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Additional information on the primitive contour and wing feathering of paravian dinosaurs

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**ABSTRACT:** Identifying feather morphology in extinct dinosaurs is challenging due to dense overlapping of filaments within fossilized plumage and the fact that some extinct feather morphologies are unlike those seen in extant birds or those predicted from an ‘evo-devo’ model of feather evolution. Here, comparisons are drawn between a range of dinosaur taxa with preserved integumentary appendages using high resolution photographs to better understand fossil feather morphology and gain insight into their function and evolution. A specimen of the basal paravian *Anchiornis* possesses contour feathers disarticulated from the plumage, revealing a novel feather type much simpler than the contour feathers of most extant birds – a ‘shaggy’, open-vaned, bifurcated feather with long barbs attached to a short rachis. In contrast, the contour feathers of the *Sinosauropteryx* contour feathers are likely simpler than those seen in *Anchiornis*; a ‘tuft’ morphology of multiple barbs connected at their bases (e.g. via a shared follicle), but lacking a rachis, is tentatively preferred. However, unless isolated *Sinosauropteryx* contour feathers are discovered in the manner of the *Anchiornis* specimen, conclusive morphological descriptions will

remain difficult. In addition to contour feathers, preserved paravian wing feathers also show potentially plesiomorphic traits. Comparison with *Confuciusornis* suggests that *Anchiornis* wing feathers were at least partially open-vaned. Combined with the interpretation of *Anchiornis* contour feathers, this suggests that differentiated barbicels are relatively derived compared to pennaceous feathers and the appearance of wings. ‘Shaggy’ contour feathers likely influenced thermoregulatory and water repellence abilities, and in combination with open-vaned wing feathers, would have decreased aerodynamic efficiency. Simplified, open-vaned wing feathers were also observed on the oviraptorosaur *Caudipteryx*, *consistent with, but not necessarily diagnostic of, its suggested flightlessness*. Taken together, these observations have broad implications for how we depict a wide variety of dinosaurs and how we view the function and evolution of feathers in these taxa.

**KEY WORDS:** dinosaur, theropod, paravian, contour feathers, wing feathers, plesiomorphy, barbules

INITIAL descriptions of feathered non-avian dinosaurs (e.g. Chen *et al.* 1998; Xu *et al.* 1999, 2000) have been followed by a flurry of fossil discoveries preserving integumentary soft tissues in this group (e.g. Norell & Xu 2005; Xu 2006; Hu *et al.* 2009; Zelenitsky *et al.* 2012). Filamentous integumentary structures have even been found on ornithischian dinosaurs (Mayr *et al.* 2002; Zheng *et al.* 2009a; Godefroit *et al.* 2014), although the homology of such structures to true feathers has not been determined (Barrett *et al.* 2015; Mayr *et al.* 2016). The evolution of feathers has become a major research topic in evolutionary biology and palaeontology. A commonly cited model for feather evolution is based on an understanding from feather development in modern birds, the ‘evo-devo’ approach (Prum & Brush 2002), but fossil feathers that do not match expected morphologies based on feather development (Zhang *et al.* 2008) show that such a model for feather evolution, while useful, is likely overly simplified and that extinct feather morphologies existed, distinct from modern feathers.

Determining the morphology of a single integumentary appendage can be difficult when such structures are preserved as dense plumage around a specimen. Descriptions can also become outdated with the discovery of more specimens that provide novel or clearer morphological details. Improved understanding of fossil feather morphology provides better insight into their function with implications for the evolution of avian flight, a key adaptation. This is important as many bizarre forms of non-avian theropods appear to have evolved aerial locomotion (e.g. gliding) prior to the evolution of the modern bird body plan, such as ‘four-winged’ forms like *Microraptor* or *Anchiornis* (Xu *et al.* 2003; Hu *et al.* 2009; Palmer 2014) or even those with proposed membranous wings (Xu *et al.* 2015). Moreover, it is possible that some non-avian theropods, like *Caudipteryx* or *short-armed or large dromaeosaurs*, might even have been secondarily flightless (Feduccia 1999; Jones *et al.* 2000; Paul 2002; Zheng *et al.* 2009b; Lü and Brusatte 2015; Mayr 2017, but see

Dyke and Norell 2005; Dececchi *et al.* 2016 for counter-positions). However, it should be noted that there is a lack of consensus on secondary flightlessness in non-avian theropods as pennaceous wings have been hypothesized to have evolved prior to biomechanical functional usage (Zelenitsky *et al.* 2012). It has been suggested that subsequent locomotory functions of the wing might have involved pre-aerial locomotion such as ‘flap running’, ‘wing-assisted incline running’, and ‘wing-assisted leaping’ (Heers *et al.* 2014; Dececchi *et al.* 2016).

Beyond investigating the evolution of flight, body contour feather evolution is particularly important. Contour feathers evolved prior to flight feathers as seen by taxa like *Sinosauroptryx*, which possess filamentous structures around the majority of its body but lack rectrices and remiges as well as skeletal adaptations for aerial locomotion (Chen *et al.* 1998; Currie & Chen 2001). Contour feathers also play key functional roles beyond aerodynamic streamlining such as thermoregulation, water repellence, or display (Lucas & Stettenheim 1972). Thus, understanding the evolution of contour feathers should provide insight into the function of the earliest feathers and the palaeobiology of extinct species beyond aerodynamic capability.

The main goal of this study is to better understand fossil feathers in non-avian theropod dinosaurs. In providing new feather data from a phylogenetic range of fossil dinosaurs, we aim to identify potential plesiomorphies, highlight challenges in their study, and gain greater insight into paravian feather function and evolution.

## **MATERIAL AND METHODS**

High resolution photographs of several non-avian and avian dinosaur taxa with preserved integumentary structures were taken using a Nikon D800 camera and a 60 or 105 mm macro

Nikkor lens in a crossed polarised light configuration with a Lowell Totalight 800W or 400W tungsten bulb: *Psittacosaurus* (SMF R 4970), *Sinosauroptryx* (NIGP 127586, NIGP 127587), *Caudipteryx* (IVPP V12344, IVPP V12430), and *Confuciusornis* (IVPP V13156). *Anchiornis* (BMNHC PH828) was photographed using the 60 mm macro Nikkor lens on a Nikon D90 under normal incandescent light at different angles. The taxa represent a phylogenetically broad sampling within Dinosauria. *Psittacosaurus* and *Confuciusornis* represent taxa whose integumentary appendages can be thought of as fairly well understood ‘end-members’ of feather-like integument evolution. *Psittacosaurus* had long, simple, non-branching, bristle-like filaments that potentially occurred in clusters (Mayr *et al.* 2016), and *Confuciusornis* is expected to have relatively more derived feathers compared to the more basal taxa (Chiappe *et al.* 1999; Prum & Brush 2002; Fucheng *et al.* 2006, but see Feo *et al.* 2015), at least with regards to its wing feathers. Importantly, the specimen of *Anchiornis* (BMNHC PH828) possesses isolated contour feathers that have been transported away from the rest of the plumage, allowing for easier interpretation of their morphology. The isolated contour feathers on this specimen were first figured by Li *et al.* (2010) in their supporting online material but were not thoroughly discussed. Using this specimen and the inclusion of relatively ‘end-member’ examples, we hope to better elucidate the less understood feather morphology of non-avian theropods through comparison.

Interpretive drawings are included to better portray certain observations. These also allow for testing the hypothesis that overlapping patterns of the plumage are influenced by the morphology (i.e., branching pattern) of a single integumentary structure.

Fig. 1A–F shows some of the studied specimens and the locations where detailed observations/comparisons of feathers were made.

Contour feathers in *Anchiornis* and *Sinosauropteryx* are first discussed to highlight possible plesiomorphies among extinct contour feather morphologies and the challenges of interpreting articulated fossil plumage, followed by a discussion of potential plesiomorphies in dinosaurian wing feathers and how feather morphology in secondarily flightless taxa may provide ecological rather than evolutionary signals. The taphonomic history of these specimens, in which they are sub-aqueously buried, should not affect feather morphology as sediment works to keep tissues in place and feather barbs only clump together when removed from water, not upon submersion.

#### *Institutional abbreviations*

BMNHC, Beijing Museum of Natural History, Beijing, China; IVPP, Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, China; NIGP, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Beijing, China; SMF, Forschungsinstitut Senckenberg, Frankfurt am Main, Germany

## **RESULTS**

#### *Anchiornis isolated contour feathers – a novel morphotype*

Isolated contour feathers in the *Anchiornis* specimen BMNHC PH828, disarticulated and transported away from the rest of the plumage, reveal the morphology of these feathers more clearly than do those in the articulated plumage (Figs. 2A–B, 3A–E). Most of the isolated feathers

are about 1–2 cm long. They appear to show two vanes of long barbs positioned at low barb angles to a relatively short rachis in a presumably pennaceous configuration. Barbs extend significantly beyond the apical tip of the rachis, resulting in a ‘shaggy’ morphology noticeably bifurcated towards its apical end in some of the isolated feathers. In those feathers that show significant bifurcation, the apical region (i.e. towards the apical tips of the barbs) are blunt or ‘squared-off’ on each vane (Fig. 3A–D), suggesting that barbs originating at different positions along the rachis terminate at a similar point and that the more basal barbs are longer than the distal barbs.

The barbs do not always show tight association to each other and can diverge and strongly curve. This suggests an open vane lacking properly differentiated proximal and distal barbules. An open vane with flexible barbs, along with variation in the angle at which the feather is exposed in the matrix, could explain why some of the isolated contour feathers do not appear to bifurcate strongly at their apical ends, although a similar disparity in *Sinornithosaurus* was attributed to the presence of two contour feather morphotypes (Xu *et al.* 2001).

