

Tracing the Evolution of Avian Wing Digits Review

Xing Xu¹ and Susan Mackem²

It is widely accepted that birds are a subgroup of dinosaurs, but there is an apparent conflict: modern birds have been thought to possess only the middle three fingers (digits II–III–IV) of an idealized five-digit tetrapod hand based on embryological data, but their Mesozoic tetanuran dinosaur ancestors are considered to have the first three digits (I–II–III) based on fossil evidence. How could such an evolutionary quirk arise? Various hypotheses have been proposed to resolve this paradox. Adding to the confusion, some recent developmental studies support a I–II–III designation for avian wing digits whereas some recent paleontological data are consistent with a II–III–IV identification of the Mesozoic tetanuran digits. A comprehensive analysis of both paleontological and developmental data suggests that the evolution of the avian wing digits may have been driven by homeotic transformations of digit identity, which are more likely to have occurred in a partial and piecemeal manner. Additionally, recent genetic studies in mouse models showing plausible mechanisms for central digit loss invite consideration of new alternative possibilities (I–II–IV or I–III–IV) for the homologies of avian wing digits. While much progress has been made, some advances point to the complexity of the problem and a final resolution to this ongoing debate demands additional work from both paleontological and developmental perspectives, which will surely yield new insights on mechanisms of evolutionary adaptation.

Introduction

A limb with five digits is considered the ground state for tetrapod vertebrates (for terms and definitions, see [Figure 1](#)) [1,2]. However, numerous tetrapod lineages exhibit digit reduction in their evolutionary history, which is a dominant theme of the tetrapod limb evolution [3]. The most controversial case pertaining to digit reduction arises in the transition from ground-living dinosaurs to flying birds ([Box 1](#)). Birds have three highly modified fingers contributing to the formation of wings for flight; their Mesozoic tetanuran ancestors (for clade definitions, see [Figure 2](#)) have three clawed fingers, which evolved to form a grasping hand for predation. Although it is assumed that the three fingers of modern birds are homologous to those of the Mesozoic tetanurans, different sets of data have resulted in contradictory homology schemes: the crown avian clade (the Neornithes) are thought to retain the middle three fingers (II–III–IV) of an idealized five-digit tetrapod hand based on embryological data [4], but extinct tetanuran dinosaurians are thought to have the first three digits (I–II–III) based on paleontological data [5]. This conflict has led to one of the most hotly debated issues on homology in evolutionary biology [6] and has

been cited, albeit invalidly, as evidence against the dinosaur hypothesis for the origin of birds (e.g., [7]).

To date, the homologies of avian wing digits have been debated for nearly 200 years [8] and still continue to generate new discussion and contributions from different fields of research [9–13]. Adding to the complexity, some recent developmental studies support a I–II–III scheme for the homologies of avian wing digits [11,14] while some recent paleontological studies suggest a II–III–IV identification of the Mesozoic tetanuran fingers [10,15]. Resolving the conflict in digit homologies will have important implications for understanding the mechanistic basis by which evolutionary adaptations arise. The ongoing work to address this question highlights the importance of integrating data from different biological disciplines to address a complex evolutionary issue [4,6,10,16–19]. Such an integrative approach is likely to yield new insights relevant to both embryonic development and evolutionary biology.

In this review, we will compare several hypotheses that have been proposed to reconcile the digit homology paradox. Other possibilities, such as a I–II–IV or I–III–IV homology scheme for avian digits will be introduced, and most importantly, the developmental processes that may have contributed to shaping the evolution of the avian wing digits will be discussed.

Homologies of the Manual Digits of Birds and other Tetanurans

The three hand-digits of non-avian tetanurans have been traditionally identified as digits I–II–III. This is because the bipedal, theropod dinosaurs have generally been considered to exhibit an unusual lateral (posterior) rather than bilateral digital reduction pattern: comparing fossil records, the first digits reduced and lost were IV and V (digit IV is highly reduced and digit V is vestigial in basal theropods), a pattern also suggested to be present in birds [20] and certain species of skink [21,22], rather than loss of digit I and V, as in most other tetrapod lineages that have undergone digit reduction, such as amphibians, turtles, lizards and mammals [5,19,23,24]. Additional morphological evidence supporting the I–II–III identities includes the shortness of the first metacarpal and the manual phalangeal formulae of non-avian tetanurans (the three digits of basal tetanurans have the same 2-3-4 phalangeal formula of digits I–III in basal theropods) [5,19]. Because three-fingered birds are widely accepted to be descendants of extinct tetanuran theropods, [5,18], paleontology in general supports a I–II–III homology for avian wing digits [19,25].

