

SUPPLEMENTARY INFORMATION

1. Preservation of STM4-1 and STM22-6

STM4-1 represents a complete skeleton with integumentary structures preserved on part and counterpart slabs. STM22-6 is a nearly complete skeleton with integumentary structures preserved on a single slab. Both specimens were collected by local farmers and purchased by the Tianyu Museum of Nature. Because many specimens of feathered non-avian dinosaurs and early birds from the Lower Cretaceous Jehol Group of western Liaoning, China have been artificially modified^{1, 2}, we carefully examined the specimens under high-magnification microscopes to guarantee that information recovered from them is reliable.

Both STM4-1 and STM22-6 were broken into several pieces, and were glued together by the collectors. This is common for specimens from the Jehol Group, because normally these specimens are preserved on relatively thin slabs of shale that are easily broken during collecting. Detailed features of both the matrix and the skeletons suggest that both specimens were correctly assembled without any manmade modifications, according to our extensive and careful observations (the observed morphological features of both the skeletal elements and the soft tissue appear entirely natural, as does the matrix). The part and counterpart slabs of STM4-1 match perfectly in all features (including soft tissue morphology), except that the counterpart slab is missing some parts (for example, the distal end of the tail). We can therefore declare that the information recovered from these specimens is authentic.

2. Identification of STM4-1 and STM22-6

Both STM4-1 and STM22-6 are referable to the Oviraptorosauria based on their general morphological features, and on several specific features uniquely shared with other oviraptorosaurs¹⁶: skull with short preorbital region; premaxilla with large main body; dorsally positioned external naris; large mandibular fenestra; long retroarticular process; and anteriorly curved pubic shaft^{16, 17}. In all known oviraptorosaurs, except those from Liaoning, in which the jaw morphology is known, the upper and lower jaws both lack dentition. STM4-1 and STM22-6 bear teeth and are thus different from toothless, relatively derived members of the group and more similar to the toothed oviraptorosaurs from the Jehol Group.

Four oviraptorosaurian genera have been previously from the Jehol Group³⁻⁵, a relatively high diversity from a single geological unit by the standards of this group⁶. Among known oviraptorosaurs from Liaoning, STM4-1 and STM22-6 differ from *Caudipteryx* in that the fourth manual digit is not reduced⁷. Furthermore, STM22-6 differs from *Caudipteryx*, *Protarchaeopteryx* and *Incisivosaurus* in several cranial features^{3, 4, 7}, including: more triangular lateral skull profile; jugal with basally constricted anterior ramus and short, posteriorly curved ascending ramus, accessory fenestra anterior to mandibular fenestra; and large surangular foramen. STM4-1 and STM22-6 are nearly identical in the morphology of all preserved overlapping elements to *Similicaudipteryx*, a basal oviraptorosaur recently reported from the Yixian Formation of Jehol Group⁵. This strong similarity exists even though the *Similicaudipteryx* holotype, a probable adult with a femur length of 220 mm, is much larger than the new juvenile specimens. Therefore, we tentatively refer STM4-1 and STM22-6 to *Similicaudipteryx*.

Admittedly there are some minor differences between STM4-1, STM22-6, and the *Similicaudipteryx yixianensis* holotype. Most of these differences pertain to the relative lengths of limb elements (Table S1), and these proportional differences can be interpreted as ontogenetic variations and are consistent with patterns of ontogenetic change in other theropods^{8, 9}. In fact, the relative lengths of the limb elements in STM4-1 are more similar to STM22-6 and *Similicaudipteryx yixianensis* holotype than to other Liaoning oviraptorosaurs, providing additional evidence for the referral of STM4-1 to *Similicaudipteryx*. However, STM4-1 lacks a pygostyle, a structure present in both STM22-6 and the *Similicaudipteryx yixianensis* holotype. The most posterior caudal vertebrae probably fused to each other to form a pygostyle relatively late in the ontogeny of basal avians (for example, GMV-2159, an enantiornithine specimen housed in the National Geological Museum of China, Beijing)¹⁰, and this was presumably also true of *Similicaudipteryx*. Consequently, the absence of a pygostyle STM4-1 is probably due to its early ontogenetic stage.

