

The foot of Archaeopteryx: Response to Feduccia et al. (2007)

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Worthy, but they both have DNA sequences of *P. elephantopus*. Worthy rightfully corrected me about misassigning *Megalapteryx* species, but nevertheless his synonymy (Worthy 1988:107) of the lineages from either end of the South Island on the basis of "a north-south cline combined with temporal variation" is clearly rejected by DNA typing (irrespective of whether the type specimen of *M. benhami* has been sequenced). Worthy (2007:1448) argues that we "did not sample any specimens that could be referred to *M. benhami* based on size," and therefore that our sequences have no bearing on its taxonomic status. This is exactly counter to the reasoning he used in synonymizing the different size forms (Worthy 1988) and is, therefore, contradictory logic. Further work is desirable before names are applied to the new lineages of *Dinornis* identified in Baker et al. (2005), but—as was pointed out in that paper—the distribution of the specimens we typed roughly coincides with previously recognized taxa that have been lumped together in more recent taxonomic revisions. The bottom line is that the assignment of taxa based on isolated bones recovered from sites with mixtures of species or composite specimens has led to numerous nomenclatural errors, including those made by Worthy and me, but this debate will no doubt make all of us more careful in the future. Ancient DNA will provide a critical source of characters in any future taxonomic revisions and, hopefully, resolve the tangled web of splitting and lumping that has characterized moa taxonomy in the past. I am sure that if Ned Johnson were still alive, he would agree that this represents a molecular advance in the study of geographic variation and speciation.—ALLAN J. BAKER, Department of Natural History, Royal Ontario Museum, Toronto, Ontario M5S 2C6, Canada. E-mail: allanb@rom.on.ca

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The foot of *Archaeopteryx*: Response to Feduccia et al. (2007).—Without examining the original specimen first-hand, Feduccia et al. (2007) questioned some observations in our recent description of a new skeleton of *Archaeopteryx* (Mayr et al. 2005, 2007). We disagree with several of their comments and believe that they gave an inaccurate account of the results of our studies in several instances.

Our statement that most specimens of the Archaeopterygidae are known from fragmentary or poorly preserved specimens was based on the fact that four of the nine specimens are known from very incomplete remains only (Maxberg, Haarlem, eighth and ninth specimens) and that only three skeletons are largely complete and have well-preserved bones (Berlin, Eichstätt, and Solnhofen specimens). Because only three of the nine specimens are well preserved, we cannot see how our statement "is easily discredited by the numerous published photographs of these specimens" (Feduccia et al. 2007:373).

Feduccia et al. (2007:373) further wrote that we reinterpreted the anatomy of the new specimen "to conform to the now largely discredited terrestrial theory for the origin of flight." This is not correct. In fact, we did not comment at all on the lifestyle of *Archaeopteryx* in our 2005 study and, in the detailed description, only concluded that *Archaeopteryx* probably "spent most of its time on the ground" (Mayr et al. 2007:114). In the latter study, we further noted that *Archaeopteryx* did not have a perching foot (i.e., a foot with a large retroverted hindtoe), but nowhere did we comment on whether or not it was able to perch.

Likewise, although we believe that the hallux of archaeopterygids was spread medially, we did not claim that it was spread "at a right angle to the other claws [*sic*]" (Feduccia et al. 2007:374). Instead, we wrote (Mayr et al. 2005:1485) that

on both feet, the first metatarsal attaches to the medial surface of the second metatarsal..., not to its plantar surface as in extant birds with a retroverted first toe.... The shaft of the first metatarsal does not exhibit the torsion that is characteristic of birds with a fully retroverted first toe.... The proximal phalanx of the first toe further exposes its mediodorsal surface.... Because the metatarsals are visible

in dorsal view, the dorsal aspect of this phalanx would not be visible if the first toe was fully reversed.... We thus conclude that the first toe of *Archaeopteryx* was spread medially and not permanently reversed as in extant birds.

This is possibly a linguistic problem on our side, but we consider "spread medially" and "spread medially at a right angle" to represent very different morphologies. The latter indeed is an unlikely position for a vertebrate toe.

Moreover, although we detailed the reasons for our interpretation of the hindtoe of *Archaeopteryx* (i.e., morphology of first metatarsal and orientation of this toe in the fossil specimen; see above), Feduccia et al. (2007:375) did not even try to refute these but simply wrote that the "hallux in Mayr et al.'s (2005) photographs opposes the other toes as it does in all other *Archaeopteryx* where the pertinent anatomy is preserved." As noted in our study, a medially spread hallux is not only preserved on both feet of the new specimen but also in the Solnhofen and Berlin ones. The feet of the London and Eichstätt specimens are preserved in lateral or medial view, and the impression of a reversed first toe in these specimens is likely to be an artifact of preservation, because the medially spread toe is pressed on the level of the sedimentation layer (Mayr et al. 2005, 2007).

Feduccia et al. (2007) also seem to be unaware that a nonreversed hallux was also reported for the early Cretaceous *Jeholornis* (Zhou and Zhang 2006:85). Their statements also conflict with the fact that the hallux was not reversed in dromaeosaurs (Feduccia et al. 2007: lower panel of fig. 2), which, in Feduccia et al.'s (2007) phylogeny, are even closer to modern birds than *Archaeopteryx*. This antilogy is not even mentioned in the text.