However, the recent discovery of the four-fingered ceratosaurian *Limusaurus* [10] demonstrates the presence of a vestigial medial digit in at least some theropods (in fact, other ceratosaurian theropods also have a somewhat reduced medial digit [10,26,27]). Furthermore, close examination of the tetanuran hand (*manus*) has resulted in the discovery of features supporting II–III–IV identities for the manual digits of basal tetanurans. In fact, there is an uncoupling of morphological features in the hands of early tetanuran theropods (including the earliest known birds): most metacarpal features support a II–III–IV identification and most phalangeal features support a I–II–III identification for the three manual digits of basal tetanurans [10]. Consequently the available

¹Key Laboratory of Vertebrate Evolution and Human Origin of Chinese Academy of Sciences, Institute of Vertebrate Paleontology & Paleoanthropology, Chinese Academy of Sciences, Beijing, 100044 China. ²Cancer and Developmental Biology Laboratory, Center for Cancer Research, NCI-Frederick NIH, Frederick, MD 21702, USA. E-mail: xu.xing@ivpp.ac.cn (X.X.), mackems@mail.nih.gov (S.M.)

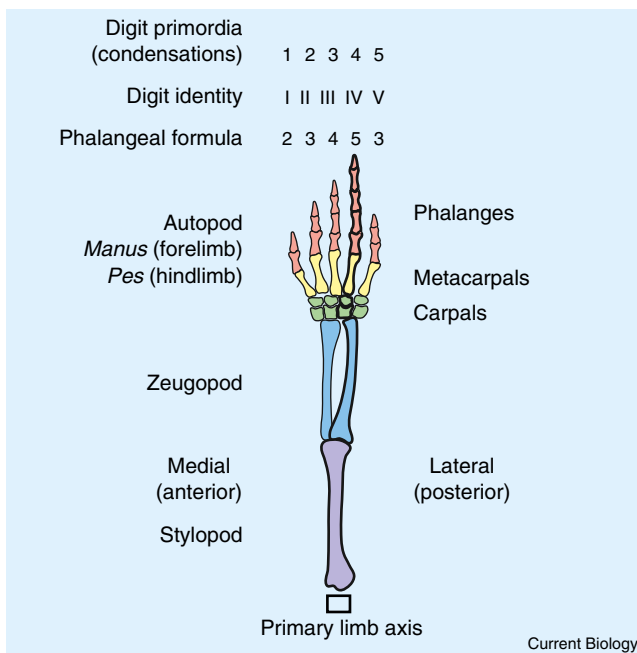


Figure 1. Diagram of components of tetrapod forelimb.

Representation of an 'idealized' five-digit ground state showing the primary limb axis (bold) and with developmental and paleontological terms compared. Roman numerals are used to indicate digit identities based on positional information (equivalent to primary homology statements for the digits). Arabic numerals are used to indicate digit progenitor (condensation) positions in early embryology, and ordinals refer to the digits actually present in a given taxon for which digit identities are unclear. Anterior and posterior are used to refer to the thumb and pinky borders of the hand when describing embryonic digit development, and medial and lateral when describing the evolution of adult digit morphology.

morphological information assessing the homologies of the manual digits of extinct tetrapod theropods is in itself contradictory, though a I-II-III homology seems to gain more support from this line of evidence [10].

The ambiguous homologies of the manual digits of extinct tetrapods can potentially be resolved by the parsimony principle. By applying the quantitative method of dynamic homology [28,29] to the available data, a parsimonious analysis shows that the II-III-IV scheme for the identifications of the manual digits of non-neornithine tetrapods, including early birds, is much more parsimonious than the I-II-III designation, under the assumption that extant birds have digits II-IV [10]. Consequently, paleontologists have turned to evidence from the morphological and developmental analysis of avian limbs to resolve this conundrum.