Table S1. Relative proportions of selected elements in Liaoning oviraptorosaurs

length ratio	<i>Caudipteryx</i>	<i>Protarchaopteryx</i>	STM4-1	STM22-6	<i>Similicaudipteryx</i>
Scapula/humerus	1.10		0.84	0.93	
Humerus/femur	0.47	0.72	0.63	0.58	*0.59
Tibia/femur	1.20	1.30	1.28	1.30	
Radius/humerus	0.90	0.80	0.86	0.85	
Manus/humerus	1.20	1.60	1.67	1.61	
Manus/Femur	0.60	1.20	1.05	0.95	

3. Additional photographs of STM4-1 and STM22-6



Figure S1 Photograph of counter slab of STM4-1.

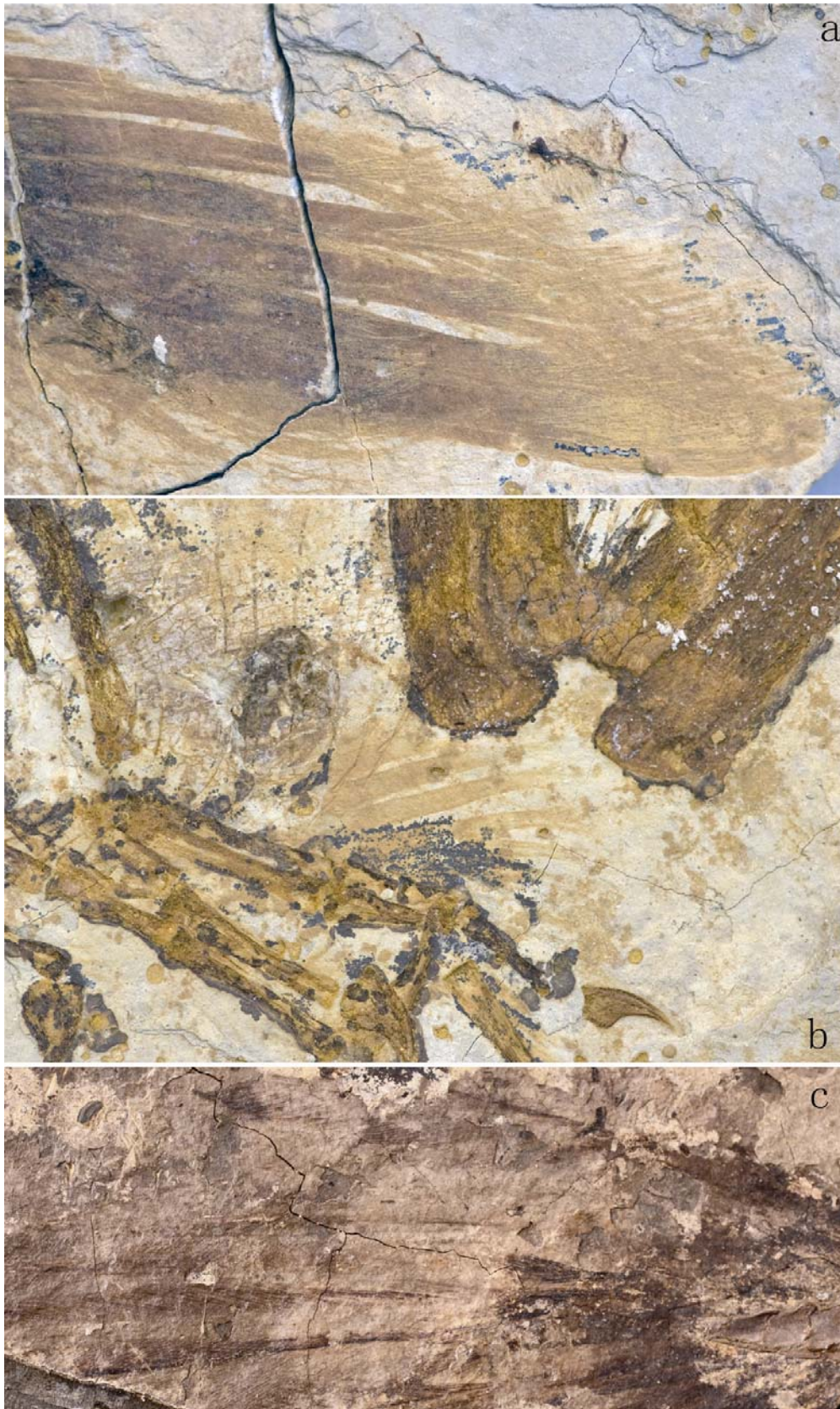


Figure S2. Photographs of remiges and rectrices in *Similicaudipteryx*. a, STM4-1, tail feathers; b, STM4-1, remiges; c, STM22-6, tail feathers

4. Additional description of proximally ribbon-like feathers and elongate broad filamentous feathers

PRPFs were first reported in a specimen of the enantiornithine *Protopteryx*¹¹, and subsequently in a specimen of the non-avian maniraptoran *Epidexipteryx*¹². They were originally proposed to represent a plesiomorphic morphotype¹¹, but this has since been questioned^{13,14}. More complete specimens indicate that the ribbon-like tail feathers reported in the holotype of *Protopteryx* are in fact incompletely preserved tail feathers with proximally ribbon-like vanes missing the pennaceous distal tip (See Figs. 1-59-1, 2, 3, 4, 5, and 6 in ref. 15)¹⁵. This is probably also true for the holotype specimen of *Epidexipteryx*. Consequently, the “ribbon-like” feathers of *Protopteryx* and *Epidexipteryx* are similar in general morphology to the PRPFs seen in the oviraptorosaurian *Similicaudipteryx*. Because PRPFs in STM4-1 are completely preserved and all display the same morphological features (i.e., proximally ribbon-like and distally pennaceous) even though they are from different body regions (limbs and tail), we can guarantee that the PRPFs in STM4-1 represent a true morphotype in *Similicaudipteryx* and information recovered from them is reliable. In addition to the above-mentioned taxa, PRPFs are also known in confuciusornithids^{2, 16} and some other basal birds^{15, 17}. Consequently, PRPFs have a wide distribution among non-avian maniraptorans and basal birds, probably representing a distinct category of early feathers.

