

# Comment on “A Well-Preserved *Archaeopteryx* Specimen with Theropod Features”

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On the basis of new information from the 10th specimen of *Archaeopteryx*, Mayr *et al.* (Reports, 2 December 2005, p. 1483) suggested that birds, or avian flight, originated twice. We investigate the statistical support for this phylogenetic hypothesis and show that it is no better supported by available morphological character data than the hypothesis of a single avian origin.

In a recent report, Mayr *et al.* (1) provided information on a new specimen of *Archaeopteryx* and posited a new classification of derived coelurosaurian theropods in which Aves (2) was either polyphyletic or required expansion to include deinonychosaurs, a clade previously considered to be nonavian dinosaurs. This novel phylogenetic hypothesis requires a complex pattern of parallel gains and/or secondary losses of flight and other “avian” features in the theropod-bird lineage. Given the controversial nature of a hypothesis suggesting that either birds, or avian flight, originated twice, we reexamined the evidence for their conclusions by determining support for the proposed phylogeny, carrying out statistical comparisons of the fit to the data between their hypothesis and competing alternatives, and investigating characters supporting the novel relationships suggested.

The new material (1) reveals osteological information unavailable from other *Archaeopteryx* specimens, permitting rescaling of eight morphological characters within an existing character matrix (3) used to resolve coelurosaur interrelationships. This principally alters the systematic relationships of *Confuciusornis*, which is no longer recovered as the sister taxon to *Archaeopteryx* within a monophyletic Aves, but placed as the sister taxon to *Microraptor*, within the dromaeosaurid clade.

We examined the relative support provided by the phylogenetic analysis of Mayr *et al.* (1) for both monophyletic and polyphyletic Aves using bootstrap proportions (4) and decay analysis (5). In general, support for the phylogeny of Mayr *et al.* is weak (Fig. 1), with that for the newly proposed clade *Microraptor*+*Confuciusornis* particularly low: Bootstrap proportions indicate that a monophyletic Aves (containing *Archae-*

*opteryx*, *Rahonavis*, and *Confuciusornis*) is recovered in more of the bootstrap replicate data sets. To examine differences in fit to the data (1) of the competing hypotheses, we used an analysis (6) in which Aves was constrained to be monophyletic. This recovered 768 constrained trees of 600 steps, just one step longer than those from the unconstrained analysis (7). We then used the nonparametric Templeton test (8) to compare the fit of polyphyletic (unconstrained) and monophyletic (constrained) avian topologies to the data. The range of probability values obtained from pairwise comparisons ( $P = 0.819$  to  $0.853$ ) indicates that the null hypothesis (9) cannot be rejected and that there is insufficient data to choose among the two alternative phylogenetic hypotheses (10).

We carried out additional analyses using more recent versions of the Theropod Working Group’s phylogenetic data matrix (11, 12), modified by the codings suggested by Mayr *et al.* (1). Although the modified analysis of (11) results in a polyphyletic Aves (13), use of a Templeton test to compare constrained (monophyletic Aves) and unconstrained trees (14) indicates that there is insufficient evidence to reject a monophyletic Aves ( $P = 0.8084$  to  $0.8474$ ). Recoding (12) did not affect the topology or number of most parsimonious trees (MPTs) recovered; *Confuciusornis* and *Archaeopteryx* group together, whereas *Rahonavis* is recovered within Dromaeosauridae rather than Aves.

Using MacClade (15), we examined the distribution of characters (16) on the strict consensus trees of Mayr *et al.* (1) and Hwang *et al.* (3). Of the five characters (17) that unambiguously support *Microraptor*+*Confuciusornis* within Dromaeosauridae, the scoring of character 111, a separate or fused scapula and coracoid, is controversial (18). Of the two characters (19) uniting *Archaeopteryx*+*Confuciusornis* in a monophyletic Aves in (3), co-ossification of the metatarsals—character 166 (20)—is also problematic (21). After consideration of other specimens (22), we reverted to the scorings of (3) for *Archaeopteryx* for characters 111 and 166 but kept other rescorings as in (1). This results in

avian monophyly with identical trees, tree lengths, and strict consensus topology to (3). Recoding of just two disputable characters in *Archaeopteryx* is sufficient to explain the hypothesis of avian polyphyly presented by Mayr *et al.* (1).

