

LETTERS

Exceptional dinosaur fossils show ontogenetic development of early feathers

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Recent discoveries of feathered dinosaur specimens have greatly improved our understanding of the origin and early evolution of feathers, but little information is available on the ontogenetic development of early feathers^{1–7}. Here we describe an early-juvenile specimen and a late-juvenile specimen, both referable to the oviraptorosaur *Similicaudipteryx*⁸, recovered from the Lower Cretaceous Yixian Formation of western Liaoning, China⁹. The two specimens have strikingly different remiges and rectrices, suggesting that a radical morphological change occurred during feather development, as is the case for modern feathers¹⁰. However, both the remiges and the rectrices are proximally ribbon-like in the younger specimen but fully pennaceous in the older specimen, a pattern not known in any modern bird¹⁰. In combination with the wide distribution of proximally ribbon-like pennaceous feathers and elongate broad filamentous feathers among extinct theropods, this find suggests that early feathers were developmentally more diverse than modern ones and that some developmental features, and the resultant morphotypes, have been lost in feather evolution.

Feathers or primitive feathers have been documented in most non-avian coelurosaurian theropod groups on the basis of numerous specimens recovered from the Lower Cretaceous Jehol Group and the Jurassic Daohugou and Tiaojishan formations^{1–4,11–13}, but exceptionally preserved specimens remain rare. Even rarer are juvenile specimens preserving integumentary tissue that can provide insights into the development of early feathers. Here we describe two small theropod specimens from the Lower Cretaceous Yixian Formation of western Liaoning⁹ that preserve significant information pertaining to this poorly understood issue (Fig. 1 and Supplementary Figs 1 and 2).

STM4-1 is a juvenile (Fig. 1a), as indicated by several features: longitudinal striations are present on the surfaces of long bones owing to incomplete ossification; the neural arches are not fused to the centra, except in posterior caudal vertebrae; and the specimen is much smaller-bodied than known sub-adult to adult oviraptorosaurian specimens (the femoral length is 38 mm, in comparison with a femoral length of about 120 mm in the smallest known specimen of the oviraptorosaur *Caudipteryx*)^{14–16}. With a femoral length of about 140 mm, STM22-6 is much larger than STM4-1, but is probably also an immature individual because the neural arches are separated from the centra in the dorsal and anterior caudal vertebrae. We suggest that STM4-1 and STM22-6 represent early and late juvenile stages, respectively.

STM4-1 and STM22-6 are referable to the Oviraptorosauria on the basis of several derived features¹⁶: a skull with a short preorbital region; premaxilla with a large main body; a dorsally positioned external naris; a large mandibular fenestra; a long retroarticular process; and an anteriorly curved pubic shaft. Comparisons with other oviraptorosaurs suggest that STM4-1 and STM22-6 are referable to

Similicaudipteryx, a basal oviraptorosaur recently reported from the Yixian Formation⁸ (Supplementary Information).

In STM4-1, two types of feather are present: large pennaceous feathers are attached to the manus and the middle and posterior caudal vertebrae but not to other parts of the skeleton, and plumulaceous feathers are seen over most of the rest of the vertebral column and near the ischia. The plumulaceous feathers associated with the ischia and anterior caudal vertebrae are long, branching filamentous structures. Eleven rectrices are present, and each is attached to the ventral side of a caudal vertebra. Most of the rectrices are wide in proportion to the size of the associated vertebrae. The proximal two-thirds of each rectrix is ribbon-like, and the distal one-third is comparable in structure to a normal pennaceous feather (Fig. 1b). About ten primary remiges are attached to metacarpal III (the middle metacarpal) and phalanx III-1, those in the middle of the series being considerably longer and wider than the remainder. As with the rectrices, the distal part of each remix is pennaceous but the proximal part is ribbon-like (Fig. 1c). No secondary remiges are observed, although they might simply have escaped preservation.

In the larger specimen, STM22-6, the feathers associated with the skull and most of the vertebral column are plumulaceous, and those near the skull and pelvis are particularly long (more than 50 mm). Pennaceous feathers are represented by proportionally large remiges and rectrices (Fig. 1d), each of which has a prominent rachis and symmetrical vanes and lacks a proximal ribbon-like portion. More than 12 bilateral pairs of rectrices are attached to the tail (Fig. 1e). At least 10 primary remiges and 12 secondary remiges are seen on each arm in STM22-6 (Fig. 1f). The distal primary remiges possess more barbs than the proximal primaries and the secondary remiges.