However, it is noteworthy that the basic ribbon-like morphology exhibits both anatomical and developmental variations among these taxa. In most taxa, the ribbon-like morphology is seen only in the rectrices, and persists at late ontogenetic stages; in *Similicaudipteryx* this morphology is present in both the rectrices and remiges of young juveniles, but is absent in older juveniles and presumably in adults. The last major difference lies in the detailed architecture of the ribbon-like structure. In *Similicaudipteryx*, the ribbon-like structure is composed of a single undifferentiated sheet of keratin in the proximal portion of the feather (Fig. S3a). In other known examples, the ribbon-like structure is composed of two vanes divided longitudinally by a median line, which was identified as a rachis by previous studies^{11,12}. However, the barbs are not attached to the identified ‘rachis’, but instead extend out from along the clearly defined edges of the sheet-like central part of the vane (Figs. S3b-d).

Elongate broad filamentous feathers (EBFFs) were first reported in two specimens of the therizinosauroid *Beipiaosaurus*¹⁸. They coexist with normal, slender filamentous feathers in the same specimens, but are limited in their distribution on the body¹⁸. EBFFs also have a wide phylogenetic distribution according to our recent observations of various non-avian theropod specimens. In a large specimen that may be a tyrannosauroid, EBFFs are attached to the caudal vertebrae and are about 10 mm in width. In a specimen that may be a compsognathid, numerous slender filamentous feathers cover the whole skeleton, but some EBFFs are present and are more than 1 mm in width.



