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1 **Pterosaur integumentary structures with complex feather-like branching**

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20 **Pterosaurs were the first vertebrates to achieve true flapping flight, but in the**  
21 **absence of living representatives, many questions concerning their biology and**  
22 **lifestyle remain unresolved. Pycnofibres, the integumentary coverings of**  
23 **pterosaurs, are particularly enigmatic: although many reconstructions depict**  
24 **fur-like coverings composed of pycnofibres, their affinities and function are not**  
25 **fully understood. Here we report the preservation in two anurognathid pterosaur**  
26 **specimens of morphologically diverse pycnofibres that show diagnostic features**  
27 **of feathers, including non-vaned grouped filaments and bilaterally branched**  
28 **filaments, hitherto considered unique to maniraptoran dinosaurs, and preserved**  
29 **melanosomes with diverse geometries. These findings could imply that feathers**  
30 **had deep evolutionary origins in ancestral archosaurs, or that these structures**  
31 **arose independently in pterosaurs. The presence of feather-like structures**  
32 **suggests that anurognathids, and potentially other pterosaurs, possessed a dense**  
33 **filamentous covering that likely functioned in thermoregulation, tactile sensing,**  
34 **signalling, and aerodynamics.**

35       Feathers are the most complex integumentary appendages in vertebrates<sup>1</sup>. Most  
36 feathers in modern birds possess an axial shaft from which branch lateral barbs and  
37 barbules. Much is known about the anatomy, developmental biology, and genomic  
38 regulation of these structures, but their deep evolutionary origin is controversial<sup>2-4</sup>.  
39 Feathers and feather-like integumentary structures have been reported in many  
40 theropod dinosaurs (including birds)<sup>3,5</sup> and ornithischians such as *Psittacosaurus*<sup>6</sup>,  
41 *Tianyulong*<sup>7</sup>, and *Kulindadromeus*<sup>8</sup>. Feather-like or hair-like structures, termed

42 pycnofibres<sup>9</sup>, have also been reported in several pterosaur specimens<sup>9-13</sup>, but their  
43 nature is not resolved.

44 Here we report remarkably well-preserved pycnofibres in two anurognathid  
45 pterosaurs and demonstrate, using evidence from morphology, chemistry and  
46 macroevolutionary analyses, that the preserved pycnofibres bear key features of  
47 feathers: monofilaments, two types of non-vented grouped filaments, bilaterally  
48 branched filaments that were previously considered unique to maniraptoran dinosaurs,  
49 and preserved melanosomes with diverse geometries. Both specimens studied are  
50 from the Middle–Late Jurassic Yanliao Biota (ca. 165–160 Mya<sup>14</sup>). NJU–57003  
51 (Nanjing University) is a newly excavated specimen from the Mutoudeng locality and  
52 CAGS–Z070 (Institute of Geology, Chinese Academy of Geological Sciences), which  
53 has been noted briefly for its feather-like branched pycnofibres<sup>13</sup>, is from the  
54 Daohugou locality. Both specimens are near-complete and well-articulated, with  
55 extensive soft tissues (Figs. 1 and 2, and Supplementary Figs. 1–5). Both specimens  
56 are identified as anurognathids<sup>17</sup> (see Supplementary text for osteological  
57 descriptions).

58 Preserved soft tissues include structural fibres (actinofibrils) and pycnofibres.  
59 Structural fibres, common in the pterosaur wing membrane<sup>9,12,18</sup>, are observed only in  
60 the posterior portion of the uropatagium in CAGS–Z070 (Fig. 1**o–p**). As reported  
61 elsewhere, they are parallel to subparallel and closely packed. Individual fibres are  
62 0.08–0.11 mm wide (ca. 5 fibres per mm) and at least 1.9 mm long. Pycnofibres are  
63 preserved extensively in both pterosaur specimens (especially CAGS–Z070; Figs. 1

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64 and 2, and Supplementary Figs. 1, 4 and 5) and are discriminated from structural  
65 fibres based on their curved morphology and overlapping arrangement. In the  
66 posterior portion of the uropatagium in CAGS–Z070, pycnofibres co-occur with  
67 structural fibres; oblique intersections reflect superposition of these features during  
68 decay (Fig. 1o–p).