The wing digits of neornithines (modern day birds) have been identified as either digits I-II-III or II-III-IV based on different lines of data. Some morphological features, such as the shortness of the first metacarpal and the manual phalangeal formulae of certain neornithines, have been suggested to provide evidence supporting I-II-III identities [19]. However, although morphological criteria are useful in digit identification in mutant contexts within a species, finding universally conserved morphological features that can serve as indicators of digital identity widely across tetrapod vertebrates is problematic. For example, the number of phalanges in a given digit is often used as a marker of identity [30], but the phalangeal formula is developmentally plastic and is

highly variable among tetrapods [16]; although most mammals have digits with either two (thumb) or three phalanges (other fingers), this ranges from one up to 14 in finned marine mammals [31].

Inferring Digit Homologies from Development

Gene expression patterns have been used to identify digits, as their spatial domains are conserved developmentally, and in certain cases correlate well with specific digit precursors. Members of the *Hoxd* gene cluster are considered to be particularly relevant because genetic studies in mice have demonstrated they play a critical role in digit development [32], and their spatial expression domains are nested posteriorly in the limb bud. Except for *Hoxd13*, expression of these genes extends from the posteriormost digit V (pinky), but does not include the anterior-most digit I (thumb). Sonic hedgehog (*Shh*), a signaling factor expressed in cells in the posterior margin of the limb bud, called the zone of polarizing activity (ZPA), acts as a morphogen that controls both the identity and the number of digits that will form in the developing limb [33,34]. Exposure of posterior limb bud progenitors to the highest levels of *Shh* specifies them to become digit V, whereas digit I arises independent of *Shh* signals [33]. Descendants of the *Shh*-expressing ZPA cells later contribute to the posterior digits (IV and V in mice) [33]. As a key regulator of digit number and identity, as well as a potential marker for 'posterior' digits, *Shh* is another gene whose expression is highly relevant to assessing digit homology.

Some recent developmental data support I-II-III identities, including expression patterns of selected individual genes (such as *Hoxd12-8*, *Mkp3* and *Sef*) as well as more recent genome-wide expression profiles comparing different digits, and lineage tracing experiments of digits arising from Sonic hedgehog (*Shh*)-expressing cells [11,14,34-40]. In tetrapod model organisms, the first digit uniquely lacks expression of all 5' *Hoxd* genes except *Hoxd13*, and expresses several very anteriorly restricted genes. These expression profiles are conserved in the most anterior digit of avian wing, and in digit I of the avian foot as well as mouse and alligator. However, this association is strictly correlative: owing to functional overlap between *Hoxd* genes, the normal expression profile is not essential for digit I specification (e.g. [30,41,42]). Comparisons of gene expression profiles of different avian digit primordia by deep sequencing reveal a high correspondence across all genes between the first digit region of the wing and the digit I region of the hindlimb, lending more support to the view that the first digit in the avian wing corresponds to digit I [40].

Recent lineage tracing studies in chick [11,38] show that in the hindlimb only the most posterior/lateral digits (IV in chick) arise from the ZPA similar to mouse [33], whereas none of the chick wing digits include ZPA cells, supporting the conclusion that digits IV and V are absent [11,33,38]. However, an underlying assumption is that the extent of the *Shh* expression domain in the avian wing is unchanged from the five-digit limb, which may not necessarily be the case [43,44]. This I-II-III interpretation also requires an axis shift (see below) in which the primary limb axis now extends through digit III rather than digit IV in the avian wing.

Another way of assessing digit homology is the pattern of digit precursor condensations in embryos. The development of the limb skeleton is highly conserved among tetrapods [16,45]: it is characterized by an initial condensation of

Box 1

Identification of manual (hand) digits of major theropod clades.

Birds and crocodiles are two living lineages of the Archosauria, which includes the extinct Dinosauria and several extinct lineages (Figure 2). It is widely accepted that birds are a subgroup of the Dinosauria. More specifically, birds are nested within tetanuran theropods, which include such famous dinosaurs as *Tyrannosaurus rex* and *Velociraptor mongoliensis*. Birds are, therefore, tetanurans.