One isolated feather has a ‘trident’ appearance (Fig. 2A). Most likely, this feather is the disarticulated apical end of a secondary remex or major covert (these being located near the isolated contour feathers observed on the specimen). The ‘trident’ appearance results from colour patterning in a feather whose morphology is consistent with the other remiges and major coverts.

#### *Sinosauropteryx non-isolated contour feathers – interpreting highly primitive morphotypes*

With a better understanding of basal paravian *Anchiornis* contour feather morphology, the contour feathers of the basal coelurosaur *Sinosauropteryx* are re-examined. Comparing filament overlapping patterns within the articulated plumage between *Sinosauropteryx* and better



understood taxa like *Psittacosaurus* and *Anchiornis* (Fig. 4) shows how integumentary appendages with different branching patterns can lead to similar overlapping patterns within the articulated plumage.

*Psittacosaurus* bristles have been suggested to be developmentally and/or structurally homologous at some level to bristle-like structures in other dinosaurs, *Tianyulong* and *Beipiaosaurus* (Xu *et al.* 1999; Zheng *et al.* 2009a; Mayr *et al.* 2016). The interpretation of *Psittacosaurus* bristle morphology here is based on that of Mayr *et al.* (2016). Non-branching *Psittacosaurus* bristles (Fig. 4A–B) show filaments that curve in the same direction and manner. Near the skin, low angle, short filaments overlap higher angle, long filaments. Filaments originating more anteriorly along the tail can overlap more posterior filaments as they curve posteriorly. As a result, there is also an overlapping pattern further away from the skin where low angle, apical portions of anteriorly erupting bristles cross over the high angle, basal portions of posteriorly erupting bristles.

Filaments of *Sinosauropteryx* contour feathers (Fig. 4C–D) show many similar overlapping patterns, although the structures are much shorter and the plumage is denser. Like *Psittacosaurus* bristles, *Sinosauropteryx* filaments separate from each other and become more easily distinguishable apically. Theoretically, simple, singular, non-branching filaments could create such overlapping patterns that might give the illusion of branching integumentary structures, especially if they are arranged in multiple tracts on the body (Saitta *et al.* 2017a).

However, filament orientations of contour feathers on the hindlimb and pes of *Anchiornis* (present in addition to remiges/major coverts on the hindlimbs) also show a similar overlapping pattern and are much closer in size to *Sinosauropteryx* feathers (Fig. 4E–F). *Anchiornis* contour feather morphology was determined above by examining isolated feathers near the torso (Fig. 2),

a method inapplicable to known *Sinosauropteryx* specimens. There are additional isolated contour feathers near the pes consistent with the interpreted morphology. Therefore, the similar overlapping pattern seen in *Psittacosaurus*, *Sinosauropteryx*, and *Anchiornis* results from a range of integumentary appendage morphologies.

Based on overlapping alone, *Sinosauropteryx* contour feathers might represent one of a range of plausible morphologies – from simple, singular, non-branching filaments, to non-branching filaments connected at their bases (e.g. via a calamus or shared follicle), to a morphology seen in *Anchiornis* with multiple barbs connected to a short rachis. Further observations are therefore needed and may benefit from additional imaging using new techniques such as the laser stimulated fluorescence (LSF) used on *Psittacosaurus* (Mayr *et al.* 2016) and other integument-bearing non-avian dinosaurs (Wang *et al.* 2017a; Xu *et al.* 2017).

As in original descriptions (Chen *et al.* 1998; Currie & Chen 2001), this study noticed a mixture of thick and thin strands close to the body (Fig. 4C–D). However:

1. Some areas show relatively thick strands away from the body. Thick strands away from the body are likely due to close-lying or overlapping thinner filaments.

2. Unlike previous descriptions (Chen *et al.* 1998; Currie & Chen 2001), streaks near the base are not always positioned at a higher angle (although thicker strands near the base do tend to be at high angles). Low angle strands near the body could be the apical ends of feathers that erupt from relatively lateral tracts.

3. Furthermore, finer strands often appear parallel to each other and usually curve posteriorly rather than branching off equally from larger strands in opposing directions as previously described (Currie & Chen 2001).

These observations might suggest that relatively simple feathers (e.g. lacking a rachis) are possible for *Sinosauropteryx*.

One perplexing observation was of several adjacent thick streaks away from the body dorsal to the cervical vertebrae in NIGP 127587 (Fig. 5A–C). They resemble modern developing feathers contained in a sheath where the apical-most barbs separate as they erupt from the sheath. Whether such a developmental pattern might suggest a relatively complex morphology in which a rachis is present is unknown. However, some of these streaks appear to curve at their basal ends, which might be less likely to occur if they were encased in a sheath (although such a sheath could have been relatively pliable). It is also unusual that several adjacent feathers would all be growing/molting in one specific region on such a large specimen. Finally, no traces of calcium phosphate are visible under normal light photography which would give strong evidence for the presence of a calcified, stiffened rachis or sheath (Pautard 1963; Vinther *et al.* 2016; Saitta *et al.* 2017b). Other fossil coelurosaurs with similar structures have been suggested to preserve developing feathers (Prum 2010).

This study corroborates previous descriptions (Chen *et al.* 1998; Currie & Chen 2001) of regularly spaced, high angle, thick streaks close to the body (Fig. 4C–D). These thick streaks suggest a morphology where multiple barbs attach at their bases but lack a rachis. Multiple filaments are present in clusters or ‘tufts’, merging downward to a basal point. The ‘tuft’ is continuous to the base, suggesting that the barbs are not attached to a short rachis. If there was a short rachis, filaments would appear to emanate from a narrow strip. Instead, filaments do not branch from a point distal to the base. The thick basal region is of uniform thickness throughout, and at the distal end, it separates into smaller filaments. The *Sinosauropteryx* ‘tuft’ (Fig. 3F–G) starkly differs from isolated *Anchiornis* contour feathers (Fig. 3A–E). Multiple filaments clumping

into ‘tufts’ with a single basal origin also provide evidence against the prevalence of single, non-branching filaments in the contour feathering of *Sinosauropteryx*.

#### *Beyond contours – possible plesiomorphic traits in wing feathers*

Not only are *Anchiornis* contour feathers of interest, but their wing feathers also show unusual morphology. The remiges have fairly symmetric vanes as described by Hu *et al.* (2009) but some primary remiges show slight levels of curvature in the rachis (Fig. 6A–B).

The barbs within *Anchiornis* remiges and major coverts do not lie close together, especially at their tips (Fig. 6A–E). As they extend away from the rachis, they separate, and this pattern is less noticeable in barbs originating very apically along the rachis. This suggests, at the very least, an open feather vane in the tips of barbs on the more basal regions of the remex and major covert. In light of the open vane of *Anchiornis* contour feathers, this suggests that, even in wing feathers, proximal and distal barb differentiation or functional barbicels were lacking.

This interpretation is bolstered by comparison with the closed vanes of *Confuciusornis* remiges (Fig. 6F–J). In these more derived feathers, barbs are closely positioned even as they extend away from the rachis, and adjacent barbs show similar patterns of displacement and curvature, indicating that they are zipped together via differentiated proximal and distal barbules.

#### *Caudipteryx simplified wing feathers – the evolutionary significance of simplicity*

The wing feathers in *Caudipteryx* are very unusual and greatly differ from remiges of modern flying birds (Fig. 7). The remiges (or major coverts) of one specimen (IVPP V12344) have an open

vane where the barbs are independent and separate from each other (Fig. 7A–B). The vanes are symmetric with a straight rachis. Another specimen (IVPP V12430) has feathers on its wings (presumably remiges or major coverts) with a more extreme open vane where long barbs curve flexibly and separate widely from each other to form a ‘frond’ shape feather (Fig. 7C–D). This specimen shows even more unusual structures near the distal end of its forelimb which might represent simplified contour feathers on the forelimb (Fig. 7E). They are disarticulated from the rest of the specimen and are long, curving, ribbon-like structures. Some potentially converge together at their base. Overall, the feathers on *Caudipteryx* wings are highly simplified compared to aerodynamically efficient modern flight feathers.

## DISCUSSION

### *Anchiornis isolated contour feathers – a novel morphotype*

Isolated contour feathers disarticulated from the plumage in *Anchiornis* allow for a much easier interpretation of their morphology. The ‘shaggy’, bifurcated morphology described here is a novel feather type (Fig. 8C) and further demonstrates how extinct feather morphologies prevent researchers from relying solely upon an ‘evo-devo’ model of feather evolution.

These feathers would have appeared open-vaned, and specialized barbicels like hooklets to differentiate proximal and distal barbules are possibly more derived characters than we may realize. Given that iridescence has been reported in paravians (Li *et al.* 2012), and iridescence is often produced in the barbules (Maia *et al.* 2011), it is plausible that *Anchiornis* did not lack barbules entirely (Li *et al.* 2010).

These contour feathers would have given at least adult *Anchiornis*, and possibly related non-avian theropods, a much ‘shaggier’ or ‘fuzzier’ appearance than typically depicted (Fig. 9), especially compared to most modern birds that have smooth, aerodynamic plumage (Fig. 8D–E), keeping in mind that plumage could have varied through ontogeny. Some non-avian theropods potentially had a superficially similar plumage to modern flightless birds like kiwis, bearing in mind that morphology differed at the level of individual feathers. Another paravian, *Serikornis*, is preserved with dramatically long, dense contour plumage (Lefèvre *et al.* 2017), consistent with the ‘shaggy’ appearance of paravian plumage suggested here. We hypothesize that the ‘shaggy’ plumage of *Anchiornis* affected physiology by altering heat retention (relative to the combination of modern down and contour feathers), decreasing water repellence, and decreasing aerodynamic efficiency by increasing drag in comparison to modern feathers, which are known to effectively function in such roles (Lucas & Stettenheim 1972). These proposed functional hypotheses should be rigorously and quantitatively tested in the future.

