Moulting tail feathers in a juvenile oviraptorisaur

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Xu *et al.*[1] describe the extraordinarily preserved feathers from two subadults of the oviraptorisaur *Similicaudipteryx* from the Yixian Formation of Liaoning, China. The preserved tail feathers of the juvenile specimen (STM4.1) show a morphology not previously observed in any fossil feathers. The tail feathers of an older, immature specimen (STM22-6) show a typical closed pennaceous structure with a prominent, planar vane. I propose that the feathers of the tail of the juvenile specimen are not a specialized feather generation, but fossilized 'pin feathers' or developing feather germs.

Xu *et al.*[1] interpret the juvenile *Similicaudipteryx* tail feathers as examples of "proximately ribbon-like pennaceous feathers" (PRPFs) that have evolved convergently in avialian confuciusornithids and enanthiornithines, and in the non-avian maniraptoran *Epidexipteryx*. They describe the differences between juvenile and immature *Similicaudipteryx* feathers as a notable example of post-nestling ontogenetic change in feather morphology, and claim that "this phenomenon is not known to occur in other birds."

Although modern birds do not show radical changes in flight-feather morphology after the nestling stage (probably owing to the functional constraints of flight), there are many examples of radical post-nestling changes in the morphology of other feathers. For example, the feather follicles on the head of a Wild Turkey (*Meleagris gallopavo*) grow plumulaceous down in nestlings, fully pennaceous contour feathers in juveniles, and specialized bristles in adults[2].

Data from Xu *et al.*[1] document that the tail feathers of the juvenile *Similicaudipteryx* specimen are very different in morphology from previously described PRPFs, in which the ribbon-like basal portion is formed completely by the lateral expansion and vertical compression of the rachis (Supplementary Fig. 3 in Xu *et al.*[1]). In contrast, the unbranched, proximal portion of the tail feathers of the juvenile *Similicaudipteryx* is not a merely a continuous, basal extension of the rachis (Supplementary Fig. 2a in Xu *et al.*[1]). Rather, the undifferentiated basal portion of these feathers surrounds the entire base of the exposed distal vane of the feather. The distal rachis does not expand laterally, and is visibly distinct from the broad base of the feather (top of Supplementary Fig. 2a in Xu *et al.*[1]). This observation is inconsistent with the conclusion of Xu *et al.*[1]

The juvenile tail feathers of *Similicaudipteryx* (STM4.1) are entirely consistent with the morphology of moulting feathers of living birds[2]. The tubular feather germ, called a pin feather, is surrounded by a keratinized sheath that falls off to expose the mature feather. Typically, the sheath begins to fall off the mature distal tip of the feather before the development of the ensheathed tubular base of the feather is complete. For a pennaceous feather, this intermediate stage of growth appears as a limited distal vane emerging from a smooth tubular base[2] (Fig. 1). These feathers are not too large to be ensheathed because feathers need to grow to their final size and may shed the sheath at different lengths. Indeed, the moulting Great Horned Owl feathers in Fig. 1 are over 6-cm long, and are mostly ensheathed. These structures are also not too wide to be ensheathed feathers; the width of pin feathers depends on the number of barbs, the size of barb ridges and the angle of barb-ridge expansion after emergence[3]. These parameters all vary among living birds. Tiny natal down feathers sometimes adhere to the distal tip of molting feathers in living birds, but this is rare after the nestling stage and would be unexpected in juvenile *Similicaudipteryx*.

I propose that the tail feathers of the juvenile *Similicaudipteryx* are similar, or identical, in morphology to those of the immature

Figure 1 | Developing primary wing feathers of a nestling Great Horned Owl. The distal tip of the planar vane of the pennaceous feathers are emerging from the tubular feather sheath. The sheath surrounds the entire base of the emergent vane, and the rachis runs under the sheath without lateral expansion. Photograph reproduced with permission from B. Hilton.

Similicaudipteryx, but in the juvenile specimen they were preserved at an intermediate stage of development during emergence from the distal portion of the vane from the feather sheath. Little is known about the evolutionary origin of feather moult, and the discovery of fossil moulting feathers is an extraordinary achievement in dinosaur palaeontology. The title of Xu *et al.*[1]—"Exceptional dinosaur fossils show ontogenetic development of early feathers"—is still entirely consistent with this interpretation, but "ontogenetic" would refer to the growth of individual feathers rather than change over life.

The apparent simultaneous moult of tail feathers in *Similicaudipteryx* is similar to the first set of flight feathers in juvenile modern birds, but differs from adult modern birds in which tail feathers moult sequentially. However, sequential moult of remiges and rectrices is proposed to have evolved as an adaptation for flight to maintain aerodynamic function. Early feathered theropods would be unlikely to have evolved sequential moult. Simultaneous rectrix molt in terrestrial theropods may have preceded the evolution of sequential rectrix moult in modern birds.

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Xu *et al.* reply

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Prum[1] 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 interpretation[2].

A feather of any generation can be expected to show different morphologies in the course of its growth[3], as noted by Prum[1]. 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 birds[3], 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 small[3], 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 generation[2], 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 birds[1]. The interpretation by Prum[1] 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.

Prum[1] 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 study[2], 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 portion[4]. Under this interpretation, the median line that typically extends along the ribbon-like portion of the feather, and which was previously identified as a rachis[5], 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 Prum[1], 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 theropods[6]. 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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