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No protofeathers on pterosaurs

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It is widely held that pterosaurs, Mesozoic flying reptiles, were covered with hair-like monofilament structures (pycnofibres) that formed a fine pelt[1–4]. Yang et al.[5] propose, on the basis of two specimens of an anurognathid pterosaur from the Late Jurassic epoch of China, that some pycnofibres were branched, exhibiting 'brush-like' and 'tuft-like' morphologies. Going further, these authors compare the branched pycnofibres to protofeathers, reported for several coelurosaurian dinosaurs[6] and argue that they share a common origin, a controversial idea that pushes back the first appearance of feathers some 80 million years, from the Late Jurassic to the Early Triassic[5,7,8]. Evidence from fossilized integument of other pterosaurs[9,10] suggests, however, that the branching reported by Yang et al. may be an artefact of preservation. When bunched up, or partially decomposed and unravelled, structural fibres (aktinofibrils) in the wing membranes of pterosaurs exhibit a variety of seemingly branched morphologies including brush-like and tuft-like strucutures[2,9,10]. Consequently, branching is not a reliable guide to the identity and homology of pterosaur integumentary structures. In support of their argument for protofeathers in pterosaurs, Yang et al.[5] cite the presence of melanosomes and keratin. Both are widely distributed in the pterosaur integument, however, and neither is unique to pycnofibres[5,11,12]. The rarity of purportedly branched pycnofibres, their restriction to a single, relatively derived pterosaur clade and the absence of uniquely shared morphologies do not support the idea of homology with feathers, as Campione et al.[13] have shown.

To date, pycnofibres have been reported in 28 specimens distributed among 17 pterosaur species, which encompass much of Pterosauria and, typically, are associated with the skull, neck, body and wings[1–4,14–17]. In almost all cases, pycnofibres consist of fine, monofilament structures typically <100 μm in diameter and often associated with more continuous integumentary tissues, 'skin'. Branched pycnofibres have been reported in just three pterosaur specimens: a single example of *Pterorhynchus wellnhoferi* from the Upper Jurassic Tiaojishan Formation of China[14] and two examples of an anurognathid pterosaur from the same deposit, CAGS–Z070 (Institute of Geology, Chinese Academy of Geological Sciences) and NJU–57003 (Nanjing University)[5,15]. In each of these examples, the vast majority of fibre-like structures are monofilament. Branched pycnofibres are comparatively rare and absent in other specimens of anurognathids from the same deposit[3,16,18].

The principal evidence for tufted and brush-like morphologies has been reported in fibres associated with the wing membranes[5,15]. The problem here is that aktinofibrils, fine, closely aligned, composite fibres, comparable in size (50–100+ μm in diameter) to pycnofibres and easily confused with them, are present throughout the flight membranes wherever these structures are well preserved in pterosaurs (Fig. 1a)[1–4,9,10,14,16,17,19]. Yang et al.[5] follow others[3] in assuming that pycnofibres can be distinguished from aktinofibrils by their curvature. However, while aktinofibrils in distal regions of the pterosaur patagia are remarkably straight and seemingly relatively stiff, those in the inner parts of the patagia, adjacent to the body, were more flexible and exhibit the same sinuosity as purported pycnofibres (Fig. 1a)[9].

When bunched up or imbricated in wrinkled or folded integument, aktinofibrils can take on the appearance of 'tufts' (type 4 fibres of Yang et al.[5]), as shown by bunched aktinofibrils in the propatagium of CAGS–Z070[5]. In addition, the composite construction of aktinofibrils means that, as they begin to decay, the fine 5- to 10-μm-thick fibrils from which they are composed unravel, resulting in branched morphologies identical to those of the type 2 pycnofibres of Yang et al. (Fig. 1b). Figured examples of branching pycnofibres in NJU–57003 and CAGS–Z070, which—with one exception—are all associated with flight patagia, are most likely misidentified aktinofibrils. Moreover, the seemingly random occurrence in these two specimens of branched pycnofibres within tracts of almost exclusively monofilament fibres is quite unlike the regionalization of specific feather morphotypes in feathered birds and dinosaurs, and further supports their interpretation as preservational artefacts.