*Anchiornis* is a basal member of paraves and is very closely related to Aves, possibly suggesting that modern contour feathers are a feature exclusive to Avialae. *Sinornithosaurus* has been described with contour feather plumage consisting of two morphotypes. One morphology was described as multiple filaments connected to a central filament (Xu *et al.* 2001). Some of these contour feathers have become disarticulated and isolated from this specimen, and closely resemble those described here in *Anchiornis*. Therefore, *Sinornithosaurus* likely possessed the same ‘shaggy’, bifurcated contour feather morphology as *Anchiornis* – a sensible conclusion given the fact that *Sinornithosaurus* is a dromaeosaur and, therefore, also a paravian. The contour feathers of the paravian *Serikornis* were described in a similar manner with two morphotypes present, one with “bundles of filaments that are joined together proximally and remain nearly parallel as they

extend distally” and the other with a “well-defined rachis and transversely inserted barbs” (Lefèvre *et al.* 2017). Some of the epidermal structures found associated with *Yi*, another taxa that has been placed within Pennaraptora (in a clade sister to Paraves), are also similar to the contour feathers observed here for *Anchiornis* (Xu *et al.* 2015, see Figure 2e within).

#### *Sinosauropteryx non-isolated contour feathers – interpreting highly primitive morphotypes*

Given contour feather morphology in relatively derived theropods like *Anchiornis*, the basal coelurosaur *Sinosauropteryx* is also expected to show primitive contour feathers, however, a lack of isolated feather fossils makes morphological determinations challenging. Currie & Chen (2001) suggested that *Sinosauropteryx* feathers had central rachises and plumulaceous barbs based on the following observations: (1) a mixture of thin and thick strands close to the body; (2) thinner strands more frequent distally; (3) thick strands positioned close to the body and typically oriented at higher angles from the body than the more distal strands; (4) areas of many fine strands adjacent and parallel to each other and sometimes kinking together; and (5) finer strands tending to angle away on both sides from thicker structures. The observations made in this study largely agree with those of Currie & Chen (2001) with some differences. Regarding observations (1) and (3), this study also observed thicker filaments farther away from the body and some low angle streaks near the body. Regarding observation (5), this study observed that finer streaks tend to lie parallel and orient in common directions rather than branching of equally in different directions. Thinner strands being more frequent distally (2) could also occur in a simple, non-branching filament (e.g. *Psittacosaurus*) if the filaments taper in thickness apically or due to less filament overlapping away from the body resulting in more thin filaments being visible. Fine, parallel strands (4) do not

necessitate the presence of a rachis, although a rachis could organize strands via parallel barbs in a vane.

A range of feather morphologies can produce similar overlapping patterns, contrary to the initial hypothesis that overlapping patterns are dictated by the morphology of the individual integumentary structures. This result confirms published claims about the difficulty in discerning a single feather's morphology within articulated plumage (Currie & Chen 2001) and highlights how important the disarticulated feathers on *Anchiornis* are to interpreting its contour feather morphology.

Although this study largely supports the observations of Chen et al. (1998) and Currie & Chen (2001), it opens up the possibility that these feathers are actually morphologically simpler than originally thought (e.g. Fig. 8A–B). Some observations might seem to suggest a relatively complex morphology with the presence of multiple barbs attached to a short rachis (e.g. regularly spaced, thick stains near the body where filaments converge or potential feathers erupting from a sheath). If correct, it could mean that the 'shaggy' contour feather morphology of *Anchiornis* was widely distributed in coelurosaurs. However, such observations more strongly suggest a 'tuft' of multiple barbs connected basally without a rachis.

Amidst a range of plausible morphologies, we assign *Sinosauropteryx* contour feather morphology as, at least predominantly, a 'tuft' of multiple barbs attached basally via a calamus or shared follicle based on the sum of the evidence of the specimens examined (Saitta *et al.* 2017a). Such a 'tuft' represents an even more primitive feather morphology than seen in *Anchiornis* contour feathers. 'Tufts' (i.e., stage II feathers) have been observed in Cretaceous amber (McKellar *et al.* 2011).



Overlapping integumentary appendages within articulated plumage can greatly obscure observations, meaning that the discovery of isolated contour feathers will likely be needed to conclusively assign a morphology to *Sinosauropteryx* feathers. Further emphasizing this point, is an indeterminate coelurosaurian tail segment preserved in amber with exceptional 3D preservation of the associated feathers (Xing *et al.* 2016a). The authors state, “none of the observed osteological features preclude a compsognathid affinity”. The feathers are weakly pennaceous and open-vented with alternating barbs attached to a poorly-developed rachis and simple, undifferentiated barbules as well as rachidial barbules. Although evidence for close phylogenetic affinity with *Sinosauropteryx* is uncertain, the feathers are morphologically more complex than those predicted for *Sinosauropteryx* here.

The second type of *Sinornithosaurus* contour feather morphology described is filaments joined in a basal tuft (Xu *et al.* 2001). This would be consistent with the morphology described here for *Sinosauropteryx* and would have given *Sinornithosaurus* an interesting combination of primitive and derived contour feather morphotypes within the plumage as well as begging the question as to whether other paravians like *Anchiornis* also possessed multiple contour feather morphotypes. However, the possibility that *Sinornithosaurus* ‘tufts’ are actually misidentified feathers of the other described morphotype (i.e., the ‘shaggy’, bifurcated morphotype possessing a rachis) may need to be investigated given that they do somewhat resemble the other feathers on *Sinornithosaurus*.

*Beyond contours – possible plesiomorphic traits in wing feathers*

The symmetric wing feathers in *Anchiornis* suggest similar barb lengths between the leading and trailing vanes and a primitive condition whereby the barbs of the trailing vane are at low angles, which may have limited their aerodynamic efficiency (Feo *et al.* 2015). In addition to ‘shaggy’, open-vented contour feathers, *Anchiornis* wing feathers appear to be at least partly open-vented. A similar observation was made for the paravian *Serikornis* (Lefèvre *et al.* 2017). The wing feathers on the forelimb and hindlimb of this taxa appear to be open-vented. Although Lefèvre *et al.* (2017) suggest that barbules were entirely lacking in *Serikornis*, this may be unlikely and represent an extreme interpretation, as discussed above where the presence of iridescence in paravians is consistent with the likely presence of barbules (Maia *et al.* 2011; Li *et al.* 2012). Evidence Lefèvre *et al.* (2017) cite includes a lack of visible barbs under optical and electron microscopy as well as a lack of basal expansions on the preserved barbs that indicated barbule insertions. However, such expansions are noted to be lacking in taxa believed to have barbules. Furthermore, carbonaceous preservation of keratinous structures like feathers derives from preserved pigments, so a lack of carbonaceously preserved barbules may simply indicate a lack of pigmented barbules *in vivo* or another taphonomic process that might eliminate fine morphological details such as weathering (Vinther 2015; Saitta *et al.* 2017b). The possibility of extinct, open-vented feathers possessing barbules is in congruence with the indeterminate coelurosaurian tail preserved in amber that possesses undifferentiated barbules and is also weakly pennaceous and open-vented (Xing *et al.* 2016a). Thus, *Serikornis*, and other paravians like *Anchiornis*, may have lacked functional barbules/differentiated barbules, resulting in an open vane, rather than lacking barbules entirely.

This hypothetically reduces aerodynamic capability and might further support differentiated proximal and distal barbules as relatively derived characters. Open-vented wing

feathers suggest that non-avian theropods had reduced aerial locomotion ability compared to modern birds or even Mesozoic aves like *Confuciusornis*. Other lines of evidence have been invoked in support of this idea (e.g. Wang *et al.* 2011, 2017a), and gliding rather than powered flight has been proposed for ‘four-winged’ non-avian theropods (e.g. Chatterjee & Templin 2007; Dyke *et al.* 2013, but see Dececchi *et al.* 2017). However, the question involves the aerodynamic functionality of the wing as a whole – could open-vaned, or partially open-vaned, feathers arranged into a wing still be aerodynamically sufficient for aerial locomotion in a way that is unpredictable from a reductionist examination of individual feathers? Such a primitive vane condition may have been countered by a primitive wing arrangement in which multiple rows of major coverts extended far down the aerofoil of the wing in *Anchiornis*, as well as *Archaeopteryx* (Longrich *et al.* 2012, but see Nudds 2014 for a counter-position). Such extensive coverts may have helped to create a less permeable lift surface despite being composed of open-vaned feathers, a feat accomplished in modern birds using tightly closed-vaned feathers but with fewer rows of such feathers in the aerofoil (i.e. less extensive coverts). This hypothesis is possibly evidenced by the fact that the major coverts in paravians like *Anchiornis* are very similar morphologically to the remiges both in overall size and shape, as well as in vane and barb morphology, suggesting similar functional roles. Furthermore, the presence of a propatagium in *Anchiornis*, and other paravians like *Serikornis*, may have also helped to compensate for aerial locomotion-related inefficiencies of the feathers and skeletomusculature (Wang *et al.* 2017a; Lefèvre *et al.* 2017), and the presence of hindlimb wings and tail rectrices in addition to forelimb wings might have compensated by increasing surface area for lift or stability during gliding (Xu *et al.* 2003; Chatterjee & Templin 2006; Alexander *et al.* 2010; Dyke *et al.* 2013; Koehl *et al.* 2011; Palmer 2014). Gliding capability prior to the evolution of functional barbicels and closed

vanes may suggest that aerodynamic functions of feathers could have predated socio-sexual display functions as the transition from filamentous feathers to closed-vane, pennaceous feathers has been suggested to have occurred through an open-vaned, pennaceous intermediate (Prum & Brush 2002), pennaceous feathers have been hypothesized to first function for display (Foth *et al.* 2014; Koschowitz *et al.* 2014), and such open-vaned, pennaceous feathers can be found in extant display feathers (Lucas & Stettenheim 1972). This question hinges upon determining whether certain, more basal non-avian theropods with pennaceous feathers represent primarily or secondarily flightless forms.

