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Reply to 'Fibre-like structures on the pterosaur integument: fur, feathers or taphonomic artefact?

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In our paper[1], we explored the morphology, ultrastructure and chemistry of the dermal structures of pterosaurs and showed that they likely had a common evolutionary origin with the integumentary structures seen widely in dinosaurs (including birds), their close relatives. Our study of two Middle Jurassic anurognathid pterosaurs from China showed that the whisker-like pycnofibres of the pterosaurs include at least four distinct morphologies, rather than one as had been assumed, and that three of these show branching, a key characteristic of feathers. Further, all four pycnofibre types are morphologically identical to structures already described in birds and non-avialan dinosaurs, not only in terms of gross morphology but also in their ultrastructure and chemistry, including melanosomes and chemical evidence for keratin; collectively these features are consistent with feathers. Mapping these data onto a phylogeny yields a single evolutionary origin for feathers minimally in the avemetatarsalian ancestor of both pterosaurs and dinosaurs. The net effect of this discovery is to shift the origin of feathers back 100 Myr before *Archaeopteryx*, one of the first birds.

In their comment[2], Unwin and Martill assert that the branched integumentary structures that we identified are not feathers or even pycnofibres. They make five arguments in favour of their point of view: (1) superposition or decomposition of composite fibre-like structures or aktinofibrils yields branched structures similar to those in the anurognathids; (2) the anatomy and anatomical distribution of the anurognathid integumentary structures is consistent with aktinofibrils, but not pycnofibres; (3) evidence for keratin and melanosomes is not indicative of pycnofibres but rather reflects contamination from epidermal tissue; (4) the branching we reported is not consistent with exclusively monofilamentous coverings in other anurognathids, and (5) homology of the branched integumentary structures with feathers cannot be demonstrated conclusively due to the simple morphology of the

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former[2]. We refute all five of their arguments.

First, the argument that superposition or partial decomposition and associated unravelling of composite fibre-like structures could produce feather-like branching structures has been raised repeatedly against the interpretation of protofeathers in dinosaurs[3-6], but this argument has been refuted[7,8]. The proposed taphonomic scenario is highly unlikely to apply to the anurognathids for three reasons: (i) contra the assertion that the pycnofibres show a 'seemingly random distribution'[2] each of the three branched morphotypes we identified is restricted to a specific body region, so the Unwin-Martill scenario would require some decay process that could produce different feather-like structures in different parts of the body; (ii) their idea of partial degradation of a single fibre type should yield an unlimited range of frayed fibres corresponding to different decay stages, but this is not seen; rather, we find only a limited number of discrete structures; and (iii) simple overlapping of fibre-like structures would produce neither the striking and consistent thickness difference between the main filament and its branches in morphotypes 2 and 3, nor the persistent occurrence of the diverging morphology in morphotype 4.

Second, the assertion[2] that the pycnofibres preserved on the patagium area are probably degraded aktinofibrils is not consistent with the gross morphology of the former. In contrast to aktinofibrils, the branched integumentary structures are sinuous, lack organization, regularly spaced throughout the patagium (Supplementary Fig. 5c in ref. 1), and, critically, extend beyond the patagium (Fig. 1o and p in ref. 1), which is confirmed in other pterosaurs, such as *Jeholopterus*[9] (Fig. 1c–d) and *Sordes* (Fig. 2 in ref. 10), where both fibre types co-occur. Indeed, the branched structures on the patagia are identical in morphology to those distributed in other body regions, strongly supporting an interpretation as pycnofibres and not aktinofibrils. As noted, we readily discriminate pycnofibres and aktinofibrils in our specimens (e.g. Fig. 1). The preservation of branched integumentary structures in distal regions of the patagia, not reported previously from other pterosaurs[1], does not automatically preclude an interpretation as pycnofibres, but may simply reflect intraspecific variations in anatomy and / or variations in the taphonomic histories of the specimens.

Third, Unwin and Martill claim[2] that the preservation of melanosomes and evidence of keratin reflects contamination from epidermal tissue. As counter to this, our study revealed that the melanosomes, and chemical spectra consistent with keratin, are restricted to the fibres and are absent from the surrounding matrix. In particular, the melanosomes are embedded within an organic matrix chemically consistent with keratinous residues (e.g. Fig. 2g and h in ref. 1). This preservation is typical of fossilized feathers of many non-avialan dinosaurs and birds and experimentally matured feathers[11,12]. In contrast, integumentary melanosomes are not embedded within a keratinous matrix *in vivo* and consistently preserve in fossils as isolated bodies (i.e. lacking an enveloping matrix[13,14]). Thus, both the melanosomes and the chemical evidence for keratin in the pterosaur pycnofibres must be integral to the tissue, not derived from elsewhere. This contamination argument had also been wielded against the identification of melanosomes and traces of keratin in dinosaur feathers[3-6] and was refuted by demonstration of close association of structures and

signals with limited tissue types[7,8], as here. The preservation of melanosomes but not pycnofibres in other pterosaur specimens referred to by Unwin and Martill[2] likely reflects relatively advanced decay in those specimens and thus is not inconsistent with our interpretations. Further, the signal for alpha keratin in the pterosaurs does not necessarily reflect the original chemistry of the structures, because the molecular configuration of keratin and other proteins is likely to alter during fossilization as we addressed in our original paper[1].

Fourth, Unwin and Martill[2] claim that the presence of branched structures is not consistent with exclusively monofilamentous coverings in other anurognathids. Extant birds, however, show remarkable interspecific variation in feather structure, so it is not unreasonable to expect integumentary structures of pterosaurs to have varied substantially. Further, among theropod dinosaurs, where most researchers accept that the dermal filaments are feathers, there is substantial variation in morphology of those feathers, including substantial differences in their presence or absence between closely related groups and including many feather morphologies not seen in birds[15].

