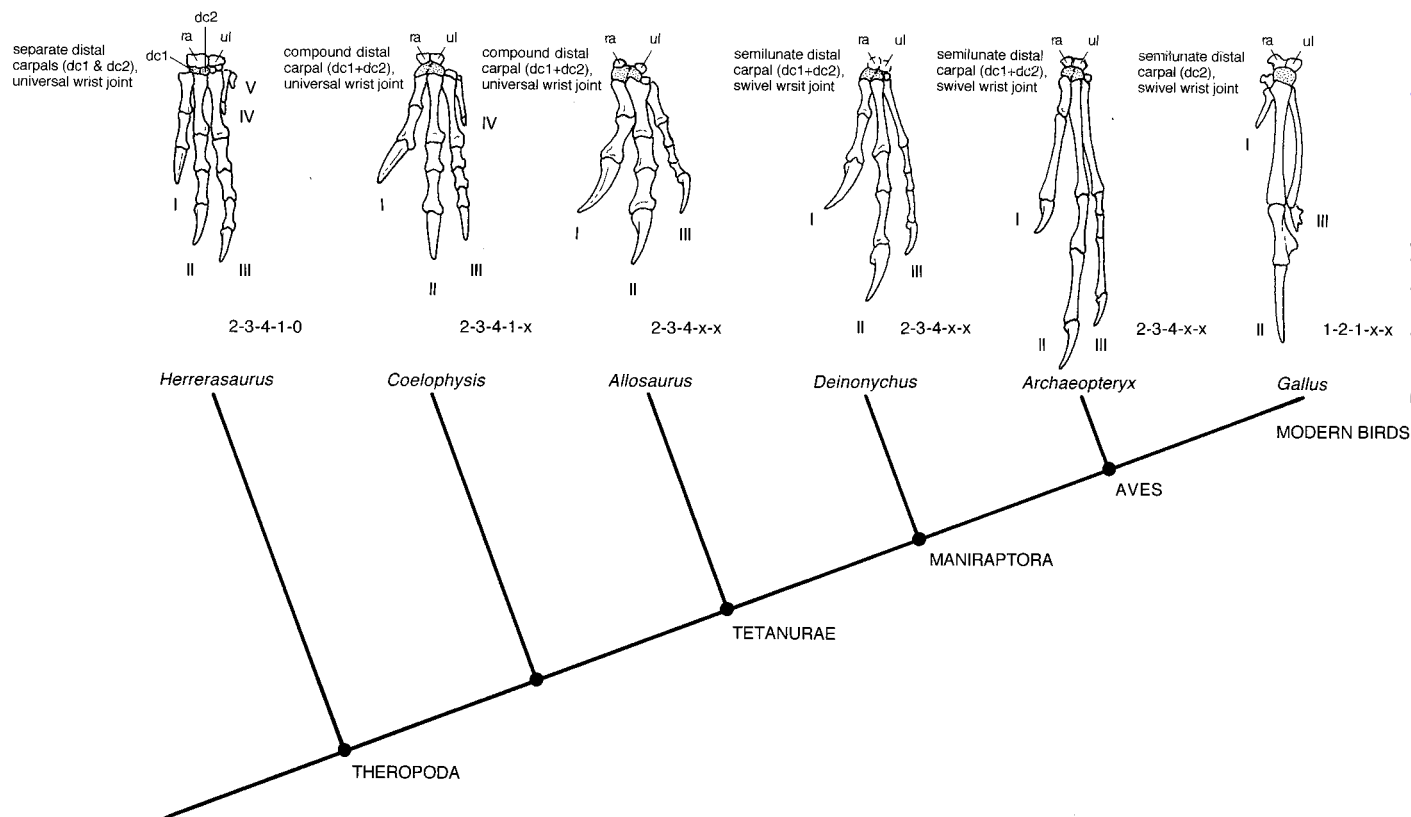


Fig. 1. Left manus of selected theropods in a phylogenetic context (2, 4) shows the pattern of digital reduction and the evolution of wrist from universal joint to swivel joint. Phalangeal counts and the topographic relationship of the

compound distal carpal (shown in stippled) support the idea that the surviving digits of maniraptoran dinosaurs and birds are I-II-III and that the semilunate bone represents fused distal carpals 1 and 2.

pentadactyl manus, the pisiform occurs adjacent to the fifth metacarpal, but this relationship is tenuous in other animals with the loss of postaxial digits. Because the pisiform occurs in the proximal row of the carpus, its topographic relation with the lateral metacarpal is not direct. It will always occur lateral to the ulnare, irrespective of loss of any digits. If so, the embryological convention that digit I is missing is not based on firm evidence.