The functional utility of wings containing partially open-vaned feathers can be elucidated by examining the silky trait in modern domesticated birds, such as pigeons and doves (Fig. 6K–L). The silky allele is a recessive mutation and leads to aberrant, disarrayed barbule formation where barbules are brittle, easily broken, and fail to properly interlock. The resulting feathers, including remiges and rectrices, take on a more open-vaned appearance in the heterozygote resulting in reduced aerodynamic capability whereby flight is lost but low perches can be reached. Insulation is not affected but water repellence is decreased. Homozygous recessive individuals show an even more extreme morphology of aberrant barbules and open-vaned feathers and are totally incapable of aerial locomotion. Silky fowl, unlike the silky pigeon, lack barbicels entirely (Cole & Willard 1939; Miller 1956; Juhn & Bates 1960; Feng *et al.* 2014; Van Grouw 2016). The fact that the overall morphology of these heterozygous silky remiges closely resembles the open-vaned pattern seen in *Anchiornis* or *Serikornis* is further evidence that fully-functional barbicels were absent in these paravians and highlights the need to compensate for open-vaned wing feathers through other adaptations (e.g., multiple feather tiers on wing surface). Understanding silky feathers in modern birds may provide insight into the functional utility of

paravian feathers in aerial locomotion, thermoregulation, and water repellence as well as provide insight into the ‘evo-devo’ of modern feathers given that the underlying genetics and development of the silky trait are well known (Cole & Willard 1939; Miller 1956; Juhn & Bates 1960; Feng *et al.* 2014; Van Grouw 2016). Open vanes are also found on the remiges of secondarily flightless ratites like ostriches and rheas as well as certain types of extant ornamental feathers (Lucas & Stettenheim 1972).

### *Caudipteryx simplified wing feathers – the evolutionary significance of simplicity*

Extinct feather morphologies give us insight into the macroevolution of feathers as they became adapted for modern avian flight. However, there is potential that rapidly-evolving ecological signals might confound broader macroevolutionary signals. Secondary flightlessness has been proposed for *Caudipteryx* (Feduccia 1999; Jones *et al.* 2000; Paul 2002; Mayr 2017, but see Dyke and Norell 2005; Dececchi *et al.* 2016 for counter-positions). *Caudipteryx* wing feathers are highly simplified compared to those of flying birds, extant and extinct (Lucas & Stettenheim 1972). Remiges were likely open-vaned, and wing feathers appeared broad and ‘frond’ shaped. Some more perplexing feathers are ribbon-like. If consensus can be built to demonstrate that some non-avian dinosaurs were secondarily flightless, then consideration must be taken when using their feather morphologies to reconstruct feather macroevolution with regards to the appearance of fully modern feathers and flight.

## **CONCLUSIONS**

Isolated *Anchiornis* contour feathers reveal a novel, extinct feather morphology, consisting of a short rachis with long, low-angle barbs in a bifurcated configuration. Functional barbicels appear to have been lacking, resulting in an open vane. *Sinosauropteryx* had simpler contour feather morphology than previously thought (i.e. lacking a rachis) and in comparison to *Anchiornis*. This study tentatively assigns a ‘tuft’ morphology to *Sinosauropteryx* contour feathers consisting of multiple barbs attached at their bases. However, conclusive interpretations likely require the discovery of isolated *Sinosauropteryx* feathers. *Anchiornis* wing feathers appear at least partially open-vaned. These observations change the way we depict paravians (i.e. with a much ‘shaggier’ appearance), and hints at their palaeobiology (e.g. reduced aerodynamic capabilities). When examining feather evolution in the future, the impact of potential secondary flightlessness on feather morphology also needs to be more carefully considered if support for secondary flightlessness in non-avian dinosaurs or basal avialans can be demonstrated based on multiple lines evidence, including quantitative biomechanical evidence.

Future work should examine the distribution of the novel contour feather morphotype identified herein. Finding such contour feathers in avialan or pygostylian stem birds would provide further support that they are likely plesiomorphic to modern contour feathers rather than a secondarily derived. When did truly ‘modern’ contour feathers first appear? Mid-Cretaceous hatchling enantiornithines in amber (Xing *et al.* 2016b, 2017) provide highly detailed glimpses of neoptile plumage. A highly complete specimen has scarce body feathers and a combination of primitive and derived plumage morphotypes. Neoptile feathers on the body either resemble “down feathers of modern birds, with elongate (plumulaceous) barbules, flexible barbs, and a poorly defined rachis [or share] the flattened (pennaceous) barb arrangement, and short rachis seen in modern neoptile feathers..., but the barbs bear barbules that are pennaceous” (Xing *et al.* 2017).

Also present are isolated bristle-like filaments (IBFs) on the crural tract and tail that are flattened structures erupting from separate follicles as well as scutellae scale filaments (SSFs) that erupt from the distal edge of the scutellae on the digits. However, this neoptile plumage may differ drastically from adult plumage. A relatively derived, yet old (Early Cretaceous), enantiornithine *Cruralspennia multidona* was described as having “hair-like and rachis-less” body feathers and peculiar crural feathers that are “proximally wire-like with a short filamentous tip (PWFDTs)”, representing a novel feather morphotype (Wang *et al.* 2017b). PWFDTs are tapered, curved proximally, and narrow for about 90% of their length, ending in visibly separated, parallel barbs at their distal end. The dark, “wire-like” portion was interpreted by Wang *et al.* (2017b) as representing fusion of barbs into a single rachis-like structure. Might the contour feathers of *Cruralspennia* or PWFDTs instead be morphologically similar to the ‘shaggy’, bifurcated morphology described here in *Anchiornis* contours? Neoptile IBFs and SSFs might be evidence that PWFDTs are indeed a single, fused structure proximally, although the narrow, solid appearance of the proximal 90% of PWFDTs could represent a closed-vane variant of the *Anchiornis* contour feather morphology, where only the distal 10% of the PWFDT is open-vaned. Contour feathers associated with the basal enantiornithine *Protopteryx* show some semblance to the those described here for *Anchiornis* (Fucheng *et al.* 2006, see Figure 1b). Ultimately, truly ‘modern’ contour feathers might be relatively more derived than originally thought.

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## DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository:

<http://datadryad.org/review?doi=doi:10.5061/dryad.h0f41>

## REFERENCES

ALEXANDER, D. E., GONG, E., MARTIN, L. D., BURNHAM, D. A. and FALK, A. R. 2010. Model tests of gliding with different hindwing configurations in the four-winged dromaeosaurid *Microraptor gui*. *Proceedings of the National Academy of Sciences*, **107**, 2972–2976.

BARRETT, P. M., EVANS, D. C. and CAMPIONE, N. E. 2015. Evolution of dinosaur epidermal structures. *Biology Letters*, **11**, 20150229.

CHATTERJEE, S. and TEMPLIN, R. J. 2007. Biplane wing planform and flight performance of the feathered dinosaur *Microraptor gui*. *Proceedings of the National Academy of Sciences*, **104**, 1576–1580.

CHEN, P. J., DONG, Z. M. and ZHEN, S. N. 1998. An exceptionally well-preserved theropod dinosaur from the Yixian Formation of China. *Nature*, **391**, 147–152.



CHIAPPE, L. M., JI, S. A., JI, Q. and NORELL, M. A. 1999. Anatomy and systematics of the Confuciusornithidae (Theropoda, Aves) from the late Mesozoic of northeastern China. *Bulletin of the AMNH*, **242**.

COLE, L. J. and WILLARD, F. H. 1939. The inheritance of silky plumage in the domestic pigeon. *Journal of Heredity*, **30**, 197–201.

CURRIE, P. J. and CHEN, P. J. 2001. Anatomy of *Sinosauropteryx prima* from Liaoning, northeastern China. *Canadian Journal of Earth Sciences*, **38**, 1705–1727.

DECECCHI, T. A., LARSSON, H. C. and HABIB, M. B. 2016. The wings before the bird: an evaluation of flapping-based locomotory hypotheses in bird antecedents. *PeerJ*, **4**, e2159.

DYKE, G. J. and NORELL, M. A. 2005. *Caudipteryx* as a non-avian theropod rather than a flightless bird. *Acta Palaeontologica Polonica*, **50**, 101–116.

— DE KAT, R., PALMER, C., VAN DER KINDERE, J., NAISH, D. and GANAPATHISUBRAMANI, B. 2013. Aerodynamic performance of the feathered dinosaur *Microraptor* and the evolution of feathered flight. *Nature Communications*, **4**, 2489.

FEDUCCIA, A. 1999. *The origin and evolution of birds*. Yale University Press, New Haven, Connecticut.

FENG, C., GAO, Y., DORSHORST, B., SONG, C., GU, X., LI, Q., LI, J., LIU, T., RUBIN, C. J., ZHAO, Y. and WANG, Y. 2014. A cis-regulatory mutation of PDSS2 causes silky-feather in chickens. *PLoS genetics*, **10**, e1004576.

FEO, T. J., FIELD, D. J. and PRUM, R. O. 2015. Barb geometry of asymmetrical feathers reveals a transitional morphology in the evolution of avian flight. *Proceedings of the Royal Society of London B: Biological Sciences*, **282**, 20142864.

