

PALAEOLOGY

Pterosaur plumage

Imaging of pterosaur skin reveals evidence of coloured feather-like structures, but whether these are homologous with true feathers is open to debate.

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Over the past two decades a wealth of fossil discoveries with remarkable preservation of integumentary structures — which include skin, feathers and scales — has revealed that the evolution of feathers is characterized by shifts from simple filamentous structures to clustered, and later branched, filaments. Outside theropod dinosaurs, the discoveries of branched filaments on the integument of *Kulindadromeus*, a small-bodied ornithischian¹, and of individual filaments ('monofilaments') on *Tianyulong confuciusi*, a heterodontosaurid positioned near the evolutionary base of ornithischian dinosaurs, suggests that these integumentary structures are basal to dinosaurs². Although integumentary filaments ('pycnofibres') have been found in numerous other pterosaur specimens, there is still substantial disagreement regarding their interpretation, in particular whether they evolved independently or are homologous to feathers. If the latter, this would imply that all Avemetatarsalia (the wide clade that includes dinosaurs, pterosaurs and close relatives) were ancestrally feathered. Writing in *Nature Ecology & Evolution*, Yang and colleagues³ describe four types of pycnofibre⁴ in two specimens outside Dinosauria, both anurognathid pterosaurs, which could support the ancestral feather hypothesis and suggest a broader evolutionary pattern of body coverings than previously thought.

Yang et al. examined two specimens of short-tailed anurognathid pterosaurs from the Middle–Late Jurassic (165–160 million years ago) Yanliao Biota of China. Of the four kinds of pycnofibre described on their bodies (Fig. 1), type 1 is interpreted as hollow, covers most parts of the body in both specimens, and is similar to previously reported monofilaments. Their ubiquitous distribution on the body could indicate a thermal insulation function⁵. The other three types of filament identified appear to be branched. Branching is the most distinctive morphological feature of feathers and thus these pterosaur pycnofibres might be of greater significance because

they may be plesiomorphic feathers⁶. The pycnofibres identified by Yang et al. are certainly integumentary in nature: they are clearly preserved as external structures and Fourier transform infrared spectroscopy showed that their chemical composition is similar to the composition of extant feathers. Scanning electron microscopy

and energy-dispersive X-ray spectroscopy of the filaments revealed they also contain packets of melanin pigment (melanosomes), which impart colour to skin structures such as feathers and mammal hairs⁷. An artistic reconstruction paints these anurognathid pterosaurs looking like brown bats with fuzzy wings.