The new *Archaeopteryx* specimen provides valuable information on the morphology of basal birds and the relationships of taxa across the theropod-bird transition. However, Templeton tests and bootstrap analyses indicate that the hypothesis of a polyphyletic Aves is no better supported by available data than that of a monophyletic Aves. That alternative codings of *Archaeopteryx* for two controversial characters shift the resulting phylogenetic hypothesis between a monophyletic and polyphyletic Aves emphasizes the lack of robustness. We conclude that statistical support for the novel hypothesis of Mayr *et al.* (1) is weak and that there is little current consensus as to the relationships between *Archaeopteryx*, *Rahonavis*, and *Confuciusornis* within Coelurosauria (Fig. 2), complicating attempts to trace the sequence of character acquisitions during the origin of flight. In noting this, we hope to draw attention to the need for further work on coelurosaurian anatomy and phylogeny.

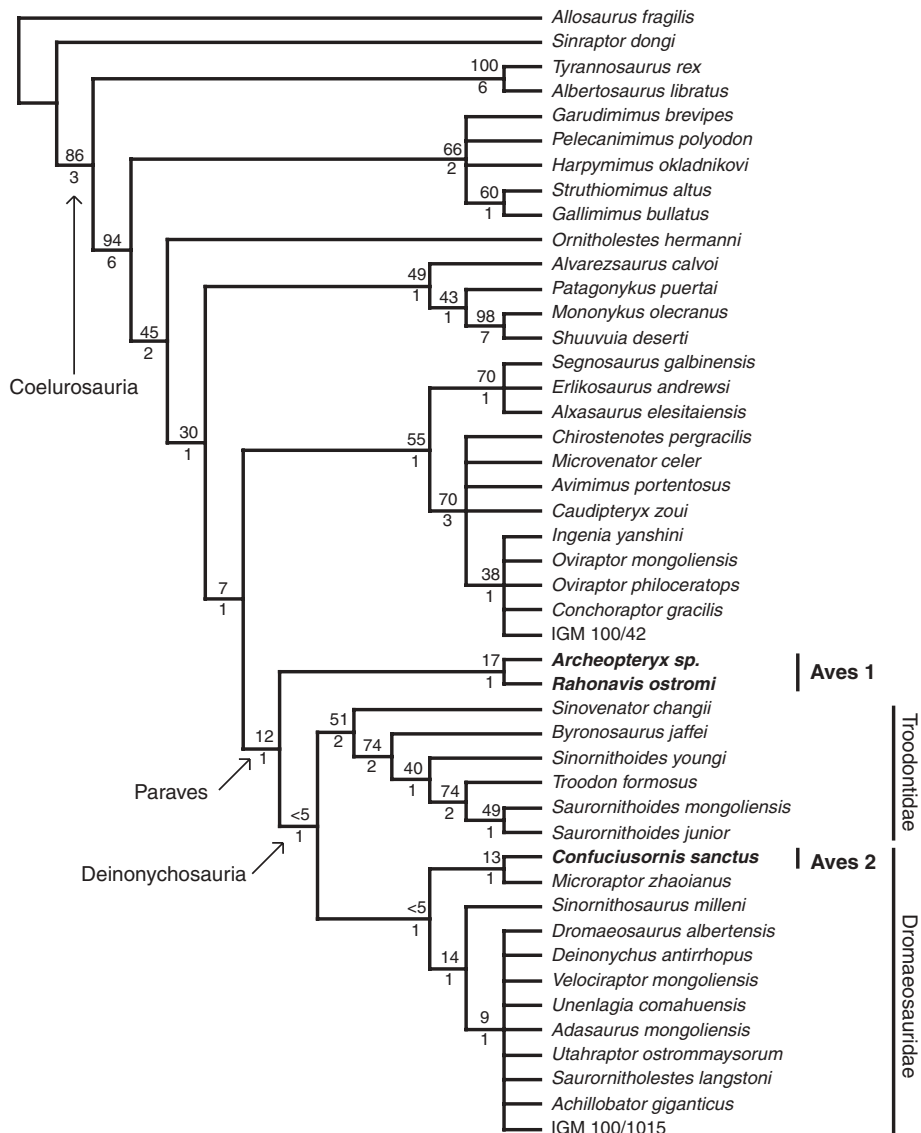
## References and Notes

1. G. Mayr, B. Pohl, D. S. Peters, *Science* **310**, 1483 (2005).
2. Aves as currently conceived contains the Mesozoic “birds” *Archaeopteryx*, *Rahonavis*, and *Confuciusornis* but excludes deinonychosaurian theropods (23).
3. S. H. Hwang, M. A. Norell, H. Gao, *Am. Mus. Novitat.* **3381**, 1 (2002).
4. J. Felsenstein, *Evol. Int. J. Org. Evol.* **39**, 783 (1985).
5. K. Bremer, *Evol. Int. J. Org. Evol.* **42**, 795 (1988).
6. D. L. Swofford, *PAUP\* Version 4.0b10* (Sinauer Associates, Sunderland, 2002).
7. The analyses of (1) and (3) used NONA (24) and collapsed branches with a minimum length of zero, which can result in trees that are not of minimal length. This was replicated in PAUP using the setting “Collapse branches if minimum length is zero (amb-).” Filtering these trees in PAUP for the best score retains only the MPTs. For example, the analysis of (1) constrained with a monophyletic Aves recovered 206,550 MPTs. Condensing by collapsing branches with a minimum length of zero returned 768 trees; filtering these by best score resulted in 120 MPTs. The resulting strict consensus was topologically similar to that of (1), other than a decrease in resolution within the clade Troodontidae. Condensed tree numbers are reported in the text for comparison with the original results of (1) and (3), but the condensed and filtered MPTs are used for Templeton test analyses.
8. A. R. Templeton, *Evol. Int. J. Org. Evol.* **37**, 221 (1983).
9. The null hypothesis of the Templeton test is that differences between the trees in their fit to the data are no greater than expected from random sampling error.
10. Constraining *Microraptor* and *Confuciusornis* together in an analysis of the data presented by Hwang *et al.* (3) resulted in 136 constrained MPTs of step-length 603 after condensing and filtering. The range of probability values ( $P = 0.491$  to  $0.568$ ) obtained from a Templeton test comparing these trees with the 36 condensed and filtered trees from unconstrained analysis of (3) indicates that for the original data set, unmodified by the codings

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**Fig. 1.** Clade support on the strict consensus tree of (1). Bootstrap proportions are above the branch, decay index values below. The 50% majority rule bootstrap tree was poorly resolved, so the bipartition table was used to identify support for the relationships considered. Important results for the phylogeny presented in (1) include bootstrap proportions for *Microraptor*+*Confuciusornis*, 12.5%; for *Archaeopteryx*+*Rahonavis*, 16.9%; for a monophyletic Aves (*Archaeopteryx*+*Rahonavis*+*Confuciusornis*), 14.2%, which is higher than the grouping *Microraptor*+*Confuciusornis*; for *Microraptor*+*Sinornithosaurus*, 16.1%, also higher than *Microraptor*+*Confuciusornis*. Decay indices are very low (1) for both *Microraptor*+*Confuciusornis* and *Archaeopteryx*+*Rahonavis*. Average bootstrap proportion, 47%; average decay index, 1.93.