Paleontologists have used two lines of evidence to support the I-II-III hypothesis: (i) conserved phalangeal formulae (2-4) and (ii) topographic relationship of the semilunate carpal with the corresponding metacarpals. The plesiomorphic phalangeal count for archosaurs is 2-3-4-5-3. Many archosaur lineages have a reduced number of digits, but have retained the original phalangeal formula in the digits that remain. The three digits of dromaeosaurs and *Archaeopteryx* have the same phalangeal formula of 2-3-4 as digits I, II, and III of basal archosaurs. Thus, the reduction of the digits in maniraptorans is believed to have occurred from the posterior to the anterior side with the loss of digits V and IV. The pattern of digital reduction becomes apparent from the phylogenetic hierarchy of theropods (Fig. 1). By extension, modern birds also possess digits I-II-III, but show further reduction of several phalanges during evolution.

The identity of the semilunate carpal provides an additional clue to the numbering of theropod digits. Ostrom (2) misidentified this bone in maniraptorans as "radiale" instead of distal tarsal and initiated the confusion. Critics (8, 9) pointed out that this bone cannot be homologous with the avian semilunate bone because the latter is a distal carpal, and thus questioned the theropod ancestry of birds. However, the articulation of the semilunate carpal in maniraptorans with corresponding metacarpals indicates that the bone in question (2) must be distal carpal, not proximal radiale, contrary to Ostrom's idea (3). The identification of the bone can be further resolved in a phylogenetic context. In *Herrerasaurus* (10), the manus is pentadactyl; the wrist shows two proximal carpals (the radiale and ulnare), one centrale, and four distal carpals (one for each inner metacarpal, I-IV). Metacarpal V is reduced and lacks its distal carpal. In *Eoraptor* (11) and *Coelophysis* (12), the next stage of manual modification can be seen; the distal carpal is integrated into a compound bone that receives metacarpals I and II, respectively. It must represent distal carpals I and 2, respectively. The fifth metacarpal is lost. Now that the homology of this compound bone is ascertained, it can be traced across the phylogeny of theropods, allowing us to number the digits. The distal

carpal becomes the semilunate carpal in maniraptorans, which allows a swivel wrist joint. The topographic relationship of the semilunate bone suggests that the surviving digits of maniraptorans are I-II-III (Fig. 1). If so, Ostrom's "radiale" actually represents distal carpals 1 and 2, whereas the true radiale and ulnare are not yet known from the wrist of *Deinonychus*. Synthesis of both neontological and paleontological data suggests that the surviving avian digits are I-II-III, and thus supports their theropod origin.

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Burke and Feduccia conclude (1) that the development of the avian hand is incompatible with a dinosaurian ancestry of birds. This conclusion, however, does not fit the data; the theropod manus has a unique and extraordinary pattern of digit reduction (1, 2) that must be based on a derived pattern of development. The identification by Burke and Feduccia (1) of the posterior digit in the avian hand as digit IV is based on the assumptions that digit IV is the first to develop, that the pattern of development in the avian hand is not extraordinary, and that the development of the avian foot and

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hand are equivalent. Because these assumptions are not correct for theropod dinosaurs, Burke and Feduccia have effectively assumed that birds are not dinosaurs, and the report's conclusion that they are not inevitably follows irrespective of the results of the experiments in the report, or of evolutionary history. Furthermore, these assumptions appear tautological—they are not independent of each other, nor of the conclusions reached in the report.

Shublin and Alberch (3) demonstrated that the ontogeny of all tetrapod limbs follows the same stereotypic pattern. Carpal