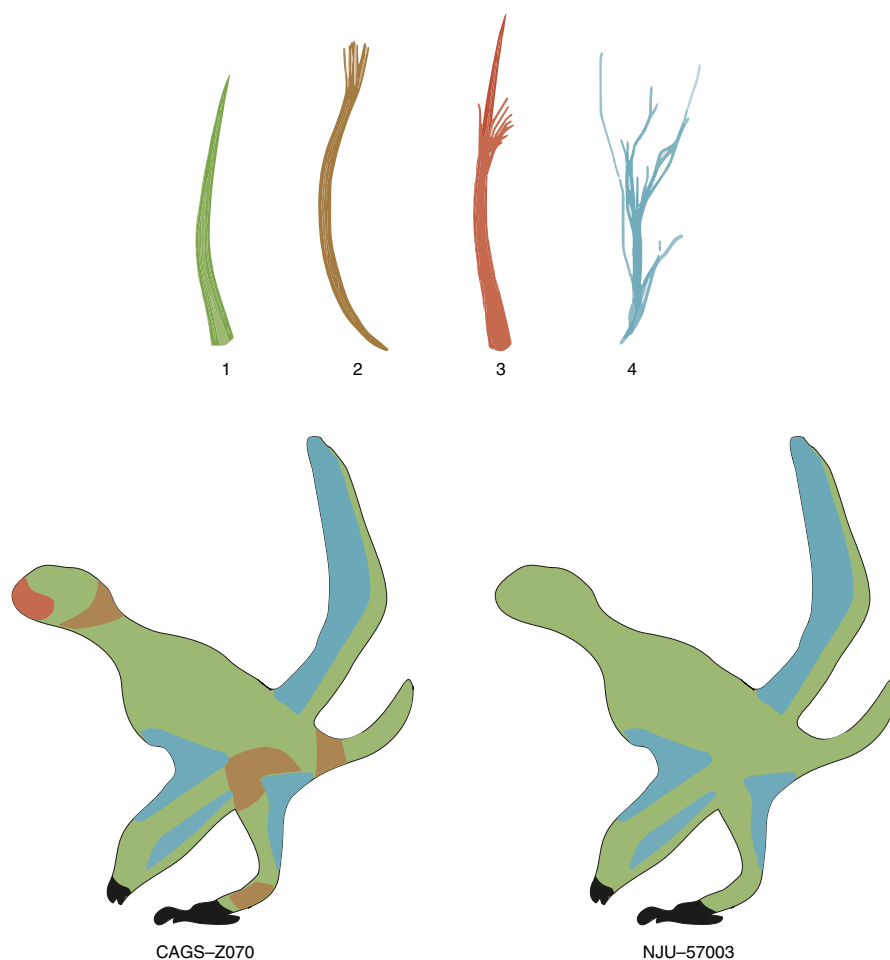


Fig. 1 | Skin filaments (pycnofibres) observed in two anurognathid pterosaurs from the Middle–Late Jurassic. Four types of pycnofibre were recognized, three of which appear to be branched (types 2, 3 and 4). Type 1 covers most of the body and type 4 was found on the wing membranes of both specimens. The presence of types 2 and 3 seems to be restricted to small body areas of one of the specimens. Credit: Zixiao Yang and Baoyu Jiang

However, the big question is still whether or not the filaments really are branched, as expected for feather precursors. As is often the case in palaeontological studies, even when the preservation of the fossils is remarkable, Yang and colleagues' interpretation of the pterosaur skin appendages is still based entirely on gross filament morphology. As a consequence, the abstraction and documentation of all the details of the filaments cannot escape some degree of subjective interpretation, which has left previous claims of pterosaur pycnofibres open to debate: the Jurassic rhamphorhynchoid pterosaur *Pterorhynchus wellnhoferi* was described as bearing branched pycnofibres on its integument in a previous claim of pycnofibre–feather homology⁸, but several authors have since argued that the filament branching in the imaging is not clear enough to support this interpretation⁴.

One method that may help reveal structural details that are otherwise undetectable is the use of backscattered electron imaging using scanning electron microscopes (SEMs)⁹. The advantages of this technique are that it is non-destructive and allows reliable identification of individual but superimposed structures in, for example, compacted stacks of filaments. The obvious limitation of this method so far is that SEMs have chambers that can fit only small specimens. Nevertheless, spatial resolution of electron microscopes has improved, and large specimen chamber and wide-field SEMs are becoming increasingly available, allowing the examination of much bigger

(~20 cm) specimens, such as an entire primary covert feather of *Archaeopteryx*¹⁰. Laser-stimulated fluorescence is another imaging method that can enhance the extraction of structural detail from fossils and is particularly powerful for analysis of fossil soft tissue. It allows a highly sensitive evaluation of structural differences signalled by the colour of the fluorescing material, and allowed the branched bristles of the ceratopsian dinosaur *Psittacosaurus* to be distinguished¹¹. Synchrotron-based computed tomography scanning has also recently arisen as a promising technique to produce three-dimensional images with submicrometre resolution of soft-tissue-like feathers¹².

Yang and colleagues' finding of differently structured filaments in the two anurognathid specimens at the very least opens up the possibility that pterosaurs could have had a range of epidermal structures that may have served varied functions, and that some of these structures may be related to feathers. But the ultimate question of when these filaments originated is much more difficult to answer. Based on the current fossil record we still know very little about pterosaur origins. The ongoing debate over pterosaur phylogeny^{13,14} complicates estimations of the emergence of lineages with confirmed pycnofibres, making it hard to say anything conclusive about the evolution of pterosaur integument. Pterosaur pycnofibres could have arisen for purposes of insulation and signalling long before pinnate feathers would have been co-opted for flight⁵. For the moment,

studies such as that of Yang et al.³ help us unveil a broad picture in which modern feathers can be seen as only part of a long history of novel integumentary structures in archosaurs. The precise nature of that history will continue to be modified through the discovery of new fossils and application of more advanced methods. □

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Competing interests

The author declares no competing interests.