FOTH, C., TISCHLINGER, H. and RAUHUT, O.W. 2014. New specimen of *Archaeopteryx* provides insights into the evolution of pennaceous feathers. *Nature*, **511**, 79–82.

FUCHENG, Z., ZHONGHE, Z. and DYKE, G. 2006. Feathers and ‘feather-like’ integumentary structures in Liaoning birds and dinosaurs. *Geological Journal*, **41**, 395–404.

GODEFROIT, P., SINITSA, S.M., DHOUILLY, D., BOLOTSKY, Y.L., SIZOV, A.V., MCNAMARA, M.E., BENTON, M.J. and SPAGNA, P. 2014. A Jurassic ornithischian dinosaur from Siberia with both feathers and scales. *Science*, **345**, 451–455.

HEERS, A. M., DIAL, K. P. and TOBALSKE, B. W. 2014. From baby birds to feathered dinosaurs: incipient wings and the evolution of flight. *Paleobiology*, **40**, 459–476.

HU, D., HOU, L., ZHANG, L. and XU, X. 2009. A pre-*Archaeopteryx* troodontid theropod from China with long feathers on the metatarsus. *Nature*, **461**, 640–643.

JONES, T. D., FARLOW, J. O., RUBEN, J. A., HENDERSON, D. M., and HILLENIUS, W. J. 2000. Cursoriality in bipedal archosaurs. *Nature*, **406**, 716–718.

JUHN, M. and BATES, R.W. 1960. Thyroid function in silky feathering. *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology*, **143**, 239–243.

KOEHL, M. A. R., EVANGELISTA, D. and YANG, K. 2011. Using physical models to study the gliding performance of extinct animals. *Integrative and Comparative Biology*, **51**, 1002–1018.

KOSCHOWITZ, M., FISCHER C. and SANDER P. M. 2014. Beyond the rainbow. *Science*, **346**, 416–418

LEFÈVRE, U., CAU, A., CINCOTTA, A., HU, D., CHINSAMY, A., ESCUILLIÉ, F. and GODEFROIT, P. 2017. A new Jurassic theropod from China documents a transitional step in the macrostructure of feathers. *The Science of Nature*, **104**, 74.

LI, Q., GAO, K.Q., VINTHER, J., SHAWKEY, M.D., CLARKE, J.A., D’ALBA, L., MENG, Q., BRIGGS, D.E. and PRUM, R.O. 2010. Plumage color patterns of an extinct dinosaur. *Science*, **327**, 1369–1372.

— GAO, K. Q., MENG, Q., CLARKE, J. A., SHAWKEY, M. D., D'ALBA, L., PEI, R., ELLISON, M., NORELL, M. A. and VINTHER, J. 2012. Reconstruction of *Microraptor* and the evolution of iridescent plumage. *Science*, **335**, 1215–1219.

LONGRICH, N. R., VINTHER, J., MENG, Q., LI, Q., RUSSELL, A. P. 2012. Primitive wing feather arrangement in *Archaeopteryx lithographica* and *Anchiornis huxleyi*. *Current Biology*, **22**, 2262–2267.

LÜ, J. and BRUSATTE, S.L. 2015. A large, short-armed, winged dromaeosaurid (Dinosauria: Theropoda) from the Early Cretaceous of China and its implications for feather evolution. *Scientific Reports*, **5**, 11775.

LUCAS, A. M. and STETTENHEIM, P. R. 1972. *Avian Anatomy Integument. Part 1*. U. S. Government Printing Office, Washington, D. C.

MAIA, R., MACEDO, R. H. and SHAWKEY, M. D., 2011. Nanostructural self-assembly of iridescent feather barbules through depletion attraction of melanosomes during keratinization. *Journal of the Royal Society Interface*, **9**, rsif20110456.

MAYR, G. 2017. *Avian evolution: the fossil record of birds and its paleobiological significance*. John Wiley & Sons, Hoboken, New Jersey.

— PETERS, S. D., PLODOWSKI, G. and VOGEL, O. 2002. Bristle-like integumentary structures at the tail of the horned dinosaur *Psittacosaurus*. *Naturwissenschaften*, **89**, 361–365.

— PITTMAN, M., SAITTA, E., KAYE, T. G. and VINTHER, J. 2016. Structure and homology of *Psittacosaurus* tail bristles. *Palaeontology*, **59**, 793–802.

MCKELLAR, R. C., CHATTERTON, B. D., WOLFE, A. P. and CURRIE, P.J. 2011. A diverse assemblage of Late Cretaceous dinosaur and bird feathers from Canadian amber. *Science*, **333**, 1619–1622.

MILLER, W. J. 1956. Silky plumage in the ring neck dove. *Journal of Heredity*, **47**, 37–40.

NORELL, M. and XU, X. 2005. Feathered dinosaurs. *Annual Review of Earth and Planetary Sciences*, **33**, 277–299.

NUDDS, R. L. 2014. Reassessment of the wing feathers of *Archaeopteryx lithographica* suggests no robust evidence for the presence of elongated dorsal wing coverts. *PloS one*, **9**, e93963.

PALMER, C. 2014. The aerodynamics of gliding flight and its application to the arboreal flight of the Chinese feathered dinosaur Microraptor. *Biological journal of the Linnean Society*, **113**, 828–835.

PAUL, G. S. 2002. *Dinosaurs of the air: the evolution and loss of flight in dinosaurs and birds*. Johns Hopkins University Press, Baltimore, Maryland.

PAUTARD, F. G. E. 1963. Mineralization of keratin and its comparison with the enamel matrix. *Nature*, **199**, 531–535.

PRUM, R. O. 2010. Moulting tail feathers in a juvenile oviraptorosaur. *Nature*, **468**, E1.

PRUM, R. O. and BRUSH, A. H. 2002. The evolutionary origin and diversification of feathers. *The Quarterly Review of Biology*, **77**, 261–295.

SAITTA, E. T., GELERNTER, R. and VINTHER, J. 2017a. Primitive contour feathers in paravian dinosaurs and interpreting feather plesiomorphies. Dryad Digital Repository. <http://datadryad.org/review?doi=doi:10.5061/dryad.h0f41>

SAITTA, E. T., ROGERS, C., BROOKER, R. A., ABBOTT, G. D., KUMAR, S., O'REILLY, S. S., DONOHOE, P., DUTTA, S., SUMMONS, R. E. and VINTHER, J. 2017b. Low fossilization potential of keratin protein revealed by experimental taphonomy. *Palaeontology*, **60**, 547–556.

VAN GROUW, H. 2016. Silky pigeons. *Aviculture Europe*, **12**, 10 p. ISSN: 2352-2445.

VINTHER, J. 2015. A guide to the field of palaeo colour. *BioEssays*, **37**, 643–656.

— NICHOLLS, R., LAUTENSCHLAGER, S., PITTMAN, M., KAYE, T.G., RAYFIELD, E., MAYR, G. and CUTHILL, I.C. 2016. 3D camouflage in an ornithischian dinosaur. *Current Biology*, **26**, 2456–2462.

WANG, M., O’CONNOR, J. K., PAN, Y., and ZHOU, Z. 2017b. A bizarre Early Cretaceous enantiornithine bird with unique crural feathers and an ornithuromorph plough-shaped pygostyle. *Nature Communications*, **8**, 14141.

WANG, X., NUDDS, R. L. and DYKE, G. J. 2011. The primary feather lengths of early birds with respect to avian wing shape evolution. *Journal of Evolutionary Biology*, **24**, 1226–1231.

— PITTMAN, M., ZHENG, X., KAYE, T. G., FALK, A. R., HARTMAN, S. A. and XU, X. 2017a. Basal paravian functional anatomy illuminated by high-detail body outline. *Nature Communications*, **8**, 14576.

XING, L., MCKELLAR, R.C., XU, X., LI, G., BAI, M., PERSONS, W.S., MIYASHITA, T., BENTON, M.J., ZHANG, J., WOLFE, A.P. and YI, Q. 2016a. A feathered dinosaur tail with primitive plumage trapped in mid-Cretaceous amber. *Current Biology*, **26**, 3352–3360.

— MCKELLAR, R. C., WANG, M., BAI, M., O’CONNOR, J. K., BENTON, M. J., ZHANG, J., WANG, Y., TSENG, K., LOCKLEY, M. G., LI, G., ZHANG, W. and XU, X. 2016b. Mummified precocial bird wings in mid-Cretaceous Burmese amber. *Nature Communications*, **7**, 12089.

— O'CONNOR, J.K., MCKELLAR, R.C., CHIAPPE, L.M., TSENG, K., LI, G. and BAI, M. 2017. A mid-Cretaceous enantiornithine (Aves) hatchling preserved in Burmese amber with unusual plumage. *Gondwana Research*.

XU, X. 2006. Feathered dinosaurs from China and the evolution of major avian characters. *Integrative Zoology*, **1**, 4–11.

— TANG, Z. L. and WANG, X.L. 1999. A therizinosauroid dinosaur with integumentary structures from China. *Nature*, **399**, 350–354.

— ZHOU, Z. and WANG, X. 2000. The smallest known non-avian theropod dinosaur. *Nature*, **408**, 705–708.

— ZHONG-HE, Z. and PRUM, R.O. 2001. Branched integumental structures in *Sinornithosaurus* and the origin of feathers. *Nature*, **410**, 200–204.

— ZHOU, Z., WANG, X., KUANG, X., ZHANG, F. and DU, X. 2003. Four-winged dinosaurs from China. *Nature*, **421**, 335–340.

