

Xu *et al.* replyREPLYING TO Richard O. Prum *Nature* **468**, doi:10.1038/nature09480

Prum¹ identifies the unusual feathers in the smaller *Similicaudipteryx* specimen as immature, and suggests that the different morphologies preserved in the smaller and larger specimens represent different growth stages of a single feather type rather than successive feather generations of different types. Although this new proposal is very interesting, we do not agree that it is better supported by the available data than our original interpretation².

A feather of any generation can be expected to show different morphologies in the course of its growth³, as noted by Prum¹. During early growth, the feather will be enclosed in a long sheath. Subsequently, the sheath will begin to open from the distal end, revealing the pennaceous feather. For simplicity, we refer to feathers at this early stage of opening as emergent feathers. The proximally ribbon-like pennaceous feathers (PRPFs) in the *Similicaudipteryx* specimen are superficially similar to the emergent feathers of extant birds³, but they are apparently different in relative size. Because feather growth is still far from complete when the sheath begins to open, emergent feathers are proportionally small³, and this is particularly true in early feather generations. The overall immaturity of the smaller *Similicaudipteryx* specimen implies that its plumage would have been of an early generation², so that emergent feathers of large size would be particularly surprising in this individual. However, the PRPFs of the smaller *Similicaudipteryx* are longer than the tibiotarsus, greatly exceeding the proportional length of early-generation emergent feathers in modern birds.

Also, the ribbon-like portion of a typical PRPF in the smaller *Similicaudipteryx* specimen is only slightly narrower than the pennaceous portion, and its width considerably exceeds the length of the associated caudal vertebra. In contrast, the ensheathed portion of an emergent feather of an extant bird is much narrower than the pennaceous portion. Also, the identification of all rectrices and remiges in the *Similicaudipteryx* specimen as emergent feathers would imply that *Similicaudipteryx* moulted all of its flight feathers simultaneously, in contrast to the sequential moulting of extant birds¹. The interpretation by Prum¹ of simultaneous moulting as a primitive condition present in non-avian dinosaurs is interesting, but at face value this is nevertheless an obstacle to interpreting the plumage of the smaller *Similicaudipteryx* specimen as a generation of emergent feathers. Finally, because new feathers physically displace old feathers during the process of moulting, a displaced mature feather will often be found hanging from the tip of the emergent feather that is replacing it. The total absence of previous-generation feathers associated with the PRPFs of *Similicaudipteryx* represents another piece of evidence indicating that the PRPFs are unlikely to represent emergent feathers, unless the replacement process was substantially different from that seen in extant birds.

Prum¹ emphasizes some differences between the PRPFs of the *Similicaudipteryx* specimen and those of basal birds and the non-avian maniraptoran *Epidexipteryx*. We noted these differences in our original study², but Prum's alternative interpretation led us to reconsider the nature of the PRPFs in the *Similicaudipteryx* specimen and those in basal birds and *Epidexipteryx*². The ribbon-like portion of the PRPFs in basal birds and *Epidexipteryx* appears to represent an extremely broad rachis, given that the definite rachis of the pennaceous portion is identifiable as a tapering extension of the entire ribbon-like portion⁴. Under this interpretation, the median line that typically extends along the ribbon-like portion of the feather, and which was previously identified as a rachis⁵, would actually represent a ventral furrow running along the rachis as in modern birds.

In contrast to both the broad proximal rachises of basal birds and *Epidexipteryx*, and the horny feather sheaths referred to by Prum¹, the ribbon-like portions of the PRPFs of the smaller *Similicaudipteryx* specimen may represent hollow structures similar to the broad monofilaments seen in more basal theropods⁶. Admittedly, two-dimensional preservation makes it difficult to judge which identification is correct, but further early juvenile *Similicaudipteryx* specimens with normal flight feathers would support Prum's interpretation. Nevertheless, differences in feather ontogeny between Mesozoic and extant taxa indicate that analogies involving specific feather structures should be drawn only with extreme caution.

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