Fifth is the assertion[2] that the simple morphology of the preserved structures precludes an interpretation of the evolutionary relationships between these and feathers. It is well documented[16,17], however, that early stages in the development and evolution of vaned feathers are characterized by simple monofilaments and various types of tufted structures with more simple branching than in a feather with a closed vane. The gross morphology of the branched integumentary structures in the anurognathids is consistent with that of feathers at early stages of evolution.

In sum, the arguments presented by Unwin and Martill[2] that the branched integumentary structures we described[1] are overlapping or degraded composite fibre-like structures or aktinofibrils are inconsistent with their morphology and ultrastructure and, critically, a complete understanding of the taphonomy of the former. Further, pycnofibres and aktinofibrils co-occur on several specimens and are morphologically distinct, as we have shown. In light of this, the most parsimonious interpretation of the simple and branched integumentary appendages in the anurognathid pterosaurs remains our original conclusion that they are feathers.

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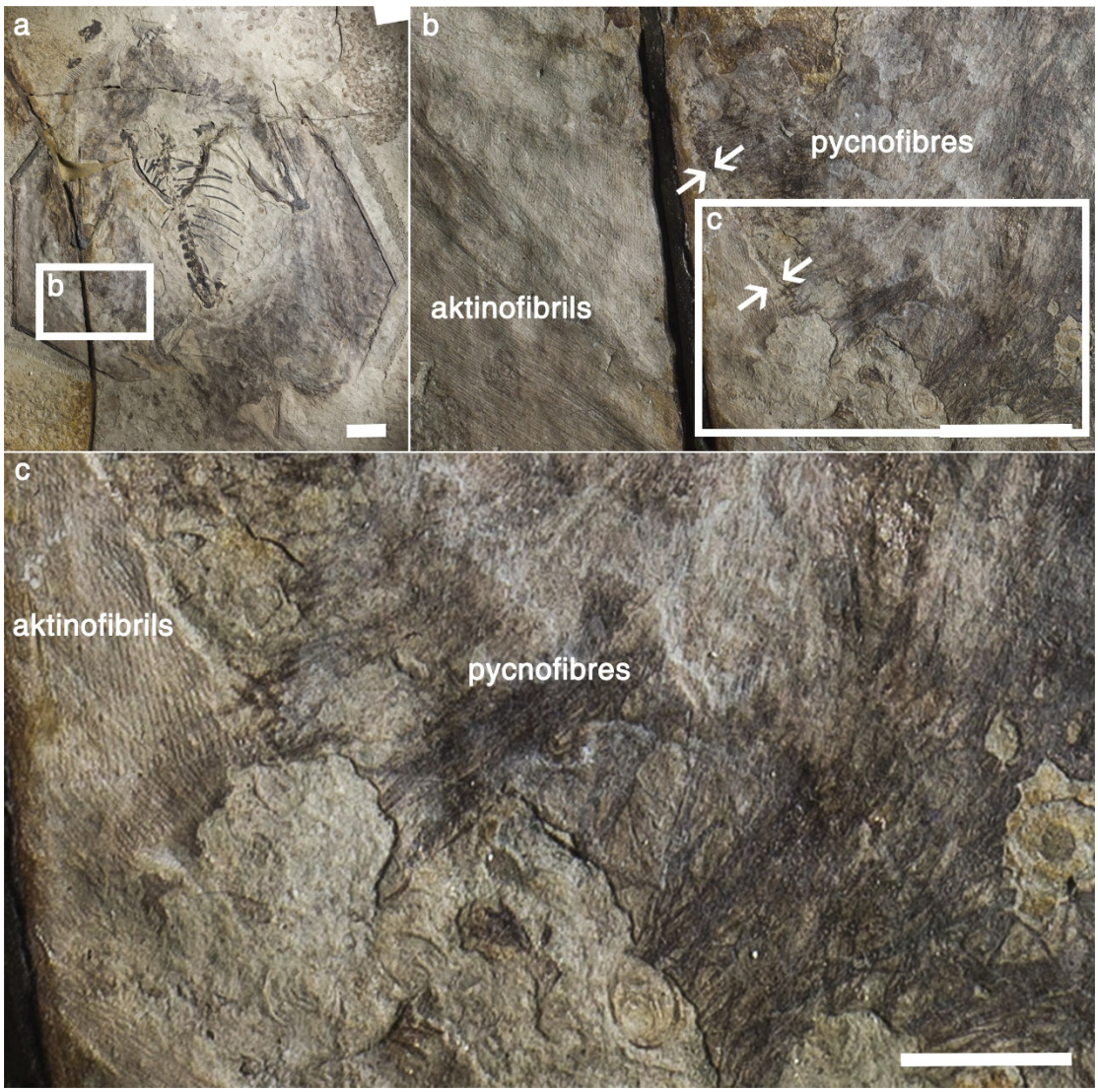


Fig. 1 | Pycnofibres and comparison with aktinofibrils in the holotype of *Jeholopterus ningchengensis*. **a**, Overview of the holotype of *Jeholopterus ningchengensis* showing extensive preservation of soft tissues. **b**, Close-up of the region indicated in **a** where both aktinofibrils and pycnofibres are preserved with an abrupt contact margin (arrows). **c**, Further close-up showing pycnofibres are covered by layers of actinofibrils which are distinctly different in morphology. Scale bars in **a**–**c**: 20 mm, 10 mm and 5 mm, respectively.