— ZHENG, X., SULLIVAN, C., WANG, X., XING, L., WANG, Y., ZHANG, X., O'CONNOR, J. K., ZHANG, F. AND PAN, Y. 2015. A bizarre Jurassic maniraptoran theropod with preserved evidence of membranous wings. *Nature*, **521**, 70–73.



— CURRIE, P., PITTMAN, M., XING, L., MENG, Q., LÜ, J., HU, D. and YU, C. 2017.

Mosaic evolution in an asymmetrically feathered troodontid dinosaur with transitional features. *Nature Communications*, **8**, 14972.

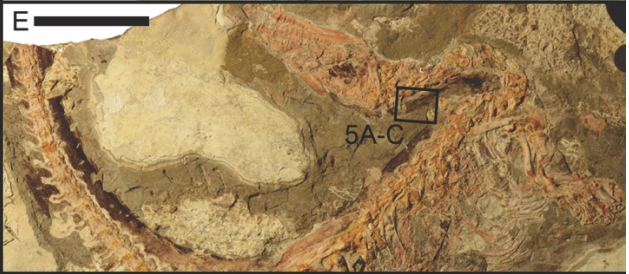
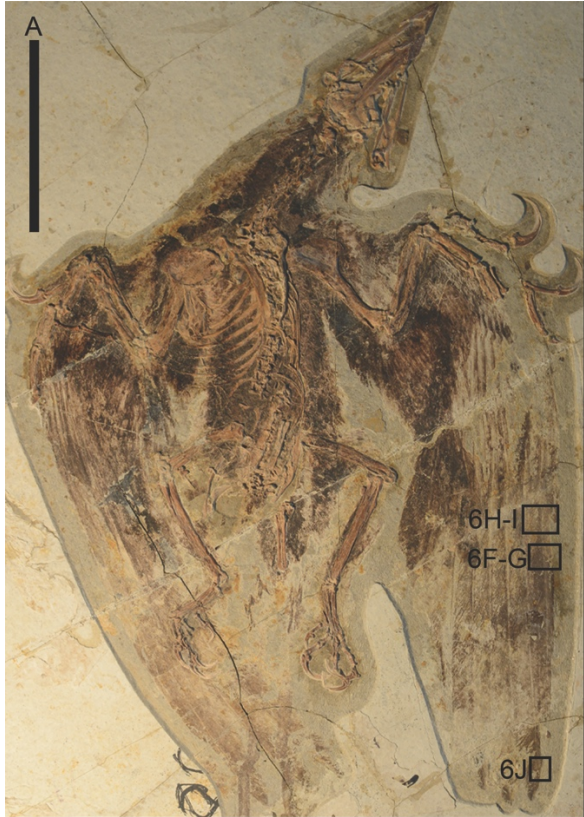
ZELENITSKY, D. K., THERRIEN, F., ERICKSON, G. M., DEBUHR, C. L., KOBAYASHI, Y., EBERTH, D. A. and HADFIELD, F. 2012. Feathered non-avian dinosaurs from North America provide insight into wing origins. *Science*, **338**, 510–514.

ZHANG, F., ZHOU, Z., XU, X., WANG, X. and SULLIVAN, C. 2008. A bizarre Jurassic maniraptoran from China with elongate ribbon-like feathers. *Nature*, **455**, 1105–1108.

ZHENG, X., XU, X., YOU, H., ZHAO, Q. and DONG, Z. 2009b. A short-armed dromaeosaurid from the Jehol Group of China with implications for early dromaeosaurid evolution. *Proceedings of the Royal Society of London B: Biological Sciences*, **277**, 211–217.

— YOU, H. L., XU, X. and DONG, Z. M. 2009a. An Early Cretaceous heterodontosaurid dinosaur with filamentous integumentary structures. *Nature*, **458**, 333–336.

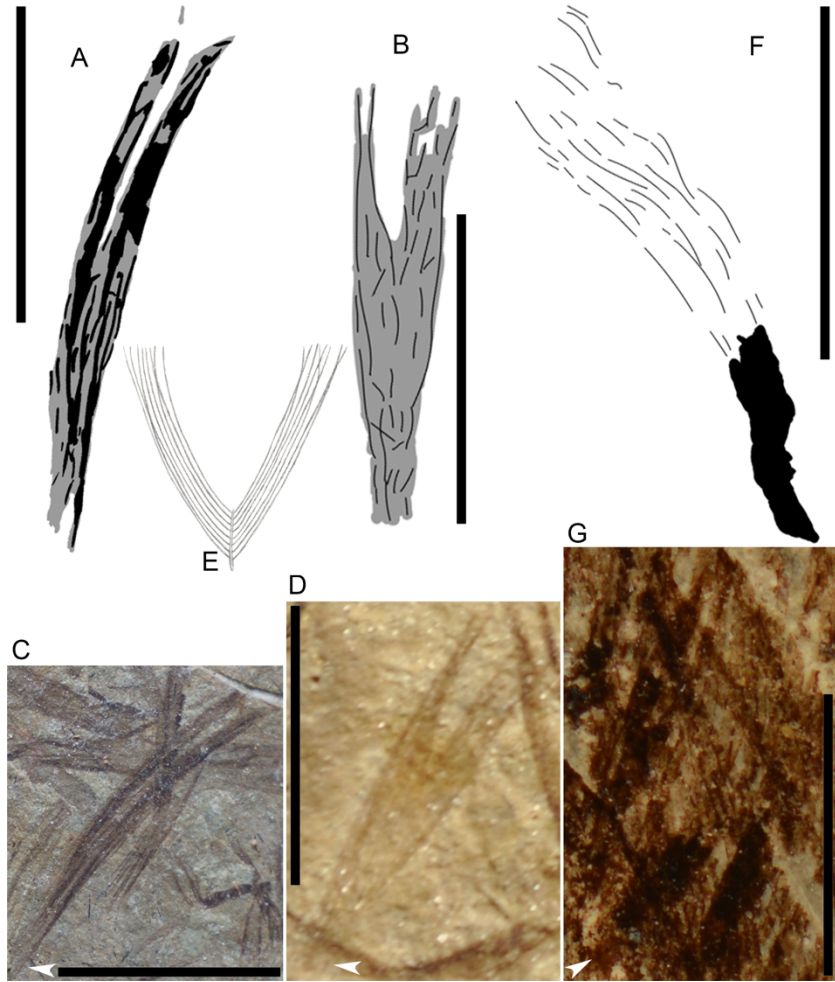
## FIGURES



**Fig. 1.** Specimens examined with boxes around locations of figure insets used in comparisons. A, *Confuciusornis* (IVPP V13156). B, *Anchiornis* (BMNHC PH828) where Fig. 6A–E panels are of counter slab. C, *Caudipteryx* (IVPP V12430). D, *Caudipteryx* (IVPP V12344). E, *Sinosauropteryx* (NIGP 127587). F, *Sinosauropteryx* (NIGP 127586). *Psittacosaurus* (Fig. 4A–B) only shows filamentous structures on the anterior portion of the tail figured therein. Scale bars represent: 10 cm (A–F).

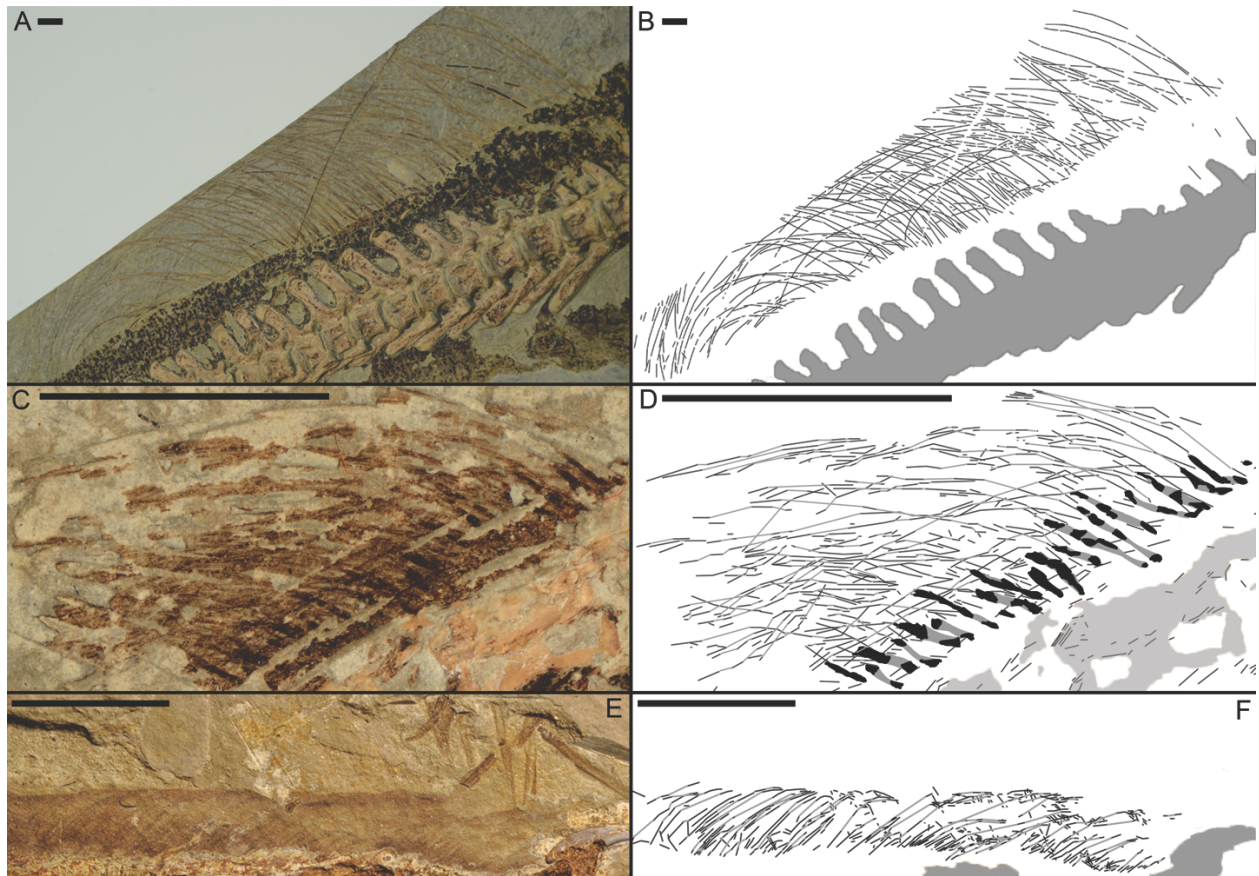


**Fig. 2.** Isolated feathers near the torso of *Anchiornis* (BMNHC PH828). A, the feather indicated by the arrow shows typical bifurcating appearance. The feather indicated by the arrowhead shows unusual ‘trident’ appearance. B, the feathers indicated by arrows show typical bifurcating appearance. See Fig. 3A–E for details and drawings of these feathers. Scale bars represent: 1 cm (A–B).