16. Although it is stated (3) that character descriptions are available online at <http://research.amnh.org/vertpaleo/norell.html>, this is not the case. Similarly, the character descriptions in (25), supposedly taken from (3), do not match those found at <http://research.amnh.org/~sunny/datasets.html>. We used the latter.
17. The five characters are 111, 123, 164, 165, and 171. Characters 123, 164, and 165 are uncontroversial. However, character 171, a reversed first toe, although absent in the new specimen, is not a definite feature of the Archaeopterygidae as a whole. The London and Eichstätt specimens offer conflicting evidence.
18. Character 111 was rescored by Mayr *et al.* (1) from fused (1) to (?) in *Archaeopteryx* and optimized as separate (0); it may, however, be fused in late ontogeny in *Archaeopteryx* (22). Considering this evidence and reverting to the scoring of Hwang *et al.* (3) for this character, but keeping all other recodings as suggested by Mayr *et al.* (1), results in 528 trees of 600 steps; the strict consensus has a polytomy between *Archaeopteryx*, *Rahonavis*, *Confuciusornis*, *Microraptor*, Troodontidae, and Dromaeosauridae, plus decreased resolution within Troodontidae. The coding of this homoplastic character (it requires 5 steps on the strict consensus tree of (1) and has a low consistency index value of 0.2) clearly affects the phylogenetic hypotheses inferred from the data.
19. Characters 165 and 166. Character 165, distal tarsal separation, changes from supporting *Archaeopteryx*+*Confuciusornis* in (3) to supporting *Microraptor*+*Confuciusornis* in (2), but the derived state (1), distal tarsals fused to metatarsals, is present in all three taxa.
20. Character 166. Metatarsals not co-ossified (0), or co-ossification of metatarsals begins proximally (1) or distally (2).
21. Character 166 was recoded in (1) from (1) to (0); (22) indicates that, although there is no evidence for proximally beginning metatarsal co-ossification, the metatarsals may have been superficially or incompletely co-ossified in some specimens. The character as currently conceived cannot represent this information. Reverting to state (1) as coded in (3) for character 166, but keeping the other recodings of (1), results in the same trees and strict consensus as when carried out for character 111 (18). Both characters 111 and 166 are osteological fusion characters, and as such are potentially prone to ontogenetic and intraspecific variation, leading to difficulties in coding observed variation in a phylogenetically meaningful way.
22. A. Elzanowski, in *Mesozoic Birds: Above the Heads of Dinosaurs*, L. M. Chiappe, L. M. Witmer, Eds. (Univ. of California Press, Berkeley, 2002), chap. 6.
23. K. Padian, in *The Dinosauria*, D. B. Weishampel, P. Dodson, H. Osmolska, Eds. (Univ. California Press, Berkeley, 2 ed., 2004), chap. 11.
24. P. Goloboff, NONA (NO NAME), ver. 2. Published by the author, Tucumán, Argentina, 1999.
25. J. M. Clark, M. A. Norell, P. J. Makovicky, in *Mesozoic Birds: Above the Heads of Dinosaurs*, L. M. Chiappe, L. M. Witmer, Eds. (Univ. California Press, Berkeley, 2002), chap. 3.
26. L. M. Chiappe, in *Mesozoic Birds: Above the Heads of Dinosaurs*, L. M. Chiappe, L. M. Witmer, Eds. (Univ. California Press, Berkeley, 2002), chap. 20.
27. C. A. Forster, S. D. Sampson, L. M. Chiappe, D. W. Krause, *Science* **279**, 1915 (1998).
28. We thank P. Barrett, M. Benton, S. Braddy, L. Sällä, M. Wilkinson, and two anonymous referees for comments on a previous version of this paper.