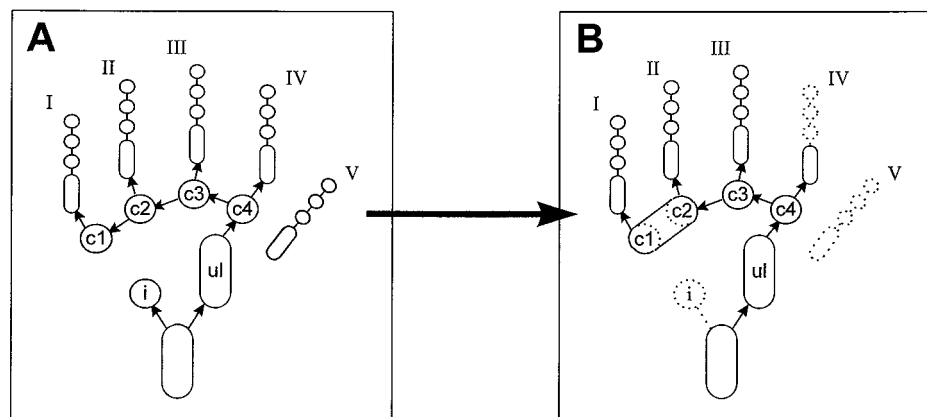


Fig. 1. (A) Development of the amniote hand. Elements developing from the radius are omitted for clarity. Bones develop from condensations of cartilage, that arise either de novo, from a Y-shaped branching event of another condensation, or from the distal budding of a cartilage condensation. Ulna gives rise to the intermedium (i), and the ulnare (ul), which in turn branches to produce a centrale (absent in crocodiles and dinosaurs) and the carpal IV (c4). Carpal IV then branches to produce metacarpal IV (and hence digit IV), and carpal III (c3), a process which is reiterated to generate the digital arch and further digits. Digit V arises from the de novo condensation of metacarpal V posterior to the ulnare (3). With the exception of theropods, digit loss occurs progressively from the anterior end of this chain (digit I), and from the isolated loss of digit V. (B) Development of the hand in early theropods. In the early theropod *Coelophysis bauri*, digit V is lost, carpals I and II are fused, reduction of digit IV is not yet complete, and the carpal and metacarpal can be seen (2). Dashed lines indicate lost or fused elements.

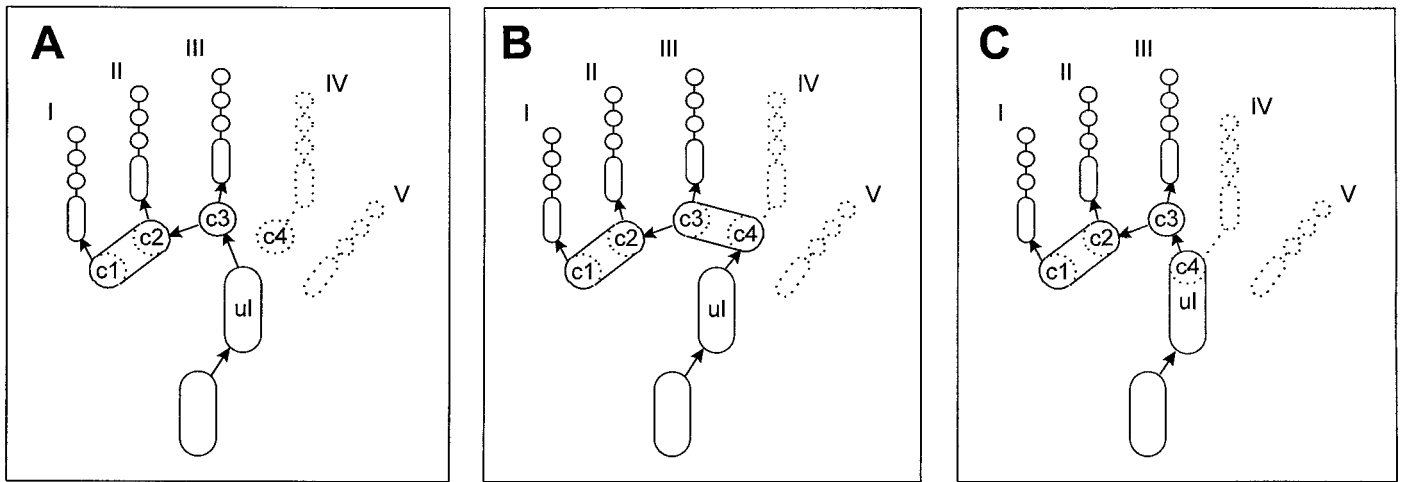


Fig. 2. Possible developmental programs responsible for the theropod hand. Labels as in Fig. 1. **(A)** Carpal IV condensation is progressively reduced, until the branching of the ulnare gives rise directly to carpal III. **(B)**

Ulnare branches to produce carpal IV, which gives rise to carpal III, but remains fused to it. **(C)** Ulnare gives rise to carpal IV, which remains fused to the ulnare.

IV is the developmental cornerstone of the hand: its Y-shaped branching to produce digit IV and carpal III initiates the digital arch (Fig. 1). The loss of digit IV and its associated carpal elements (2) makes the theropod manus extraordinary, for without carpal IV the remaining digits could not develop. The unique and extraordinary pattern of digit reduction in theropods implies a unique developmental pattern.