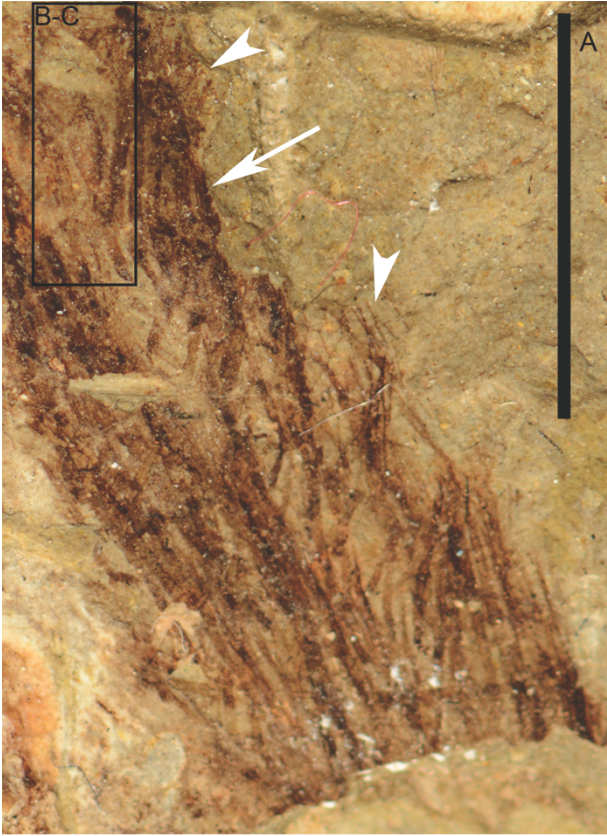


**Fig. 3.** Drawings of contour feathers arranged with basal ends downward. A–B, *Anchiornis* (BMNHC PH828) bifurcated contour feathers as they appear in the rock. Black areas represent darkly pigmented regions of the fossil. Grey areas represent faintly preserved pigmented regions. A, the feather in Fig. 2A indicated by arrowhead. The darkly pigmented, non-striated ‘block’ apical to the bifurcation of the feather is the result of overlapping adjacent feathers that intersect at this location. B, a feather in Fig. 2B indicated by rightmost arrow. C–D, corresponding photographs of drawn feathers in A–B, respectively, indicated by arrowhead. E, *Anchiornis* contour feather interpretation by Rebecca Gelernter. F, filaments representing the basal portion of one *Sinosauropteryx* ‘tuft’ (NIGP 127586) within the region depicted by Fig. 4C–D as it appears in the rock. The finer filaments extended much farther apically than illustrated here. G, corresponding

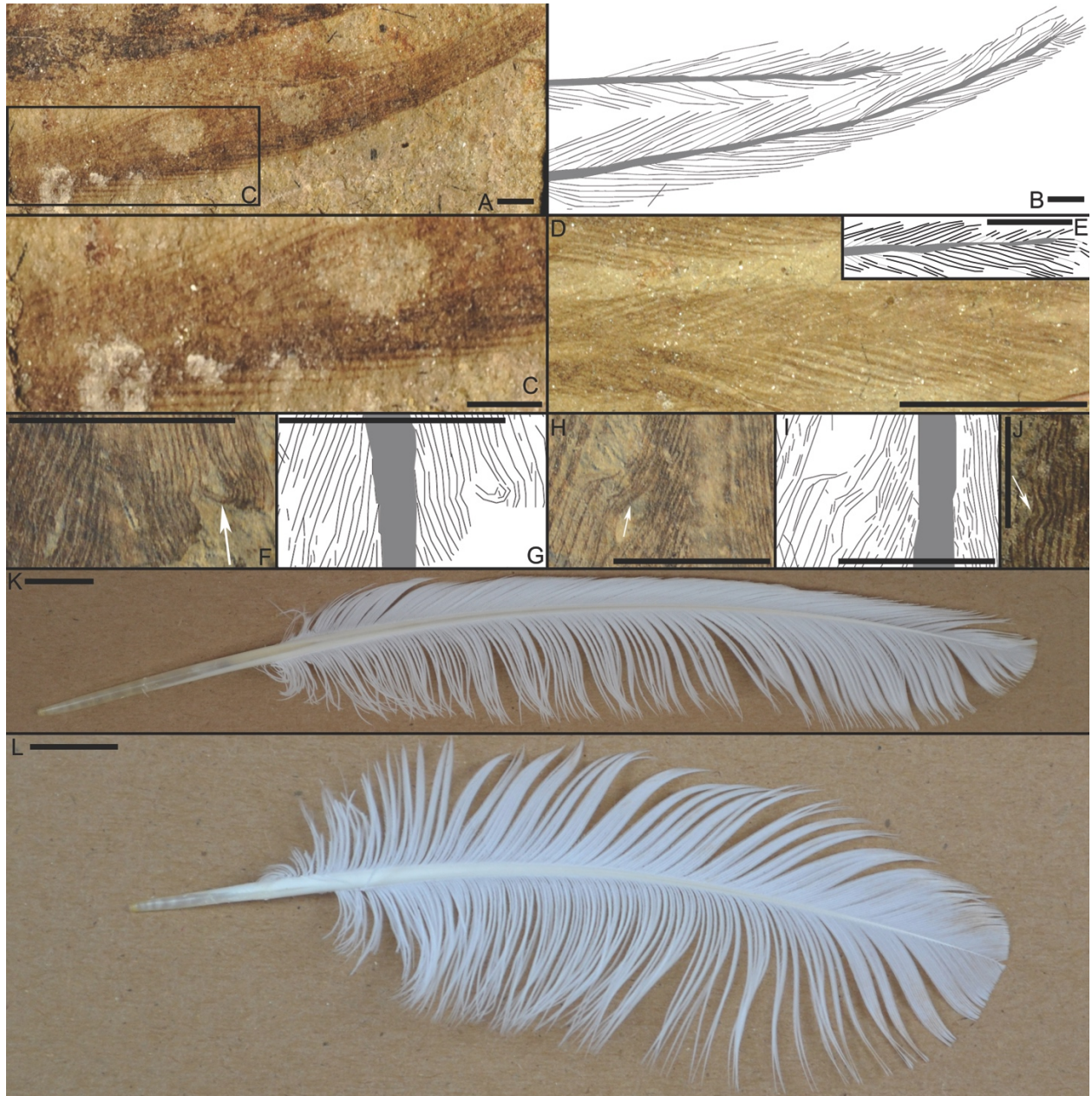
photograph of drawn feather in F indicated by arrowhead. Scale bars represent 1 cm (A, C), 0.5 cm (B, D), 0.25 cm (F–G).



**Fig. 4.** Non-avian dinosaur integumentary appendages. Photograph, A, and corresponding drawing, B, of *Psittacosaurus* (SMF R 4970) tail bristles (see also Mayr *et al.* 2016, Figure 2). Photograph, C, and corresponding drawing, D, of *Sinosauropteryx* (NIGP 127586) contour feathers dorsal to the caudal vertebrae. Thick strokes in C indicate high-angle, dark, thick streaks. Thin grey lines connect incomplete filaments. Photograph, E, and corresponding drawing, F, of *Anchiornis* (BMNHC PH828) contour feathers anterior to the hindlimb and pes with isolated contour feathers also present in the top-right corner of the panels. Thin grey lines connect incomplete filaments. Large grey areas indicate regions where bone is visible (B, C, F). Scale bars represent: 1 cm (A–F).