Tetanuran theropods have three fingers, but the three fingers of non-bird tetanurans are clawed and differ considerably from those of most birds. The four-fingered ceratosaurian theropods are the sister-group to the three-fingered tetanuran theropods. The first finger of ceratosaurians is reduced [8] and has no phalanges in some taxa such as *Aucasaurus* [9], and is completely vestigial in *Limusaurus* [10]. More basal theropods such as coelophysids have five fingers with a reduced fourth digit, and at least in *Coelophysis bauri* [5] a vestigial metacarpal V. Theropod manual digits are also identified based on anatomical position, morphology, and gene expression patterns. Although position is arguably the most definitive criterion for identifying and comparing homologous digits in different species, it is based on the assumption that the position of adult structures is unperturbed relative to early embryonic progenitors. In fact, when a central digit is removed genetically in the mouse embryo, the remaining digits come closer together in the mature skeleton, showing that positional identification can be difficult [54,55]. Given the variation in normal digit number and morphology of homologous digits between various classes of amniotes, universal criteria for comparing digit homologies are hard to define. Expression domains of developmental genes are another way to distinguish the identity of digits that look similar morphologically, as gene expression domains tend to be conserved during development of homologous structures. However, these comparisons also have limitations; unless there are genes that are essential to specify individual digit identities, expression profiles of genes used as 'markers' are necessarily only correlative, and cannot define digit identity.

pre-cartilage cells along the limb axis (shoulder to finger), which extends through the stylopod (humerus or upper arm) and the posterior zeugopod (ulna, posterior forearm) and this is termed the 'primary limb axis' (Figure 1). Digit IV is generally always the first and largest digit condensation to appear, as a direct continuation of the primary limb axis. Other skeletal elements (anterior forearm-radius, digits) arise secondarily relative to this primary axis. Hence, by monitoring the appearance of digit condensations in the embryo, digit IV can serve as a reference for the positional identity of other digit condensations. Contrary to morphological and gene expression data, the early condensation patterns of wing digit progenitors in birds support II-III-IV identities [4,6,8,9,17,45–53]. These studies suggest that the neornithine hand contains five digit pre-condensations of which the middle three are presumed to form the three wing digits of the adult bird, although the very transient, anterior-most of these appears very late developmentally and it has been disputed whether this element represents a digit precursor [11,49]. Four of the condensations are more clearly demonstrated by evidence of early chondrogenic differentiation (interpreted as II-V). Although these results have been considered to be conclusive [53], they assume that early transient structures represent vestigial digit condensations (not tendons, ligaments, etc.), and also that observed stable condensations are contiguous digits (i.e. digit loss only occurs from the anterior/medial or from posterior/lateral sides, not from the middle of the hand).

Another possibility for homologies of avian wing digits are I-II-IV or I-III-IV digit patterns, which would entail the loss of a middle digit, a scenario that has not been considered by paleontologists. Genetic modulation of Shh-signaling in mice results in the selective loss of middle digits [44,54,55]. Thus, from a developmental perspective, I-II-IV or I-III-IV digit homology patterns are also plausible and could reconcile the contradictory gene expression and condensation data for the avian wing. The I-II-IV or I-III-IV scheme would solve the problem of retaining the digit IV condensation that extends the primary limb axis, while at the same time retaining the medial digit with homology features of digit I in the three-digit adult, without necessitating identity

transformations in the course of evolution to explain how the dinosaurian digit I becomes avian wing digit II. Furthermore, at least in mice, newer approaches show that the middle digit (digit III) is the last condensation to form [54]. If a central digit is also the last to form in five-digit tetanurans, then a I-II-IV pattern for the remaining avian digits would also be congruent with Morse's law for evolutionary loss of structures: the last element to form during ontogeny (embryonic development) is the first to be lost in phylogeny (during evolution) [12,56].

In summary, despite recent advances, paleontological and developmental data offer some support to both sides of the debate. The bird wing digits are best identified as II-III-IV if adopting positional criteria, but as I-II-III based on some morphological and gene expression data; those of non-neornithine tetanuran dinosaurs can be inferred to represent digits II-III-IV based on the principle of parsimony under the assumption that extant birds have digits II-III-IV, but represent digits I-II-III if extant birds have digits I-II-III. Recent developmental studies also suggest new formulas (I-II-IV). The debate is basically derived from the conflict between different lines of data, which has also led to discussions on which criteria are more reliable [57]. While this paradox persists, several hypotheses have proposed developmental mechanisms that might reconcile the apparently conflicting avian and dinosaurian data.

Hypotheses for the Evolution of Theropod Manual Digits

Theropods are a group of primarily carnivorous, bipedal dinosaurs that reduced and lost their manual digits from the primitive five digits to three seen in tetanuran theropods. Several hypotheses aim to explain how this occurred and how evolutionary adaptation led to the digit features present in modern birds.

