Reply to "*Limusaurus* and bird digit identity"

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Vargas et al. agree with us that a lateral shift in theropod dinosaur digits occurred prior to the origin of birds, but contend that it occurred as a single "frameshift" with little outward change to the three main digits involved[1]. We consider the digital morphology of *Limusaurus*, other ceratosaurs, and non-avian tetanurans to provide evidence that the shift was stepwise, and that a stepwise shift better explains theropod maual morphology than a hidden frameshift.

Morphological data from extinct theropods, even without considering *Limusaurus* and ceratosaurs, clearly contains two contradictory signals for the identification of tetanuran manual digits. Thus, neither our hypothesis nor the frameshift hypothesis is able to avoid a substantial number of homoplasies. The discovery of *Limusaurus* led us to re-examine all available data, including gene expression, morphology, and embryology, regarding the homologies of the tetanuran manual digits, which together indicate the II-III-IV hypothesis is more parsimonious than the I-II-III hypothesis. The basal ceratosaur *Limusaurus* is best explained as displaying an intermediate condition rather than being derived.

Vargas et al. decry our use of all of the data to identify bird digits as II-III-IV, preferring instead to consider morphology (identity) and position as being completely separate categories of homology[1]. We recognize that homeotic shifts in identity are possible, but we do not agree that in this situation a homeotic shift should be assumed to have occurred. The assumption of a homeotic shift is the basis of their frameshift hypothesis, and we suggest that other modes of evolution should be considered.

Experimental manipulations of embryos show the presence of homeotic changes in avian digital development[2, 3], but it remains unclear why these observations should imply that a gradual transition is less plausible than a quantum and complete shift. For example, in those embryos in which the phenotypes of digits I and II are experimentally developed in positions III and IV a vestigial digit medial to phenotype digit I sometimes remains[2], and Hox expression patterns in vertebrae do not have rigid phenotypic boundaries[4]. Moreover, unlike classic examples of homeotic changes, such as segmentation in *Drosophila*[5], Hox genes are involved in determining both digit number and digit identity rather than just identity[6]. Rather than assuming that suites of digital morphology shifted en masse from one embryological position to another, we suggest that each digit underwent morphological change in response to developmental signals of evolutionarily variable strength.

Vargas et al hypothesize that the course of theropod hand evolution involved a saltational shift such as the one they produced experimentally[2], a shift unrecognizable in the morphology of the three main digits of theropods. Our hypothesis instead recognizes evidence for a stepwise change, such as the reduction of the first digit in ceratosaurs and newly recognized metacarpal features. As fans of Sherlock Holmes we concede that sometimes a lack of evidence, like a dog that doesn't bark in the night[7], can be informative. However, Holmes also inveighed against holding too tightly to preferred hypotheses in the face of contradictory evidence.

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