In later theropods, digit IV is completely reduced, and carpal IV is lost. In development, however, the digital arch must either pass through the cartilaginous precursor of carpal IV or be initiated with carpal III. Because carpal IV is not visible in the theropod wrist, its cartilaginous precursor must be subsumed within, or fused to, carpal III or the ulnare (Fig. 2). In either case, the ulnare would give rise to a distal condensation, which branches to form a digit and the

next carpal element in the digital arch; the first digit would be digit III, not IV, as in all other tetrapods (1). Burke and Feduccia's identification of this first digit as IV is based on the assumption that the first digit to develop is digit IV in birds as well as other tetrapods, but this is the very hypothesis that they are testing.

Furthermore, Shubin and Alberch (3) describe a unique pattern of development for digit V in birds. In all other tetrapods, digit V arises from a de novo condensation, but in birds it arises from a Y-shaped branching of the ulnare, exactly as if carpal IV does not separate from the ulnare (Fig. 2C). Labelling the posterior, transient digit as V rather than IV would require a fundamental rewriting of the developmental program, with the ulnare producing a trifurcation, the most anterior branch of which has been suppressed.

The developmental aspects of the avian hand reported by Burke and Feduccia are, despite their conclusion to the contrary, entirely consistent with a theropod origin of birds.

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Response: The identification in the report (1) of the digits of the avian hand as II-III-IV is based on a highly conserved pattern of development among amniotes (Fig. 1) and is at odds with a proposed theropod origin of birds. The comments by Chatterjee and by Garner and Thomas argue that the reigning hypothesis of avian origins renders our developmental interpretation impossible. Chatterjee cites the large number of synapomorphies uniting birds and dromeosaurid-theropods and then states "Burke and Feduccia apparently regard these similarities as convergence, not homology." Such a statement was not made in the report (1), although it was discussed in the accompanying Perspective (2). However, this criticism highlights an important aspect of our discussion. Convergence will be present in some characters, whichever

cladogram one favors. The convergence, wherever it may lie, is at least as interesting and important as the homologies, and deserves attention.

Chatterjee mentions that "the correspondence between primary axis and digit IV appears to break down" in salamanders, for example. This is correct, and for this reason we have limited our comparison to amniote patterns. It is also correct, in this regard, that the unusual mode of development of the urodele hand and foot is a precedent for alteration in developmental patterns. Salamanders are a remarkable exception. They do not represent a "simple" variation wherein the primary axis shifts to extend through digit II, as implied by Chatterjee. Salamanders violate the proximal to distal pattern exhibited by all other tetrapods and have no primary axis (*sensu stric-*

to). The polarity of this character in salamanders as opposed to frogs and amniotes has even lead to hypothesis about the parphyly of the Lissamphibia.

The characteristic pattern we describe in the report involves early cartilaginous condensations that form the anlagen of the skeleton during development. Actual ossification occurs long after the initial pattern forming stages, and subsequent patterns of fusion do not always reflect the original cartilaginous pattern. Therefore, without reversing causality, it is difficult to see how ossification of distal carpal elements could have an effect on a more rudimentary stage to the degree of shifting a developmental axis. The ulnare is present in avian embryos as a precartilagenous element that can be seen between the condensation of the ulna and a distal element that represents distal



Fig. 1. Early chick left forelimb bud showing the primary axis, which corresponds to digit IV. Image by S. Whitfield.

carpal and metacarpal IV. The fact that its individual identity is then obscured by later regression does not eliminate its initial significance based on connectivity.

Garner and Thomas center their criticism on the fact that the theropod hand is highly unusual and must represent a total

alteration on the stereotyped pattern we describe for amniotes. A radical change is certainly possible, but not necessary. The theropod hand is unusual, not because of the loss of digit IV, but because of the loss of digit I. It is the latter character that is most significant. We suggest that it is possible that the theropod hand developed in a fashion consistent with the early developmental pattern in other amniotes, with a primary axis running through digit IV. Subsequently during development, digit IV is totally reduced. As mentioned in our report, there are several extant lizards that have almost completely reduced digit IV [see the references in (3)].

The other issue raised by Garner and Thomas involves the development of digit V. In snapping turtles and alligators, digit V appears as a *de novo* condensation. Garner and Thomas cite the appearance of digit V as a branch off of the postaxial carpal element in chicks as evidence that it must actually be digit IV. In fact, digit V develops with strong connectivity to the postaxial carpal in mammals and in lizards, so a *de novo* appearance does not diagnose this digit.

In sum, one can argue that the primary axis shifted in birds and theropods during evolution, but at present there is no developmental data to support such a model. We have made our identification of avian

digits based on the conservation of developmental patterns seen in amniotes. To say that this pattern remains exactly the same in birds and other amniotes, except for the numbering of the digits, would seem to require "special pleading" and would be inconsistent with the observations and current evidence of comparative embryology. The relationship of birds and dinosaurs is an hypothesis, and our report points out an inconsistency in this popular idea.

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