The 'axis shift hypothesis' assumes I-II-III identities for tetanuran manual digits. This hypothesis suggests that digit III in tetanuran hands developed precociously [58], so that the primary limb axis extends through digit III rather than through digit IV as in most other amniotes [6,45,58,59]. The axis shift hypothesis is supported by a recent lineage tracing study suggesting that the primary axis of the neornithine

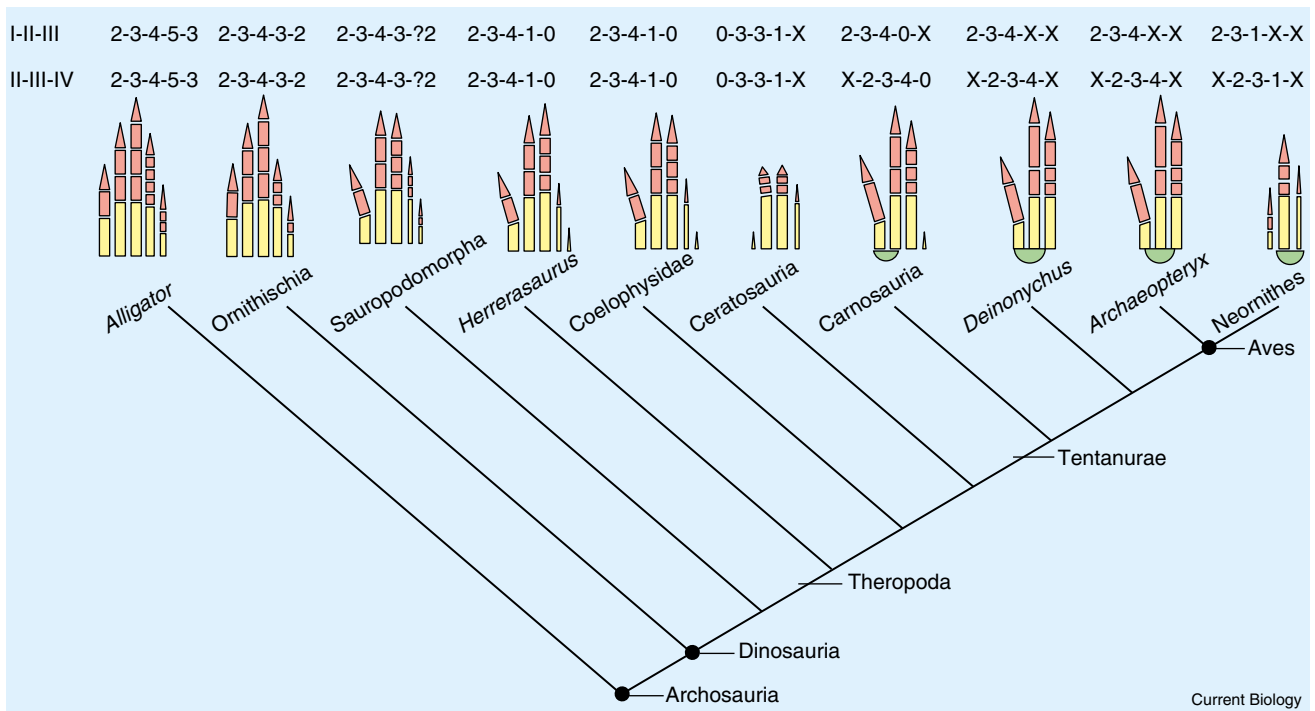


Figure 2. Hand evolution across theropod phylogeny.

The diagram shows a comparison of the I-II-III and II-III-IV identifications for the neornithine wing digits. The former relies on morphological information and selective spatial expression patterns of developmental genes and the latter emphasizes positional information. We adopt the following definitions of several higher-level dinosaurian taxa used in this paper: Theropoda, the most inclusive clade containing *Passer domesticus* [76] but not *Saltasaurus loricatus* [77]; Tetanurae, the most inclusive clade containing *Passer domesticus* [76] but not *Ceratosaurus nasicornis* [78] or *Carnotaurus sastrei* [79]; Aves, the least inclusive clade containing *Passer domesticus* [76] and *Archaeopteryx lithographica* [80]; Neornithes, the least inclusive clade containing *Struthio camelus* [76] and *Passer domesticus* [76].

forelimb extends through digit III [11]. However, its suggestion that the three manual digits of neornithines develop from positions 1, 2 and 3 is inconsistent with the accepted early condensation patterns for digit progenitors, which show that the three hand digits of adult neornithines develop from the three middle positions [9,16,38,51]. A remaining caveat is that traditional methods might not correctly reveal avian condensation patterns, which has turned out to be the case in mice using newer approaches [15].

