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 resoring 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 Archaeopteryx, 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. (13). Of the five characters (17) that unambiguously supported 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 (23).

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References and Notes

2. Aves as currently conceived contains the Mesozoic “birds” Archaeopteryx, Rahonavis, and Confuciusornis but excludes deinonychosaurian theropods (23).
7. The analyses of (2) 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 (2) 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 320 MPTs. The resulting strict consensus was topologically similar to that of (2), 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 (2) and (3), but the condensed and filtered MPTs are used for Templeton test analyses.
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.
Fig. 1. Clade support on the strict consensus tree of (J). 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 (J) include bootstrap proportions for Microraptor + Confuciusornis, 12.5%; for Archaeopteryx + Rahnavis, 16.9%; for a monophyletic Aves (Archaeopteryx + Rahnavis + 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 + Rahnavis. Average bootstrap proportion, 47%; average decay index, 1.93.

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 (J). The strict consensus resembles that of (J) in positioning Microraptor as the sister taxon to Confuciusornis instead of within 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.
16. Although it is stated (J) that character descriptions are available online at http://research.amnh.org/vertpaleo/norell.html, this is not the case. Similarly, the character descriptions in (J), supposedly taken from (J), 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 specimens, is not a definite feature of the Archaeopterygidae as a whole. The London and Eichstätt specimens offer conflicting evidence.
18. Character 111 was rescoped by May et al. (J) from fused (J) to (J) in Archaeopteryx and optimized as separate (J); it may, however, be fused in late ontogeny in Archaeopteryx (J). Considering this evidence and reverting to the scoring of Hwang et al. (J) for this character, but keeping all other recodings as suggested by May et al. (J), results in 528 trees of 600 steps; the strict consensus has a polytomy between Archaeopteryx, Rahnavis, Confuciusornis, Microraptor, Troodontidae, and Dromaeosauridae, plus decreased resolution within Troodontidae. The coding of this homoplasy character (J) requires 5 steps on the strict consensus tree of (J) 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 (J) to supporting Microraptor + Confuciusornis in (J), but the derived state (J), distal tarsals fused to metatarsals, is present in all three taxa.
20. Character 166. Metatarsals not co-ossified (J), or co-ossification of metatarsals begins proximally (J) or distally (J).
21. Character 166 was recoded in (J) from (J) to (J); (J) 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 (J) as coded in (J) for character 166, but keeping the other recodings of (J), results in the same trees and the strict consensus as when carried out for character 111 (J). 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.
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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).
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