

# Comment on “Narrow Primary Feather Rachises in *Confuciusornis* and *Archaeopteryx* Suggest Poor Flight Ability”

Gregory S. Paul

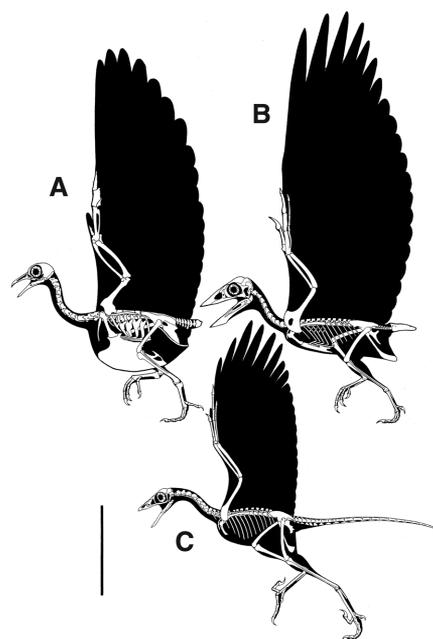
Nudds and Dyke (Reports, 14 May 2010, p. 887) reported that the primary features of the early birds *Archaeopteryx* and *Confuciusornis* were too weak to power flight. This conclusion is not supported because the authors overestimated the mass of the subjects and understated the strength of the primary shafts in at least one example. The total biology of the birds indicates that they could achieve flapping flight.

In their attempt to estimate the aerial performance of the early birds *Archaeopteryx* and *Confuciusornis* based on the strength of their primary feathers, Nudds and Dyke (1) correctly observe that accurate body mass estimates are crucial to their calculations that flight feathers were not strong enough for powered flight. However, they used excessive mass values that underestimated the flight potential of the ancient fliers. They also did not test their methods by estimating the mass and feather strength of derived fossil avians with more highly developed flight adaptations.

A number of problems prevent restoring the flight of *Archaeopteryx* using feather shaft dimensions. The absence of feathers adorning the largest skeleton, the Solnhofen specimen weighing a little over half a kilogram with a 68-mm-long femur, bars assessing the fully mature aerial abilities of the adults. Other specimens are juveniles whose mass varies by a factor of more than 7 (2, 3). With a 46-mm-long femur, the Munich specimen examined by Nudds and Dyke (1) is a small juvenile of just ~140 g (2, 4). A same-scale comparison confirms that it is not possible for it to have weighed as much as a pigeon (Fig. 1, A and C) as assumed by Nudds and Dyke, who incorrectly applied the quarter kilogram that a number of researchers agree was the mass of the much larger-bodied Berlin specimen (1–6) to the little juvenile. The primary feathers of the Munich specimen are poorly preserved. Nudds and Dyke did not provide high-resolution images showing that the shaft base diameter of the longest primary is only 0.75 mm, and I cannot confirm such a low value using large-format, high-resolution photographs of the Munich slabs. Somewhat more medial primary shafts measuring 1.25 to 1.4 mm across at shaft mid-length are clearly present (Fig. 2), and those rachises were probably even more robust at their bases. The rachises of the Berlin specimen’s well-preserved primaries do not show evidence of becoming more slender progressing laterally toward

the outer wing, and the maximal diameter of the proximal shafts is obscured by other feathers (7). The buckling resistance of the longest outer primaries therefore cannot be estimated in any *Archaeopteryx*, but the thickness of some of the primary rachises of the Munich juvenile combined with its low mass indicate that its immature wings were strong enough for flapping flight, and the flight capacity of adults may have been much better.

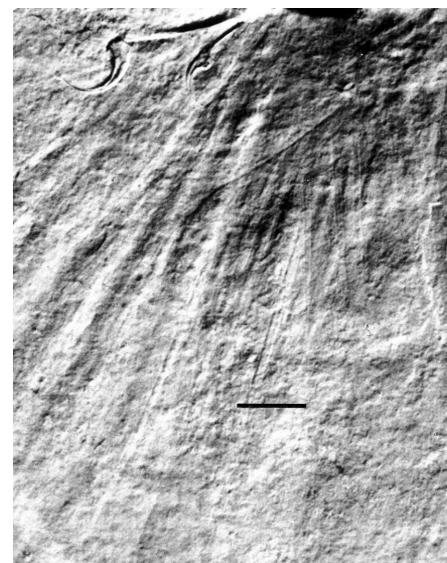
Lacking high-resolution images of the well-preserved, unobscured proximal shafts of the longest primaries of *Confuciusornis*, the 1.2-mm



**Fig. 1.** Same-scale comparison of the skeletons with muscle profiles and wing feathers of (A) rock pigeon, 250 g, 43 mm femur; (B) *Confuciusornis* of the size of the specimen in figure 1A in (1), 47 mm femur; (C) Munich juvenile *Archaeopteryx*. Scale bar, 100 mm.

average diameter reported by Nudds and Dyke is not sufficiently documented. The mass of the specimen in figure 1A in (1) could not have been close to the authors’ estimate of 0.5 kg, which equals the weight of some teals and ducks (8–10). Instead, at ~180 g, the shallow-bodied basal bird was intermediate in mass to the Munich *Archaeopteryx* and the deep-bodied pigeon, so the feathers were a number of times stronger than calculated by Nudds and Dyke (Fig. 1, A to C).

