

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

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We agree that statistical support for our proposed phylogeny is weak, but the monophyly of Aves favored by most current researchers is also weakly supported. In the absence of unambiguous apomorphies of a clade including *Archaeopteryx* and *Confuciusornis* but not deinonychosaurs, we do not believe that the statistical comparisons made by Corfe and Butler challenge our hypothesis regarding the ancestry of birds.

Corfe and Butler (1) take issue with our statement that the data obtained from the new specimens “challenges the monophyly of Aves as currently recognized” (i.e., a clade including *Archaeopteryx* and modern birds but not deinonychosaurs) (2).

They recoded two characters included in our analysis, the co-ossification of metatarsals and the presence of a scapulocoracoid, referring to (3) for the presence of fused metatarsalia in *Archaeopteryx*. However, (3) explicitly states that the metatarsalia of *Archaeopteryx* were “reported to be proximally fused” in two specimens only—the now-lost third specimen and the sixth specimen. In the same study, the alleged fusion in the third specimen is then shown to be based on spurious evidence. The feet of the sixth specimen are very poorly preserved, and the original description (4) notes that in “the right foot fusion seems to be possible proximally” and in “the left foot, metatarsals II and III cannot be clearly distinguished and might be partially fused.” Given that the metatarsalia are unfused in all other specimens, we do not consider this to be a convincing base for coding fused metatarsalia as present in *Archaeopteryx*. Likewise, the alleged fusion of

scapula and coracoid is far from being certain, and these bones “appear to articulate firmly” in only three of the ten archaeopterygid specimens (3); certainly scapula and coracoid were not fused in *Rahonavis* (5, 6).

Corfe and Butler correctly note that the statistical support for the tree resulting from our analysis is weak, but this is also true for the competing hypothesis favored by most current researchers, that is, monophyly of a group including *Archaeopteryx* and pygostylians and excluding deinonychosaurs. In our study, we listed derived characters in which *Microraptor* agrees with *Confuciusornis* and other pygostylians, including the presence of ossified uncinat processes and an ulna that is much wider than the radius (2). These characters are not challenged by Corfe and Butler who, unfortunately, did not discuss the character evidence for a clade including *Archaeopteryx* and pygostylians to the exclusion of deinonychosaurs.

Corfe and Butler incorrectly state that we suggested “birds, or avian flight, originated twice.” We do not assume that flight was gained independently more than once within theropods but consider it more likely that flight ability was lost several times independently in the clade including *Archaeopteryx*, deinonychosaurs, and pygostylians (7). This is a reasonable assumption irrespective of the position of *Archaeopteryx*, because the presence of modern-type wing feathers in the dromaeosaur *Microraptor* (8) alone

suggests secondary loss of flight ability in the larger species of Deinonychosauria.

A clade including deinonychosaurs and more derived birds, to the exclusion of *Archaeopteryx*, has been discussed in detail previously (7), and there are also hypotheses that consider oviraptorosaurs, traditionally considered “non-avian” theropods, to be closer to crown group Aves than is *Archaeopteryx* (9).

We are not aware of any derived character shared by *Archaeopteryx* and *Confuciusornis* that is not also present in the deinonychosaur *Microraptor*. However, and as noted above, *Microraptor* shares derived characters with *Confuciusornis* that are absent in *Archaeopteryx*, and we thus do not agree with Corfe and Butler’s comment that “the hypothesis of a polyphyletic Aves is no better supported by available data than that of a monophyletic Aves.” One of the essentials of phylogenetic systematics, which makes it superior to other methods of phylogenetic reconstruction, is the naming of apomorphies of the clades in question. Purely statistical comparisons reduce it to just another numerical approach. Unless Corfe and Butler can present unambiguous apomorphies of a clade including *Archaeopteryx* and *Confuciusornis*, to the exclusion of deinonychosaurs, we do not believe that their argument poses a robust challenge to our hypothesis of bird ancestry.

References

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