Response to Comments on "Narrow Primary Feather Rachises in *Confuciusornis* and *Archaeopteryx* Suggest Poor Flight Ability"

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Paul and Zheng *et al*. challenge our conclusions regarding the flight of *Confuciusornis* and *Archaeopteryx*, which derive from our method of assessing flight ability from estimated feather strength. They suggest that our mass and rachis data for these fossil birds are incorrect. Neither comment, however, invalidates our method nor alters conclusions of poor flight ability based upon our original data. We encourage researchers to use our method before critiquing our conclusions regarding early bird flight.

We recently published a method for estimating the strength of primary feather rachises and extrapolating this to the maximum lift forces sustainable by a bird, thereby providing a quantitative, and novel way of estimating the flight abilities of fossil birds (*1*). Our model is, of course, dependent on the data fed into it. Here, we respond to the comments of Paul (*2*) and Zheng *et al*. (*3*) challenging our conclusion that *Confuciusornis* and *Archaeopteryx* were not capable of powered flight. Paul suggests that our mass estimates for these fossil birds and our methodology are unsound, whereas Zheng *et al*. present new data that highlight potential errors associated with feather taphonomy or open the possibility that the Confusciusornithidae may be composed of more than one species—neither of which confounds our original conclusion of poor flight ability based on data from our original specimens.

Zheng *et al*. (*3*) present measurements that add a new twist to the debate over the flight capabilities of Mesozoic birds based on feather morphology. However, we cannot fully assess the importance of their alternative rachis diameters because measurements of primary feather length relative to overall wing length for individual specimens are also required to repeat our calculations. Nonetheless, if we use a rachis diameter of 2.15 mm and assume everything else is equal to the data in our initial study (*1*), the primary feather safety factor for the specimens reported by Zheng *et al*. (assuming hollow feathers) is 3.2, implying that their specimens of *Confuciusornis* were capable of flapping. We do not agree with the statement of Zheng *et al*. that confuciusornithids have considerably thicker rachises than we measured, because what they have shown is only that some confuciusornithids may have thicker rachises, which is a potentially interesting development. Other work has indicated that the known specimens of this taxon show a bimodal size distribution (*4*, *5*). This would either suggest that *Confuciusornis* was sexually dimorphic or that this bird, currently represented by one predominant species, needs to be further split. Differences in feather morphology may also indicate different flight abilities, which could most parsimoniously be explained by the data being extracted from separate species, based on what we know about extant birds.

It is also worth balancing the debate about preservation influencing the dimensions of the rachis diameters by considering what could lead to overestimates, for example, flattening of the rachises or measuring the calamus, which is embedded and supported by soft tissue. Of course, we are also assuming that the feather rachises are cylindrical in cross section and that the dorsal or ventral orientation of the feathers that is measured from the fossils is representative of the lateral dimension. Feather and rachis preservation remains an interesting area for future work, as it is also possible that rachis apparent diameters are increased during fossilization.

As Zheng *et al*. (*3*) acknowledge, a rachis diameter of 2.1 to 2.3 mm is still very thin compared to an extant bird with a similar wingspan, and this alone certainly implies relatively poorer flight abilities. We hope that as more specimens are found with preserved feathers, the methodology we described (*1*) will prove important and useful in assessing the flight capabilities of fossil birds—not least because it provides a direct quantitative assessment, as opposed to often qualitative and subjective conclusions drawn from morphological shape and palaeoecology data.

In a second comment on our study (*1*), Paul (*2*) states that our conclusion of poor flight ability in *Confuciusornis* and *Archaeopteryx* is incorrect because both our mass estimates for these fossil birds and our methodology were unsound. Paul, however, did not present any new primary feather safety factors based on his body mass estimates, so exactly how his contradictory conclusion was reached is puzzling. In our paper (*1*) we were explicit about our model, its assumptions, and the measurements used to feed it. Researchers (including Paul) can use our method to input alternative measurements from fossil birds and calculate primary feather safety factors.

In response to Paul's criticisms, consider first his suggestion that unless we test our methods against other fossil avians the method we use is flawed. This logic is problematic: You cannot test predictions from a model against an organism in which flight ability is unknown. This is why we used extant birds with known and observable flight abilities to test our predictions of primary feather safety factors.

Paul (*2*) argues that we have overestimated the size of both *Confuciusornis* and *Archaeopteryx* and suggests that his estimates for the body masses for these extinct avians are more valid. If, however, we use Paul's (*2*) lower mass estimates in our model, then the safety factor for a hollow primary-feathered *Archaeopteryx* with a 140-g body mass is 1.1, which is still not sufficient for flapping flight and barely enough for gliding under static forces. Similarly, if we use 180 g for the body mass of *Confuciusornis*, then the calculated safety factor is 1.4—again, barely enough to sustain a glide and certainly nowhere near sufficient to allow flapping or any flight maneuvers, which involve sudden high dynamic forces.

Paul's third criticism is that the rachis measurements we present for *Archaeopteryx* (*1*) are inaccurate. A rachis diameter of 1.4 mm, suggested by Paul based on a photograph, would yield a safety factor of 3.6, below that of modern birds (almost always >4.8), but probably enough to sustain some level of flapping. The suggestion that heavier adult *Archaeopteryx* were likely better at flapping than juveniles (*2*) implies that adult feathers are thicker than those of juveniles, which is unlikely and has not yet been shown for fossil or modern birds.

The final four paragraphs of Paul's comment (*2*) outline other lines of evidence as to why our conclusion of poor flight ability in the two Mesozoic birds may be incorrect. As we have already argued, the one clear advantage of our method is that it is quantitative as opposed to being qualitative or subjective, as are many discussions about the lifestyles of fossil taxa based on anatomy and palaeoecology. Such arguments may be extraneous anyway: If the feathers of early birds were too weak to withstand the forces of flight, then we know (thanks to the laws of physics) that they could not fly regardless of any other morphological features they might, or might not, have possessed.

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