



CLADISTICS AND THE ORIGIN OF BIRDS: A REVIEW AND TWO NEW ANALYSES

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ABSTRACT.—The hypothesis that birds are maniraptoran theropod dinosaurs (the “BMT hypothesis”) has become widely accepted by both scientists and the general public. Criticism has usually been dismissed, often with the comment that no more parsimonious alternative has been presented with cladistic methodology. Rather than taking that position, we ask here whether the hypothesis is as overwhelmingly supported as some claim. We reanalyzed a standard matrix of 46 taxa and 208 characters from a recent paper by Clark, Norell, and Makovicky, and we found statistical support for the clades Coelurosauria and Maniraptoriformes and for a clade of birds and maniraptorans. Note, however, that because the matrix contains only birds and theropods, it assumes that the origin of birds lies within the Theropoda. In addition to this problem, Clark et al.’s (2002) matrix contains problematic assumptions of homology, especially in the palate, basipterygoid, manus, carpus, and tarsus. In an attempt to avoid these two major problems and to evaluate the BMT hypothesis and four alternative hypotheses in a comparative phylogenetic framework, we followed the recommendations of Jenner, Kearney, and Rieppel by constructing and analyzing a larger but more conservative matrix. Our matrix includes taxa from throughout the Archosauria. When the ambiguous characters were excluded, parsimony analyses with bootstrapping and successive pruning retrieved a weak clade of birds and core maniraptorans (oviraptorosaurs, troodontids, and dromaeosaurs) that also contained the early archosaur *Longisquama* and was not unambiguously associated with other theropods. When the ambiguous characters were included but coded as unknown where appropriate, the results were virtually identical. Kishino-Hasegawa tests revealed no statistical difference between the hypothesis that birds were a clade nested within the Maniraptora and the hypothesis that core clades of Maniraptora were actually flying and flightless radiations within the clade bracketed by *Archaeopteryx* and modern birds (*Aves*). Additional statistical tests showed that both the “early-archosaur” and “cro-dylomorph” hypotheses are at least as well supported as the BMT hypothesis. These results show that Theropoda as presently constituted may not be monophyletic and that the verificationist approach of the BMT literature may be producing misleading studies on the origin of birds. Further research should focus on whether some maniraptorans belong within *Aves*, and whether *Aves* belongs within Theropoda or is more closely related to another archosaurian taxon. At present, uncertainties about the hypothesis that birds are maniraptoran theropods are not receiving enough attention. Received 28 July 2008, accepted 25 January 2009.

RESUMEN.—La hipótesis de que las aves son dinosaurios maniraptos terópodos (la teoría de BMT) ha sido extensamente aceptada por científicos y el público en general. Críticas en contra de esta hipótesis han sido usualmente rechazadas basándose en el hecho de que una alternativa mas parsimoniosa no ha sido presentada usando metodología cladística. Nosotros cuestionamos si la hipótesis esta realmente tan bien respaldada como ha sido indicado previamente. Se reanalizó una matriz estándar de 46 taxones y 208 caracteres basados en el artículo publicado por James Clark, Mark Norrell y Peter Makovicky, encontrando resultados estadísticos positivos que respaldan los clados de Coelurosauria y Maniraptoriformes y para los clados de aves y Maniraptora. Sin embargo, es importante notar que ya que la matriz contiene solamente aves y terópodos, esta

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