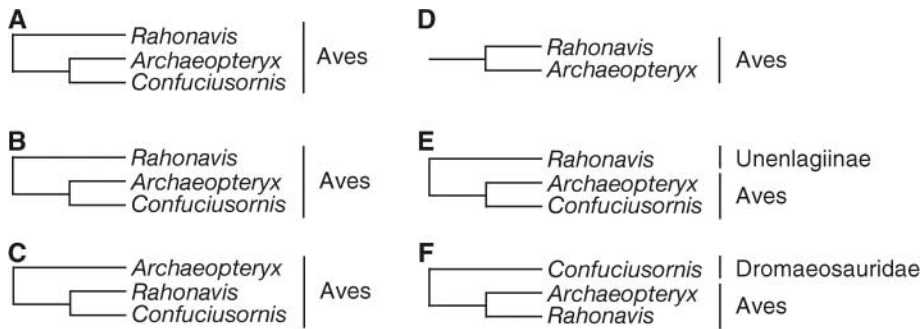
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10.1126/science.1130800

suggested in (1), there is insufficient data to reject the alternative hypothesis of avian polyphyly.

11. S. H. Hwang, M. A. Norell, Q. Ji, K. Gao, *J. Syst. Pal.* **2**, 13 (2004).
12. P. J. Makovicky, S. Apesteguia, F. L. Agnolin, *Nature* **437**, 1007 (2005).
13. Analysis of the modified data set resulted in 864 trees of 627 steps, compared with the 2592 trees of 629 steps from the original analysis presented in (1). The strict consensus resembles that of (1) in positioning

*Confuciusornis* as the sister taxon to *Microraptor* instead of in the monophyletic Aves from the unmodified data set. Constraining Aves as monophyletic on this modified data set returns 1727 constrained trees of 628 steps.

14. Because of the large number of trees, each individual tree was not considered; rather, every 10th of the 160 trees was compared to the 280 trees.
15. D. R. Maddison, W. P. Maddison, *MacClade 4: Analysis of phylogeny and character evolution* (Sinauer Associates, Sunderland, MA, 2003), version 4.06.



**Fig. 2.** The relationships of the three avian taxa considered in (1) are subject to considerable uncertainty. Examining six recent phylogenies, all possible combinations of relationship are seen across either a monophyletic Aves or within Paraves (other taxa are not shown). **(A)** Hwang *et al.*, 2002 (3). **(B)** Hwang *et al.*, 2004 (11). **(C)** Chiappe, 2002 (26). **(D)** Forster *et al.*, 1998 (27). **(E)** Makovicky *et al.*, 2005 (12). **(F)** Mayr *et al.*, 2005 (1). Four of the analyses (A, B, E, and F) are based on different iterations of the same basic data matrix. (C) and (D) are independently derived but may share characters (though the latter does not include *Confuciusornis*).