Figure S3 Ribbon-like feathers in *Similicaudipteryx* and other extinct theropods. a, reconstructed proximally ribbon-like feather of *Similicaudipteryx*; b, reconstructed proximally ribbon-like tail feather of the type present in other known extinct maniraptorans; c, proximally ribbon-like tail feather of an enantiornithine specimen (STM34-7, Figure 1-59-6 in ref. 15); d, proximally ribbon-like tail feathers in a confuciusornithid specimen (STM13-53, Figure 1-59-2 in ref. 15).

5. Homologies of elongate broad filamentous feathers (EBFFs) and other primitive feathers

Immediately after the initial reports of the first feathered dinosaur *Sinosauropteryx*^{19, 20}, questions were raised as to whether the filamentous structures preserved on *Sinosauropteryx* specimens were homologous to modern feathers²¹. Subsequently, a series of studies by Lingham-Soliar and colleagues provided further arguments against the identification of filamentous integumentary structures including EBFFs as primitive feathers, suggesting instead that these structures represent decayed collagen fibers²²⁻²⁵.

Here we briefly comment on the evidence against the identification of filamentous integumentary structures as primitive feathers adduced by Lingham-Soliar and colleagues, and demonstrate that filamentous integumentary structures including EBFFs are indeed best regarded as primitive feathers. There are numerous misinterpretations of our previous studies in publications by Lingham-Soliar and colleagues²²⁻²⁵, but we will not address these points here. We will simply list a few lines of evidence supporting our previous identifications and refuting the hypothesis that the filamentous integumentary structures are collagen fibers.

1) The relatively large size of the filamentous integumentary structures in non-avian dinosaur specimens supports the feather interpretations. We agree that collagen fibers are superficially similar in general morphology to the filamentous integumentary structures, and both are somewhat similar to downy feathers. However, the examples of collagen fibres that have been presented, including those from ichthyosaur specimens, are proportionally very small relative to the organisms in question. In contrast, the filamentous integumentary structures on all non-avian theropod specimens are proportionally much larger (in terms of both the length and the width of each individual filament) and in fact are more comparable in size to feathers²⁶.

2) The anatomical distribution patterns of the filamentous integumentary structures in various non-avian dinosaur specimens support the feather interpretations. Although many specimens of non-avian dinosaurs preserve feathers of primitive or modern aspect, exceptionally well preserved specimens are still rare. For example, only a few *Microraptor* specimens preserve feathers of different types around the whole skeleton, and in most *Microraptor* specimens soft tissue is either absent or restricted to large pennaceous feathers near the limbs and tail. Nevertheless, a characteristic general distribution pattern of feathers of primitive or modern aspect is present in non-avian dinosaur specimens. The longest feathers are always those near the limbs and the distal end of tail, a pattern similar to that seen in modern birds. Also, the feathers are almost invariably more or less perpendicular to the long axes of the limbs and tail. A striking example is provided by the long filamentous integumentary structures on the forearms of the *Beipiaosaurus inexpectus* holotype, which are very long and perpendicular to the forearms. There is no evidence supporting a similar distribution pattern for collagen fibres.

3) The taphonomic characteristics of the filamentous integumentary structures in non-avian dinosaur specimens support the feather interpretations. Nearly all filamentous integumentary structures and feathers of modern aspect are preserved as dark carbonized impressions in both non-avian and avian specimens from the Jurassic and Cretaceous sediments of northeastern China. This pattern might be related to the keratinous nature of

feathers of primitive and modern aspect and the unique preservational processes associated with these strata (involving, for example, volcanic activity), but this needs further work. However, there is no evidence that collagen fibres can be preserved as dark carbonized impressions.

4) The presence of melanosomes in the filamentous integumentary structures supports the feather interpretations. Feathers can be easily differentiated from collagen fibers by the presence of melanosomes, structures that are important for the colouring of the feathers. Melanosomes have recently been identified in some specimens of avian feathers^{27, 28}, and most recently even in feathers of both primitive and modern aspect in non-avian dinosaurs²⁹. The discovery of melanosomes in the filamentous integumentary structures of some non-avian dinosaurs provides unambiguous evidence supporting the feather interpretations for these structures²⁹.