The ‘pyramid reduction hypothesis’ assumes II-III-IV identities for neornithine manual digits and postulates the existence of a conservative five-digit pattern with a gradual, bilateral reduction of phalanges and metacarpals in avian evolution [9]. One proposed mechanism postulates that an elevation in peripheral *BMPs*, signaling factors that modulate cell survival and proliferation [60,61], drove bilateral medial and lateral digital reduction [9]. This hypothesis is developmentally plausible, and is also consistent with the phalangeal reduction pattern seen in basal birds [9,23]. However, it predicts that the direct avian ancestor had a five-fingered hand with dominant digits II, III, and IV [9], which is inconsistent with the digital reduction data from basal theropods (e.g., all known basal theropods, including ceratosaurs, have a vestigial digit IV) [5,62–64]. In fact, the pyramid reduction hypothesis implies that either birds are not descended from theropod dinosaurs, or that some as yet to be discovered basal theropods were five-fingered with dominant digits II, III, and IV.

The ‘polydactyl hypothesis’ assumes II-III-IV identities for tetanuran manual digits and suggests that limbs of the

Archosauria (Figure 2) were primitively polydactylous [49]. Under this assumption, the two small lateral digits of basal theropods are likely to be digits V and VI, and the three manual digits of neornithine and non-neornithine tetanurans would then represent digits II-III-IV [49]. However, there is no direct evidence for primitive polydactyly in archosaurs [49,65], and recent developmental studies instead strongly support a fundamental five-digit structure in living archosaurs and presumably in their common ancestor [53].

The ‘frameshift hypothesis’ and its variants accept I-II-III identities for tetanuran digits [12,13,19] and propose a mechanism in which theropod digit I-II-III morphologies arise from digits in positions 2–4, via simultaneous, complete homeotic transformations of three neighboring digits in theropod evolution [12,13,19]. In principle, a change in the *Shh* morphogen gradient in the limb bud could accomplish such a sudden simultaneous evolutionary change [37,55], as *Shh* levels regulate both digit number and digit identity in concert during limb development. Indeed, natural variation in digit number has been shown to correlate with altered duration of embryonic *Shh* expression in limb buds of different species of skinks with evolutionary loss of digits [43]. The original [19] and modified versions [12] of the frameshift hypothesis differ in the timing of the frame shift: the former suggests a shift in a three-fingered hand of early tetanuran theropods and the latter in a four-fingered hand of more basal theropods.

The ‘lateral shift hypothesis’ accepts II-III-IV homologies for tetanuran digits and suggests that the three functional manual digits took on features that primitively characterized more medial ones in theropod evolution via three

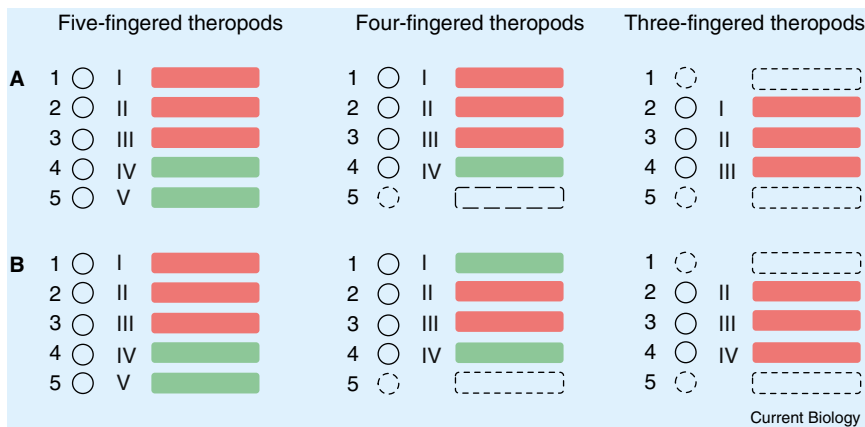


Figure 3. Frameshift hypothesis and lateral shift hypothesis.

