Comment on "Embryological evidence identifies wing digits in birds as digits 1, 2, and 3."

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Tamura et al. (Science, 11 Febuary 2011, p. 753) claim that the three avian wing digits should be identified as digits I-III based on new embryological data and suggest that these identifications help to remove the conflict between the paleontological data and developmental data concerning the homology of the avian digits. However, their results are not novel, and the authors fail to address the critical problems relating to this interesting issue.

Tamura et al. [1] provide embryological data on digital development in living birds. They claim that the three avian wing digits should be developmentally identified as digits I-III and suggest that these identifications help to remove the conflict between the paleontological data and developmental data concerning the homology of the avian digits. While Tamura et al. present information of significance, their study fails to address larger questions of digit homology and the paleontological record.

First, the authors state without discussion that paleontological data indicate the loss of digits IV and V in extinct and living tetanuran theropods, but they do not mention published evidence to the contrary. Previous studies have provided morphological evidence supporting a II-III-IV identification for the three manual digits of extinct tetanuran theropods [2]. Our recent study demonstrates a decoupling of morphological features in the hands of extinct 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 [3]. The updated paleontological data thus clearly contain two contradictory signals relating to the identification of the tetanuran manual digits. The strikingly conservative phalangeal formula of 2-3-4 seen in tetrapods has been given primacy in identifying these digits as I-II-III, overshadowing other morphological features that favor the II-III-IV identification. The significance of the latter evidence for the problem of digital identification was only recognized following the recent discovery of the unusual theropod *Limusaurus*, which has a vestigial digit I [3].

Second, some important embryological data have not been fully appreciated by Tamura et al., which weakens the significance of their study. Given that several recent embryological studies also support the I-II-III hypothesis [4, 5], the authors' identification of the avian wing digits as I-II-III is not novel. Furthermore, except the embryological evidence from the primary limb axis, there are other lines of evidence supporting a II-III-

IV identification for the avian wing digits [6, 7]. Tamura et al.'s refutation of “the primary axis-digit D4 hypothesis” has weakened the developmental evidence for the II-III-IV hypothesis, but is far from representing the final word on the identities of the avian wing digits.

Paleontological and developmental data concerning the identifications of the avian wing digits are not simply in direct conflict, as the authors claimed [1]. Instead, the I-III-III and II-III-IV hypotheses can each claim some support from both paleontological and developmental data. There must have been complex changes in the development and evolution of the hand of theropods on the lineage to modern birds.

Finally, in assessing different digital homology hypotheses, it might not be proper to use anatomical features as the main criterion, as the authors did [1]. Positional information is often the main operational criterion for delineating statements of primary homology [8], though caution is warranted because positional information can be as ambiguous for homology assessment as morphological and developmental information, particularly in the case of serially repetitive structures. In the tetrapod autopodium, however, the conservative pentadactyl pattern provides unambiguous positional information for digital identities. The extant avian wing digits are clearly identified as digits II-II-IV based on the observed congruence between the ossified digits and the condensations observed in the development of an avian embryo. In comparison, developmental and morphological features of the digits are ambiguous in providing digital identity. For example, in those avian embryos in which the phenotypes of digits I and II are experimentally induced in positions III and IV, a vestigial digit medial to phenotype digit I sometimes remains [9]; and in extinct tetanuran theropods, manual digits display a mixture of anatomical features favoring different identifications [3]. Consequently, Tamura et al.’s conclusion that both extant and extinct tetanuran theropods have digits I-II-III based on new embryological evidence is not necessarily justified.

However, the available data do show an interesting pattern: some developmental and morphological features have shifted their expression positions in a coordinated fashion, a phenomenon usually called a "frame shift". How this shift occurred in developmental and evolutionary terms is key to our understanding of the evolution of the avian wing digits. The research findings of Tamura et al. do little to elucidate the evolutionary timing of the presumed digital “frame shift,” nor do they resolve whether this “shift” was a sudden, discrete event or a piecemeal transition. Although the early development of the manus in theropods has no known fossil record, rigorous assessment of these two questions must explain paleontological findings as well as developmental evidence.

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