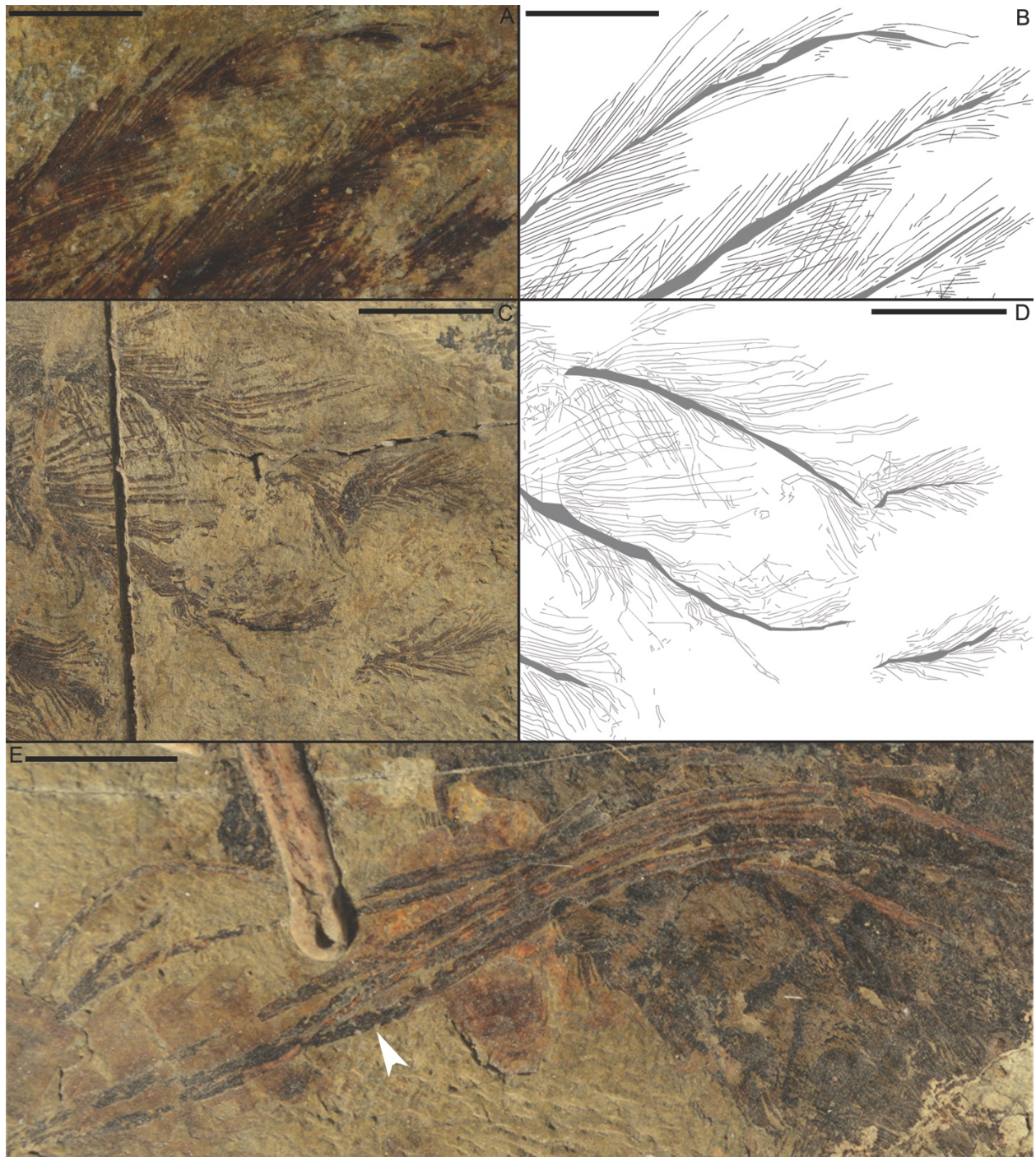


**Fig. 5.** A, Feathers with potential developmental sheaths dorsal to the cervical vertebrae in *Sinosauropteryx* (NIGP 127587). Arrow indicates region containing several of these structures. Arrowheads indicate filaments splaying out as if erupting from sheaths. Vertebra is partly visible in the bottom-left corner. Scale bar represents 1 cm. B–C, A single such feather and associated drawing, respectively. Thin grey lines connect incomplete filaments. Scale bar represents 25 mm. D–E, Another single feather and associated drawing, respectively. Thin grey lines connect incomplete filaments. Scale bar represents 25 mm. F–G, Close-up of a feather and its drawing, respectively. Thin grey lines connect incomplete filaments. Scale bar represents 25 mm. H–J, Another close-up of a feather and its drawing, respectively. Thin grey lines connect incomplete filaments. Scale bar represents 25 mm. K and L show two complete feathers with scale bars representing 1 cm.



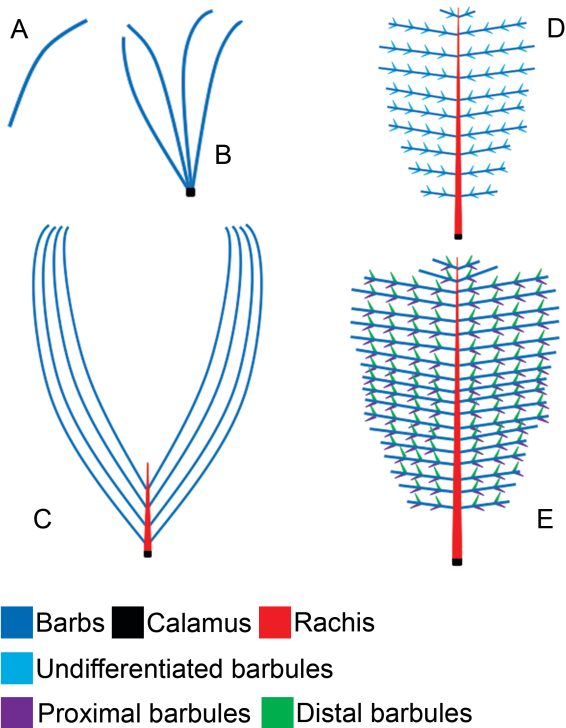
**Fig. 6.** *Anchiornis* (BMNHC PH828 counter slab) and *Confuciusornis* (IVPP V13156) wing feathers compared to modern remiges. Drawing, A, corresponding to photograph, B, of *Anchiornis* primary remex. The feather crossing the panel from the bottom-left and extending to the top-right demonstrates rachis curvature and unzipped barbs. Thin grey lines connect incomplete barbs. Large grey areas indicate preserved rachis. C, close-up image of the basal region of the primary remex feather depicted in A–B. D, barbs on *Anchiornis* major coverts and secondary remiges. E, drawing of major covert in D. Thin grey lines connect incomplete barbs. Large grey area indicate preserved rachis. F–J, *Confuciusornis* remex barbs. Photographs, F & H, correspond to drawings, G & I, respectively. Large grey areas indicate preserved rachis. Arrows indicate jointly deflected barbs. K, Primary and, L, secondary remex of the Barbary Dove, *Streptopelia risoria* (i.e., domesticated African Collared Dove, photographs courtesy of Hein Van Grouw) that is a heterozygous for the silky trait and shows similarly open vanes to those seen in *Anchiornis*. Scale bars represent: 1 cm (A–C, K–L), 0.5 cm (D–I), 0.25 cm (J).





**Fig. 7.** Feathers associated with *Caudipteryx* forelimbs. Photograph, A, and corresponding drawing, B, of the remiges of IVPP V12344. Thin grey lines connect incomplete barbs. Large grey areas indicate preserved rachis. C–E, feathers associated with the forelimb of IVPP V12430. Photograph, C, and corresponding drawing, D, of feathers on the wing showing a ‘frond’ shape.

Thin grey lines connect incomplete barbs. Large grey areas indicate preserved rachis. E, long, ribbon-like structures (arrowhead) near the distal end of the forelimb. Phalange visible at the top of the panel. Scale bars represent: 1 cm (A–E).



**Fig. 8.** Idealized diagrams of contour feathers in order of increasing complexity. A, simple, non-branching filaments reminiscent of those in *Psittacosaurus* (although their homology to feathers is unsure). B, multiple non-branching filaments connected basally (e.g. via a hypothetical calamus or emerging from a single follicle). C, ‘shaggy’, bifurcated contour feather of *Anchiornis* with a short rachis and long barbs, hypothetically depicted with a calamus and lacking barbules (although undifferentiated barbules are possible). *Sinosauropteryx* may plausibly possess feathers ranging in morphology from A to C, although morphology B is most supported. D, ‘modern’, open-vaned feather without differentiated barbules. E, ‘modern’, closed-vaned feather with differentiated proximal and distal barbules.



**Fig. 9.** Life reconstruction of *Anchiornis* and one of its contour feathers by Rebecca Gelernter that includes several accepted, novel, and hypothetical aspects, representing a bold departure from previous paravian artwork. Body outline (e.g., soft-tissue-joined fingers) is based on the reconstructed high-detail LSF study of Wang *et al.* (2017a). Present are the novel contour feathers described here, resulting in a ‘shaggy’ appearance to the plumage. The digits of the hands and feet are fully covered in feathers, as in fossil specimens. The colour pattern is based on Li *et al.* (2010). The wings have multiple rows of long, major coverts that closely resemble the remiges (Longrich *et al.* 2012) as well as long major coverts on the hind limb that also resemble the hind limb remiges, as in fossil specimens. The major coverts, remiges, rectrices are drawn as fairly open vaned as described here. As a four-winged, gliding paravian, *Anchiornis* is presented as an, at least facultatively, arboreal animal climbing in the style of juvenile hoatzins rather than perching as would be consistent with its lack of a reversed hallux and its well-developed, clawed hands.

## **SUPPORTING INFORMATION**

S1. Diagram showing how simple, non-branching filaments could result in the observed overlapping patterns seen in *Sinosauropteryx*. A, simple, non-branching filaments arranged in multiple, parallel tracts *in vivo* with some tracks more latero-ventral on the tail than others. B, filaments in A copied but where the area representing the flesh of the tail *in vivo* is not preserved. Only filaments dorsal to the tail are visible, as is mostly the case in such fossil specimens. Selective preservation of filaments dorsal to the vertebra gives the illusion of branching structures.

S2. Table of observations on *Sinosauropteryx* contour feathers and how they are expected support various plausible morphologies. Does the observation support a particular morphology? Y, yes. “?”, maybe or uncertain. N, no. Scoring system is arbitrary with Y=1, “?”=0.5, and N=0. Highest score is the tentatively preferred morphology.