Red shading refers to fully formed digits, green shading refers to highly reduced digits, and dashed lines indicate vestigial digits that are absent in the adult. Note that both the frameshift hypothesis (A) and lateral shift hypothesis (B) require re-emergence of a fully formed, functional digit at position 4. However, the lateral shift hypothesis suggests that the homeotic changes are piecemeal and incomplete, and thus digits II, III, and IV of the first three-fingered theropods are not identical to the digits I, II, and III of four-fingered theropods.

partial homeotic changes [10,15,66]. It suggests a three-stage scenario of manual evolution in theropods: first, reduction of digits IV and V near the base of the Theropoda; second, reduction of digit I by the point of divergence between ceratosaurs and tetanurans; third, complete loss of digit I and reappearance of a fully functional digit IV in early tetanuran evolution (Figures 2 and 3). The core proposal of the lateral shift hypothesis is that, while a frameshift took place, it was incomplete and piecemeal in nature [13], so that the transformed digits retained vestiges of their original morphology (Figure 3). The lateral shift hypothesis has been considered to be a modified version of the pyramid reduction hypothesis [12,13], but this reflects a misunderstanding of both. The pyramid reduction hypothesis requires a gradual, bilateral reduction of phalanges and metacarpals from a condition of five-fingered hand that has dominant digits II, III, and IV [9], while the lateral shift hypothesis suggests re-evolution of a fully functional digit IV by enlarging the small metacarpal IV in basal theropods and adding more phalanges, rather than losing phalanges.

In summary, the axis shift, pyramid reduction and polydactyl hypotheses are inconsistent with certain key developmental and/or paleontological data. The frame shift and lateral shift hypotheses can better explain the available data concerning the evolution of the theropod hand, if one accepts current views that the theropod fossil record accurately indicates that basal theropod digit reduction was entirely lateral-sided, that the primary limb axis extending through digit position 4 must be preserved during evolution, and that current methods for evaluating embryonic digit primordia provide an accurate picture of remaining digit positions in avian species. The frame shift and lateral shift hypotheses adopt different criteria for assessing primary homologies: the frame shift hypothesis relies on morphological information and selective spatial expression patterns of developmental genes, whereas the lateral shift hypothesis emphasizes positional information. However, the two hypotheses are similar, as both require genes that regulate digit pattern to shift their expression domains for the developing hand and the re-emergence of a fully functional digit in position 4, but differ in proposed mechanism of homeosis.

Homeosis and Theropod Hand Evolution

The frameshift hypothesis introduced homeosis to resolve the conflict between morphological and positional data [19]. In a strict sense, homeosis is defined as ectopic

development of a whole structure or organ, but some studies use it in a loose way, i.e., referring to homeosis as ectopic development of at least some features of a structure or organ [67]. Here we follow this loose definition.

The frameshift hypothesis requires a specific type of complete homeosis involving the simultaneous occurrence of complete homeotic transformation of three adjacent digits. Several recent studies suggest that homeotic changes are involved in the development of the neornithine hand [14,35–37]. Changes in the *Shh* morphogen gradient could in principle produce a seamless and simultaneous transformation to more anterior/medial identities of all digits, as has been proposed [37]. In fact, the effects of *Shh* dosage on digit number and identity can be uncoupled; there is clear evidence that *Shh* roles in regulating digit identity and digit number (proliferation) are temporally distinct: digit identity is specified by early, transient *Shh* activity and later attenuation of *Shh* activity in the limb bud impacts only digit number [34,54]. The natural variation in digit number without associated transformations in digit identity in different skink species correlates with altered duration of *Shh* expression [43]. Likewise, shortening the duration of *Shh* expression in mice reduces digit number without identity transformations [54]. These studies argue that *Shh* can be modulated to reduce digit number without affecting identity of remaining digits; however, the converse does not occur: any ‘early’ change in *Shh* that affects identity will necessarily also reduce digit number [68]. Consequently, a change in *Shh* activity level during theropod evolution as envisioned in the frameshift hypothesis would necessitate the simultaneous, rather than sequential, loss of posterior digits, re-emergence of a robust digit 4 condensation and medial/anterior identity shifts.