STM4-1 and STM22-6 show that some interesting ontogenetic variations are present in *Similicaudipteryx*. STM4-1 has primary remiges but possibly lacks secondary remiges, whereas both primary and secondary remiges are present in STM22-6. If the absence of secondary remiges is a true feature, this would suggest that secondary remiges developed ontogenetically later in *Similicaudipteryx* than in modern birds (for example, a chicken already has secondary remiges even at hatching)¹⁰. Another major ontogenetic change relates to the relative sizes of the rectrices and remiges. The remiges are much smaller than the rectrices in STM4-1, but in STM22-6 the size difference is much less significant. This implies that the rectrices and remiges developed at unequal rates in *Similicaudipteryx*, possibly reflecting an increase in the functional role of the remiges as the individual approached adulthood.

However, the most striking ontogenetic difference is the contrast between the fully pennaceous remiges and rectrices of STM22-6 and their unusually constructed counterparts in STM4-1, which are proximally ribbon-like but have pennaceous distal tips. In modern

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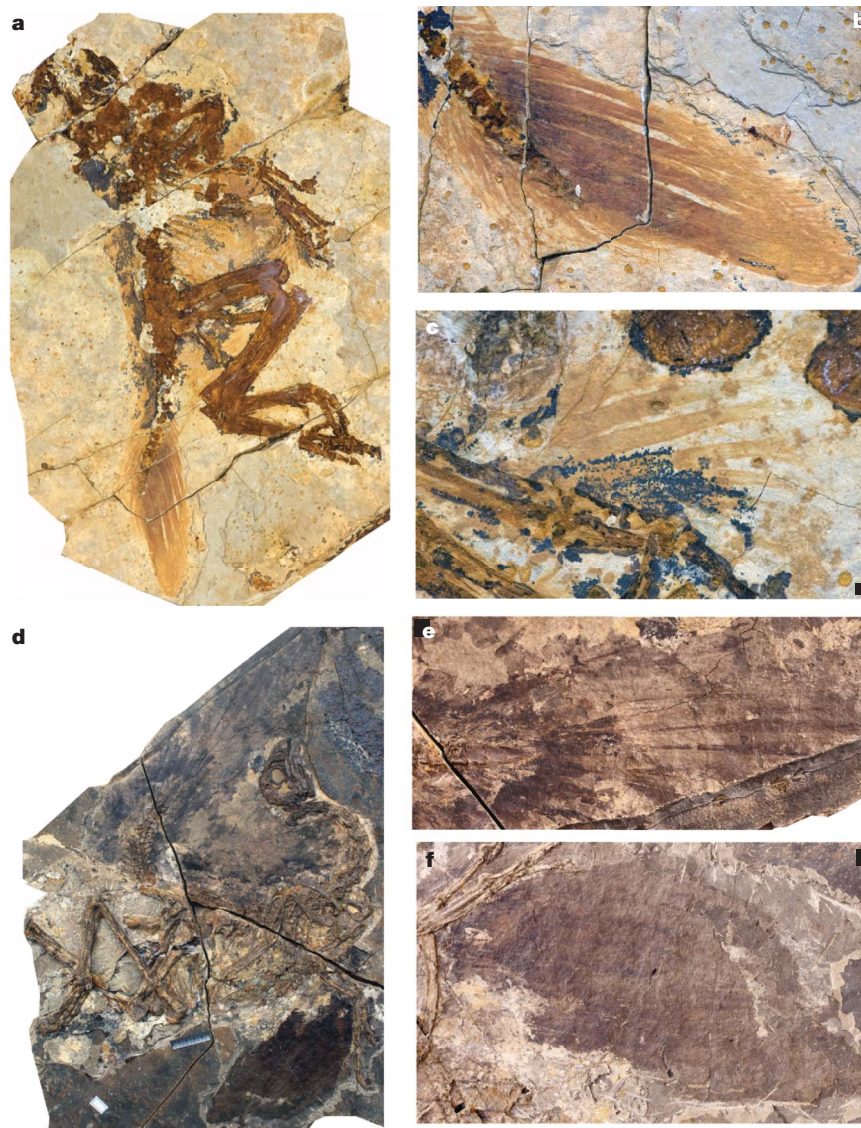


Figure 1 | Feathers of two *Similicaudipteryx* specimens. **a**, Slab of specimen STM4-1; **b**, rectrices of STM4-1 (slab); **c**, primary remiges of STM4-1 (counterslab). **d**, *Similicaudipteryx* specimen STM22-6; **e**, rectrices of STM22-6; **f**, remiges of STM22-6.

birds, remiges and rectrices change little in general morphology after the first feather generation (natal down)¹⁰. The remiges and rectrices in STM4-1 and STM22-6 are apparently not natal down, but they are

significantly different from each other, suggesting that significant morphological changes took place in feather development even after the hatching stage. This phenomenon is not known to occur in modern birds.