6. Major feather morphotypes documented in non-avian theropods

Feathers of either primitive or modern aspect have been documented in most non-avian coelurosaurian theropod groups²⁶. However, these feathers have been identified purely on the basis of morphological information. Although the morphological evidence for these identifications is overwhelming, extending even to the microscopic level²⁹, it is admittedly true that morphological features of fossil feathers in non-avian theropods can sometimes be ambiguous owing to imperfect preservation and the difficulty of observing some structural details. For example, in most feathers found in non-avian theropod specimens, it is not known whether barbules and after-feathers are present²⁶, or whether the vanes of the pennaceous feathers have a basal downy portion. Consequently, drawing correspondences between fossil and modern feathers is sometimes difficult, although some typical features of modern feathers such as branching and planar form can be confirmed in some fossil feathers. In context of the present study, it is currently hard to determine whether EBFFs are homologous to filoplume feathers and whether PRPFs are homologous to the highly specialized barbless tail feathers that occur in some modern birds, although some morphological similarities are definitely present in each of these cases. If these homologies are indeed valid, the phylogenetic and ontogenetic distribution patterns of the EBFFs and PRPFs would support the primitive nature of the filoplume feathers and barbless tail feathers of some modern birds.

Nine major feather morphotypes have been reported and identified in non-avian dinosaurs and Mesozoic birds²⁶, and only some of these morphotypes can be easily determined to correspond with modern feather types. A lack of correspondence does not, however, necessarily refute a homologous relationship, as discussed above.

Morphotype 1 is known from the heterodontosaurid *Tianyulong*³⁰ and possibly the ceratopsian *Psittacosaurus*³¹, and is characterized by its monofilament structure and relatively great length and rigidity. Morphotype 2 (EBFF) is also monofilamentous but differs from Morphotype 1 in its great width. It is seen in the therizinosauroid *Beipiaosaurus*¹⁸, a large unnamed tyrannosauroid, and a large compsognathid specimen. Morphotype 3 is a compound structure composed of multiple filaments joined basally. This morphotype is present in the dromaeosaurid *Sinornithosaurus*³² and the troodontid *Anchiornis*³³, and probably also in the compsognathid *Sinosauropteryx*, the tyrannosauroid *Dilong*, and *Beipiaosaurus*. Morphotype 4 is seen in the holotype of the dromaeosaurid *Sinornithosaurus millenii* and probably also in *Beipiaosaurus*³⁴, and is characterized by short barbs that radiate from the tip of a central filament. Morphotype 5 is a compound structure consisting of multiple filaments branching laterally from most of the length of a central filament, and is known in *Sinornithosaurus*, *Anchiornis*, the oviraptorosaurians *Caudipteryx* and *Protarchaeopteryx*, and probably *Dilong*. Morphotype 6 is only known in the basal avialan *Epidexipteryx*, and is characterized by parallel barbs arising from the edge of a membrane structure¹². Morphotype 7 (PRPF) is present in the oviraptorosaurian *Similicaudipteryx*, in *Epidexipteryx*, and in many basal birds, and is characterized by a flat, broad, barbless proximal shaft with a pennaceous distal portion. It is noteworthy that some minor variations exist among different taxa displaying this morphotype (see discussion above). Morphotype 8 is known in *Caudipteryx*, *Protarchaeopteryx*, *Anchiornis*, and the dromaeosaurid *Microraptor*, and comprises fully pennaceous feathers that each have a prominent rachis and well

organized, symmetrical vanes. Morphotype 9 is only known in *Microraptor* among non-avian theropods (though some feathers of *Anchiornis* resemble Morphotype 9 in having a slightly curved rachis) and is similar to Morphotype 8 in general morphology, but differs in that the vane is asymmetric and the rachis curved.

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