Some recently obtained fossil data are not supportive of the frameshift hypothesis. The frameshift hypothesis postulates a seamless change in the structure of the three functional digits, so that the digits that develop in positions 2–4 in tetanuran theropods are morphologically identical to digits I–III of more basal theropods [12,13]. However, the hands of basal tetanurans possess a combination of features originally associated with digits I–II–III and II–III–IV, respectively, i.e., most metacarpal features supporting II–III–IV identities and most phalangeal features supporting I–II–III identities [10]. This demonstrates that any homeotic shift at the base of the Tetanurae must have been incomplete. Also, it is difficult to identify plausible selective pressures that would drive this type of homeotic shift, considering that the post-frameshift adult hand

would be morphologically identical to the pre-frameshift condition [69].

The lateral shift hypothesis postulates that the homeosis was partial and piecemeal. In fact, partial homeosis is an important factor in the morphological diversity among the major groups of multicellular eukaryotes, including plants [67] and mammals [70]. Moreover, in contrast to classic examples of complete homeosis [71], Hox genes are involved in determining both digit morphologies and digit number and both roles involve the regulation of growth of elements [72,73], suggesting that anatomical features of digit identity may be achieved by differential proliferation rather than a homeotic 'selector' type of function. This suggests that partial dissociation between positional and phenotypic identities is at least equally plausible as complete dissociation, and partial dissociation has indeed been observed in some experimental animals [19].

The lateral shift hypothesis fits better with the distribution of manual morphological characters across the currently accepted theropod phylogeny. As mentioned above, a combination of manual features supporting both I-II-III and II-III-IV identities in basal tetanurans suggests that the homeosis is incomplete. Furthermore, the mostly unchanged nature of the metacarpals but changed morphologies of associated phalanges are consistent with the proximal-to-distal temporal progression of developmental patterning of tetrapod digits [30,74], and a late-acting developmental signal might have repatterned the tetanuran phalanges selectively [10]. Such a late-acting developmental signal could provide a mechanistic basis for a partial homeosis. Interestingly, a second, independent homeotic change appears to have contributed to the evolution of the foldable avian wing given that this involved a shift in the position of the 'semilunate' carpal from the medial to the lateral side of the hand in tetanuran evolution (Figure 2) [75].

Compared to the frameshift hypothesis, the Lateral Shift Hypothesis is also more plausible from the perspective of adaptation. The unusual lateral reduction of the theropod manual digits has been interpreted as a consequence of a functional constraint favoring retention of a grasping hand [19]. However, the forelimbs of *Limusaurus* and other ceratosaurian theropods almost certainly had no predatory function [10]. Consequently, it is possible that the functional constraint associated with predation relaxed near the base of the Ceratosauria–Tetanurae clade, resulting in the reduction and loss of digit I as dictated by the conservative developmental pathway for digit loss among amniotes [16,45,56]. Subsequently, the hand in tetanuran theropods would have re-evolved features for a grasping hand.

Homeosis represents a plausible route for theropod hand evolution and recent developmental and genetic studies have revealed possible mechanisms for the inferred shift in developmental regulation of morphological features from positions 1, 2, and 3 to 2, 3, and 4 [12,21,37,38]. Comparatively, partial and piecemeal homeosis as postulated by the lateral shift hypothesis seems to be more likely to have occurred in theropod hand evolution than complete homeosis based on a comprehensive analysis of both paleontological and developmental data.

Future Directions

The evolution of the theropod hand is a complex process. While there is still debate over whether I-II-III or II-III-IV homologies for tetanuran manual digits are more valid, new

possibilities are also worth considering. For example, given the developmental plausibility of central digit loss, it would be of interest to re-examine the tetanuran fossil record and assess whether a I-II-IV or I-III-IV homology may be even more parsimonious than the II-III-IV proposed by the lateral shift hypothesis.

Several models have been proposed to interpret theropod hand evolution in light of the contradictory interpretations of avian wing digit homologies, but a fully consistent and plausible developmental–evolutionary scenario has yet to be proposed. It will be particularly important to determine how loss of condensation 1 in archosaurs may have driven the evolution of the developmental program for digit specification. From a paleontological perspective, better taxon sampling near the base of the Tetanurae will be critical for testing the lateral shift hypothesis and frameshift hypothesis. Because the lateral shift hypothesis predicts that the loss of digit I was a key event in the evolution of the tetanuran hand, more taxa with a highly reduced digit I are expected to be present near the base of the Tetanurae.

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