The existence of these two different morphotypes suggests that *Similicaudipteryx* displayed moulting of feathers during development, as in modern birds. Alternatively, the morphotypes may represent changes in a single feather generation, but this is much less likely given the striking difference between them and the considerable size difference between the two specimens (STM4-1 is less than 30% as large as STM22-6, judging by femoral length). Furthermore, these two morphotypes are inferred to represent relatively early generations of remiges and rectrices, given the juvenile status of both STM4-1 and STM22-6, but it is likely that an even earlier generation represented by a different morphotype (that is, natal down) was present in *Similicaudipteryx* and that additional generations were present between the ones seen in STM4-1 and STM22-6.

Proximally ribbon-like pennaceous feathers (PRPFs) similar to those seen in STM4-1 are also known in confuciusornithids^{4,17} and some other basal birds¹⁸. The ribbon-like tail feathers previously reported in a specimen of the enantiornithine *Protopteryx*¹⁹ and a specimen of the non-avian maniraptoran *Epidexipteryx*¹² are in fact incompletely preserved tail feathers that are proximally ribbon-like

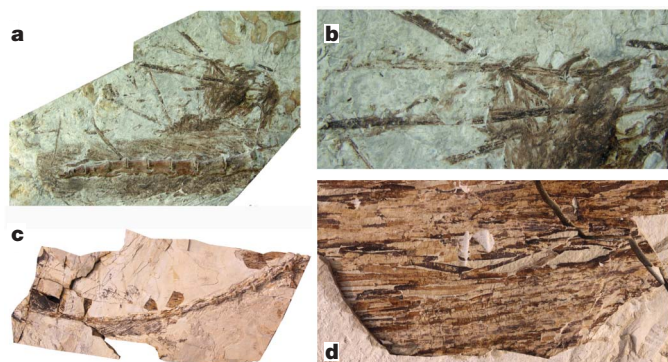


Figure 2 | Elongate broad filamentous feathers in selected non-avian theropods. **a**, Series of posterior caudal vertebrae and associated integumentary structures in a specimen of the therizinosauroid *Beipiaosaurus* (IVPP V11559); **b**, close-up of elongate broad filamentous feathers in IVPP V11559; **c**, series of posterior caudal vertebrae and associated integumentary structures in a large specimen that may represent a tyrannosauroid (STM1-5); **d**, close-up of EBFFs in STM1-5.

and do not show the pennaceous distal tip, as indicated by more complete specimens (Supplementary Information). Accordingly, PRPFs have a wide distribution among basal avians and non-avian maniraptorans. Although the primitive nature of PRPFs has been questioned^{1,5}, the developmental and phylogenetic distribution of this morphotype among basal avians and non-avian maniraptorans seems to record an early stage of feather evolution that is not represented in any surviving taxon (Supplementary Information).

In modern feathers, a synergistic system involving bone morphogenetic protein, noggin and sonic hedgehog has a key role in regulating the formation of the rachis and barbs, and the balance between these elements of the feather^{20–22}. Altering activation and expression of barb-specifier and interbarb-apoptotic genes could result in different morphotypes²³. For example, suppression of *SHH* could generate continuous feather vanes—essentially sheets of keratin not divided into barbs²¹. PRPFs are therefore likely to have developed as a result of low *SHH* expression and/or incomplete expression of barb-specifier and interbarb-apoptotic genes. In modern birds, these genes are activated and expressed very early in the growth of even very early generations of feathers. By comparison, activation of the equivalent genes during the growth of early feather generations in *Similicaudipteryx* was probably delayed and spatially incomplete, resulting in a partially, rather than fully, pennaceous morphology. In late juveniles of *Similicaudipteryx*, and presumably in adults, the barb-specifier and interbarb-apoptotic genes seem to have been expressed during feather growth as extensively as is the case in modern birds.