Because focusing on one narrow aspect of a fossil organism increases the risk of error, the whole biology should be considered. The gross degree of powered flight in animals with well-developed brachial airfoils is primarily determined by the muscle power of the arms (2, 3). Because gliding does not require the arms to have more strength than is needed to hold the animal off the ground, major adaptations for increasing the arm musculature above normal levels are not present in nonflapping gliders, and increasing adaptations for expanded forelimb muscles is indicative of increasing powered flight performance. The wings of *Archaeopteryx* and *Confuciusornis* were large enough for powered flight (1–3, 5, 6, 10). In *Archaeopteryx*, the large furcula and greatly expanded pectoral crest indicate an expanded musculature beyond the tetrapod norm and are indicative of some level of flapping flight beyond simple gliding, albeit well below that typical of most birds (2, 3, 11). The presence of a large sternal plate anchored by ossified sternal ribs, an even larger pectoral crest, and the flattening of the hand and fingers to better anchor the primaries shows that *Confuciusornis* was markedly better adapted for powered flight than was *Archaeopteryx*, and was approaching derived fliers in performance (2).



**Fig. 2.** Detail of primary feathers of the Munich specimen counterslab, including some rachises at mid-shaft. Lateral is to the left; finger elements are near the top. Scale bar, 10 mm.

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Because *Confuciusornis* is preserved as enormous numbers of complete specimens that lack evidence of substantial hydrodynamic transport in lake bottom deposits, with volcanic aerial pollutants probably being the killing mechanism (12), it appears that the birds formed large flocks able to fly out over large bodies of water (13). Flocking and over-water flights are common attributes of capable powered fliers, not of gliders that live singly or in small groups and must avoid flying over large stretches of water. The less-developed flight abilities of *Archaeopteryx* are compatible with its scarcity in the Solnhofen lagoonal deposits.

The thesis that large-winged basal avians with primary feathers large and asymmetrical enough to produce lift and thrust had shafts that would buckle under the load is a priori illogical, and it can be presumed to be correct only if it is conclusively shown that the adults were sufficiently massive to overstress the flight feathers. Because the hypothesis that basal avians were not powered fliers due to weak feathers is entirely dependent

on mass estimates that are controversially high, implausible for the specimens examined, and impossible to verify; is contradicted by the anatomy and lifestyle of the early birds; and in one case is based on a small juvenile specimen, the hypothesis cannot be sustained. It follows that powered flight was probably further improved, not initiated, in more derived birds.

#### References and Notes

1. R. L. Nudds, G. J. Dyke, *Science* **328**, 887 (2010).
2. G. S. Paul, *Dinosaurs of the Air* (Johns Hopkins Univ. Press, Baltimore, 2010).
3. G. S. Paul, *Predatory Dinosaurs of the World* (Simon and Schuster, New York, 1988).
4. That the volumetric mass estimates in (2) and (3) incorporate high specific gravities of 0.85, large flight muscles, and feathers reduces the possibility that they are too low. Using the method of Christiansen and Farina (14), the mass estimate for the Munich specimen is a similar 135 g.
5. D. W. Yalden, *Zool. J. Linn. Soc.* **82**, 177 (1984).
6. A. Elzanowski, in *Mesozoic Birds: Above the Heads of Dinosaurs*, L. M. Chiappe, L. M. Witmer, Eds. (University of California Press, Berkeley, 2002), pp. 129–159.
7. The visible rachises of the Berlin specimen primaries are up to 1.3 mm in diameter, but they taper strongly proximally, so their maximum widths are probably much higher.
8. Mass estimates based on extrapolations from skeletal dimensions as used by Nudds and Dyke regarding *Confuciusornis* are less reliable than volumetric estimates because of very large variations in mass/dimension ratios in different animals (2, 3, 9, 10). The mass estimate in (2) for *Confuciusornis* is too high for specimens of the size examined herein.
9. G. S. Paul, *Dinofest International*, D. L. Wolberg, E. Stump, G. D. Rosenberg, Eds. (The Academy of Natural Sciences, Philadelphia, 1997), pp. 129–154.
10. The wings of *Confuciusornis* are exceptionally large relative to mass (Fig. 1), perhaps an adaptation for achieving sustained flight with its grade of flight adaptations (2).
11. S. L. Olson, A. Feduccia, *Nature* **278**, 247 (1979).
12. M. Chang, *The Jehol Biota* (Shanghai Scientific and Technical Publishers, Shanghai, 2003).
13. Preservation of large numbers of nonaquatic, nonflocking flying vertebrates over large areas of lake bottoms is rare at best, while this taphonomic event is fully compatible with power flying in groups.
14. P. Christiansen, R. A. Farina, *Hist. Biol.* **16**, 85 (2004).

28 May 2010; accepted 20 September 2010  
10.1126/science.1192963

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*Science* **330** (6002), 320.  
DOI: 10.1126/science.1192963

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