Feduccia et al. (2007:375) correctly noted that the proximal end of the penultimate phalanx of deinonychosaurs forms an "extended ventral joint surface," which is absent in *Archaeopteryx*. However, we also recognized this difference and coded the morphologies of archaeopterygids and deinonychosaurs as two different, unordered character states. The second toe of archaeopterygids lacks a hypertrophied claw and clearly served a different function than in the deinonychosaurs (Mayr et al. 2007). However, differences do not prove nonrelationship of taxa, and we still consider it possible that the proximodorsal expansion of the distal end of the first phalanx of the second toe is a shared derived character that unites archaeopterygids and deinonychosaurs.

Feduccia et al.'s (2007: fig. 3) imaginative phylogeny avoided any character conflict by omitting all dromaeosaurs other than *Microraptor*. By contrast, and without listing any supporting evidence, the enigmatic and very incompletely known *Pedopenna daohugouensis*, which was described as a manirap-

toran dinosaur of uncertain affinities (Xing and Zhang 2005), is shown as sister taxon of *Microraptor*. If the authors had also included other dromaeosaurs in their phylogeny, such as *Velociraptor* or *Deinonychus*, it would have become all too obvious that character transformation in the lineage leading to extant birds is not as straightforward (e.g., notes above concerning the hallux).

The statement that the teeth of *Microraptor* are "avian style" (Feduccia et al. 2007:377) is incorrect; the teeth of *Microraptor* are serrated on their caudal carina and more closely resemble the teeth of the troodontid *Sinovenator* (Hwang et al. 2002). This statement is even more misleading, because Feduccia et al. (2007) did not mention that other dromaeosaurs, which are deliberately left out of their phylogeny (Feduccia et al. 2007: fig. 3), have typical theropod teeth.

Although Feduccia and his coauthors have until recently been among the most prominent opponents of a theropod ancestry of birds (e.g., Prum 2002), they now state that there is "little question that *Archaeopteryx* and, therefore, birds, are closely related to dromaeosaurids, particularly Chinese Lower Cretaceous microraptors, which we regard as a derived group of birds" (Feduccia et al. 2007: 377). They further list alleged problems with a "strict theropod ancestry" of birds (Feduccia et al. 2007: 377), but conclude with the statement that the "great challenge for archosaurian paleontology is to tease out the exact avian clade from early theropods with superficially similar structure" (Feduccia et al. 2007: 379). Although we agree with Feduccia et al. (2007) that the interrelationships between *Archaeopteryx*, deinonychosaurs, and more advanced birds are far from being understood fully (Mayr et al. 2005), we do not believe that such confusing statements shed new light on the ancestry of birds. —GERALD MAYR and D. STEFAN PETERS, *Forschungsinstitut Senckenberg, Sektion Ornithologie, Senckenberganlage 25, D-60325 Frankfurt a.M., Germany*. E-mail: gerald.mayr@senckenberg.de

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Response to Mayr and Peters.—We welcome the reply by Mayr and Peters (2007) to our article on the relationships and morphology of early birds (Feduccia et al. 2007), because such discussion may lead to a better understanding of avian evolution. We believe that the figures in their original papers adequately illustrate the points we discussed, but we look forward to actually examining the specimen when it becomes available for study. It now appears that they did not intend their description of the new *Archaeopteryx* to indicate that *Archaeopteryx* had a terrestrial lifestyle and was unable to perch in trees. If they also believe that the hallux of their specimen was only inclined medially (but not at a nearly right angle), their description corresponds to the reflexed hallux of most other birds and we would not disagree with it. However, if that was their intention, they should have used a term such as “postero-medial” to describe its position.

The expansion of the hallux ungual in *Archaeopteryx* is not a character of birds adapted to an aquatic or terrestrial habit, but is characteristic of arboreal birds. Other *pes* characters that they use include a supposed expansion of phalangeal condyles that is not clearly evident in *Archaeopteryx*, and a proper understanding would necessitate comparison of scaled measurements between theropod dinosaurs, birds, and other archosaurian taxa that are not provided. Mayr and Peters (2007) agree with us that *Archaeopteryx* does not have the special morphology characteristic of deinonychosaurs on *pes* digit two and did not code these features as a synapomorphy with *Archaeopteryx*, although they did claim that this is a morphology “uniting archaeopterygids and deinonychosaurs.”

The presence or absence of serrations on the teeth varies widely among related groups, but the avian character of maniraptorian teeth is demonstrated by the waisted crown and expanded root seen in at least some examples. We are sure that there is still significant disagreement between our interpretations and those of Mayr and Peters, but the explanations they now offer seem to greatly diminish those differences. Perhaps these discussions will lead to a better exchange of ideas among students of avian evolution with contrary views, and contribute toward new and better hypotheses concerning the ancestry or sister-group relationships of birds.

Our phylogeny is only slightly modified from that of Nick Longrich, as we noted (Feduccia et al. 2007), by moving *Archaeopteryx* to a basal position with respect to microraptors and other Mesozoic birds, a position that conforms to its temporal occurrence. This view of superficially theropod-like Mesozoic birds being derivatives of the early avian radiation is not new to us, but was suggested in some form or other as early as 1911 by O. Abel, and most recently by Gregory Paul, George Olshevsky, Stephen Czerkas, A.F., L.M., and others. By our interpretation of the current evidence, birds are monophyletic and are nicely defined by their unique possession of feathers.—ALAN FEDUCCIA, *Department of Biology, University of North Carolina, Chapel Hill, North Carolina 27599, USA (e-mail: feduccia@bio.unc.edu)*; LARRY D. MARTIN, *Museum of Natural History, University of Kansas, Lawrence, Kansas 66045, USA*; and SAM TARSITANO, *Biology Department, Worcester State College, Worcester, Massachusetts 01602, USA*.

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