The presence of melanosomes was cited by Yang et al.[5] in support of their interpretation of branched pycnofibres as protofeathers. However, melanosome-like bodies have been reported throughout the pterosaur integument[11], including in association with fibres in the cranial crest[12] and in regions such as the distal wing tips where aktinofibrils are prominent, but pycnofibres have never been observed[5,11,19]. The ubiquity of melanosomes in the pterosaur integument and their co-occurrence with different types of fibre render them uninformative with regard to the identity of particular fibres.

Yang et al.[5] describe a chemical signature for α-keratin from a sample of the cruropatagium preserved with fibres in NJU–57003, the size, morphology, orientation and packing of which are consistent with aktinofibrils[9,20] rather than pycnofibres. The keratin, if indeed keratin has been preserved, is probably derived from the epidermis, a continuous layer that enclosed the aktinofibrils, preserved as a dark shadow in NJU–57003. The presence of α- rather than β-keratin is inconsistent with protofeathers[21] but is typical of more pliable regions of the epidermis in reptiles[22] and consistent with the glabrous, non-scaled integument of pterosaurs.

A few of the bristle-like integumentary structures fringing the jaws of CAGS–Z070[5,15] have been interpreted as a distinct type of branched pycnofibre by Yang et al.[5]. These tapering, relatively straight and seemingly rather stiff structures, also reported for *Batrachognathus volans*[2] and seemingly unique to anurognathids, appear to be distinctly different from other pycnofibres. The peculiar branching morphology exhibited by these structures in CAGS–Z070 most likely reflects fraying or the accidental overlap of multiple bristles.

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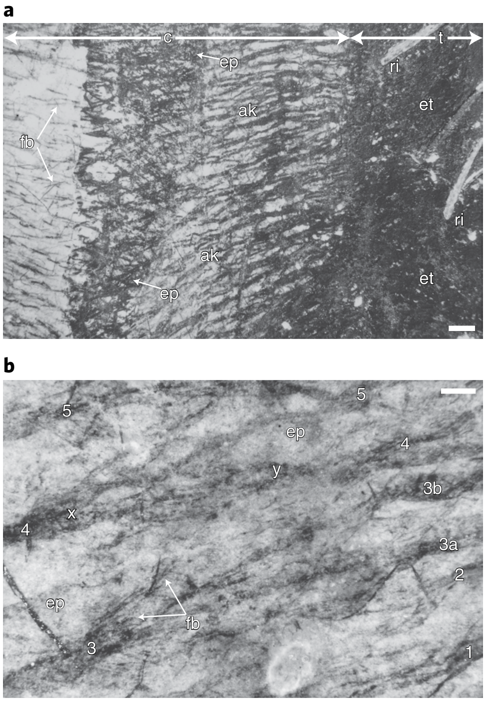

Fig. 1 | Integumentary structures in *Sordes pilosus*, PIN-2585/36 (Palaeontological Institute, Moscow). a, The inner region of the cheiropatagium adjacent to the body anterior to the pelvis. The dark, slightly granular epidermal surface of the integument (et) covering the torso (t) contrasts with the remarkably thin epidermal surface (ep) of the integument forming the proximal region of the cheiropatagium (c). Much of the epidermis covering the cheiropatagium has been lost, exposing closely packed and aligned aktinofibrils (ak) now slightly decayed. On the far left, much of the cheiropatagium has been pulled away, leaving a few incomplete aktinofibrils and numerous fine fibrils (fb) from which they were composed. ri, rib. **b**, Five aktinofibrils (1–5), short sections of which are partially unravelled (for example, x–y), exposing fine fibrils in the proximal part of the cheiropatagium. The aktinofibrils were approximately 60–80 μm in diameter, before unravelling, the fibrils are <5 μm in diameter. Patches of epidermis preserved as irregular dark background stains. Scale bars, 1 mm (**a**) and 0.1 mm (**b**).

Data availability

The data that support the findings of this study were collected from the literature cited and examination of specimens mentioned in the text.

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Author contributions

D.M.U. and D.M.M. conceived the project, conducted the research, constructed the figures and wrote the paper.

Competing interests

The authors declare no competing interests.

Additional information

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