A limited expression of barb-specifier and interbarb-apoptotic genes might also have characterized the growth of certain more primitive feather morphotypes, such as the elongate broad filamentous feathers (EBFFs) first reported in two specimens of the therizinosauroid *Beipiaosaurus*²⁴ (Fig. 2a, b). Although the EBFFs and other recently reported primitive feather morphotypes have been claimed to represent partially decayed dermal collagen fibres rather than homologues of modern feathers²⁵, these claims are refuted by the presence of melanosomes in these filamentous integumentary structures²⁶ and by other lines of evidence (Supplementary Information). EBFFs have now also been observed in a large specimen that may be a tyrannosauroid (Fig. 2c, d), and an additional specimen that may be a compsognathid (Supplementary Information). EBFFs differ from the typical slender filamentous feathers of non-avian theropods in that they appear as broad, planar structures, and have been interpreted as monofilamentous feathers that had an elliptical cross-section before taphonomic compression²⁴. The EBFFs were probably simple in developmental terms, in that they might have developed without the expression of barb-specifier and interbarb-apoptotic genes and thus might each have grown from an epidermal collar that never differentiated into barb ridges²⁴.

Owing to the conservative nature of some developmental mechanisms, experimental data can have a key role in reconstructing the evolutionary history of important structures such as feathers^{7,27}. Our observations show, however, that the oviraptorosaurian *Similicaudipteryx* differs from modern birds in some aspects of remigial and rectricial development. In combination with data from other theropod fossils that preserve PRPFs and/or EBFFs (Supplementary Information), the discovery of the two oviraptorosaurian specimens described in this Letter suggests that early feathers were less constrained and more flexible in some developmental features than were their counterparts in modern birds. The PRPFs of many maniraptoran theropods, and the EBFFs seen in other, more basal, taxa, may have been produced by a developmental programme in which the expression of barb-specifier and interbarb-apoptotic genes was reduced, delayed or even absent. In any case, these feather types have been lost in the course of evolution, implying that the developmental mechanisms underlying their morphologies are also extinct (Fig. 3 and Supplementary Information). Although our observations are largely consistent with the concept of a barbs-to-rachis-to-vane evolutionary sequence (Fig. 3) that has been supported by data from

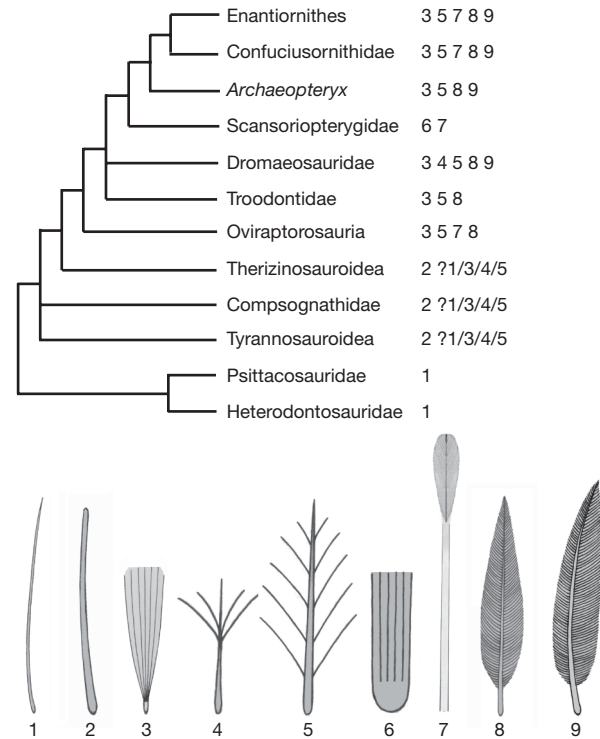


Figure 3 | Known feather morphotypes across a simplified dinosaurian phylogeny. Many dinosaurian groups, such as most ornithischians, the sauripodomorphs and the basal theropods, are not included in this simplified dinosaurian cladogram. The available specimens suggest that members of these groups have scaly skin, but the possibility that they are partially covered by filamentous integumentary structures cannot be completely excluded. Preservational factors make it difficult to observe the detailed structure of the filamentous feathers in available specimens of compsognathids, tyrannosauroids, and therizinosauroids, and thus we use a '?' to indicate uncertainty regarding the presence of morphotypes 1, 3, 4 and 5 in these groups. On the basis of the anatomical, ontogenetic and phylogenetic distribution patterns of known feather morphotypes among non-avian dinosaurs and early birds, morphotypes 1, 2 and 7 are inferred to have been lost in feather evolution, along with their associated developmental mechanisms. (For a more detailed interpretation, see Supplementary Information.)

both palaeontology and developmental biology^{5,20,28,29}, the real pattern seems to have been more complex in both evolutionary and developmental terms.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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