69 Pycnofibres are categorized here into four types. Type 1 occurs around the head,  
70 neck, shoulder, torso, all four limbs and tail of both specimens (Figs. 1c–e, o–p, 2b–c  
71 and f). It comprises curved monofilaments that are 3.5–12.8 mm long and 70–430  $\mu\text{m}$   
72 wide. Some short, distally tapering examples discriminate between dark-toned lateral  
73 margins and light-toned axial regions, especially near the filament base where the  
74 light-toned axis is wider, suggesting a tube-like morphology (Fig. 1c–e). Type 2 is  
75 preserved in the neck, proximal forelimb, plantar metatarsus and proximal tail regions  
76 of CAGS–Z070. It consists of bundles of curved filaments of similar length that  
77 appear to form brush-like structures at the distal ends of thicker filaments (2.0–13.8  
78 mm long and 80–180  $\mu\text{m}$  wide) (Fig. 1f–h). The latter may represent individual thick  
79 filaments or fused proximal regions of thinner distal filaments. Type 3 occurs around  
80 the head of CAGS–Z070. It comprises straight to slightly curved, distally tapered,  
81 central filaments (4.5–7.0 mm long and 50–450  $\mu\text{m}$  wide) with short lateral branches  
82 that diverge from the central filament near the midpoint (Fig. 1i–k). There are five  
83 Type 3 filaments identified on the head, next to five similar filaments likely of the  
84 same nature but obscured by overlapping filaments (Supplementary Fig. 5b). Type 4  
85 occurs on the wing membrane of both specimens. It comprises tufts of curved

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86 filaments (2.5–8.0 mm long and 70–130  $\mu\text{m}$  wide) that diverge proximally (Figs. 11–n  
87 and 2d–e), in contrast to the clear separation between Type 1 filaments (Fig. 1o–p).

88 Filamentous integumentary structures in extant and fossil vertebrates commonly  
89 contain melanin-bearing organelles (melanosomes). Scanning electron microscopy  
90 (SEM) of the filamentous structures of NJU–57003 reveals densely packed  
91 microbodies  $0.70 \pm 0.11 \mu\text{m}$  long and  $0.32 \pm 0.05 \mu\text{m}$  wide (Fig. 2g–h,  
92 Supplementary Figs. 4a–f, 6 and 7, and Supplementary Table 2). As with most  
93 melanosome-rich fossil feathers<sup>19-21</sup>, energy dispersive X-ray spectroscopy (EDS)  
94 spectra of the filaments are dominated by a major peak for carbon (Supplementary  
95 Fig. 8). These carbonaceous microbodies resemble fossil melanosomes in terms of  
96 their geometry, dense packing, parallel alignment relative to the long axis of the  
97 integumentary structure (i.e. barbules in Paraves), and preservation within the matrix  
98 of the filament (see Supplementary text). Most of the microbodies are oblate and  
99 morphologically similar to those that are usually interpreted as phaeomelanosomes in  
100 fossils<sup>19</sup> (Fig. 2h). Rod-shaped examples, usually interpreted as eumelanosomes in  
101 fossils<sup>19</sup> (Fig. 2g), are rare.

102 Fourier transform infrared spectroscopy (FTIR) of samples of pterosaur filaments  
103 shows four major peaks unique to the filaments (Fig. 2i). These peaks are consistent  
104 with the absorption regions of amide I at ca.  $1650 \text{ cm}^{-1}$  (principally the C=O  
105 asymmetric stretching vibration with some C–N bending), amide II at ca.  $1540 \text{ cm}^{-1}$   
106 (a combination of N–H in-plane bending and C–N and C–C stretching as in indole  
107 and pyrrole in melanin and amino acids), and aliphatic C–H stretching at  $2850 \text{ cm}^{-1}$

108 and 2918  $\text{cm}^{-1}$ <sup>22</sup>. These peaks also occur in spectra obtained from extant feathers<sup>21,23</sup>,  
109 fossil feathers of the paravian *Anchiornis*<sup>20</sup>, and melanosomes isolated from human  
110 hair<sup>24</sup>. Further, spectra of the pterosaur filaments more closely resemble those of  
111 pheomelanin-rich red human hair in the stronger absorption regions at ca. 2850  $\text{cm}^{-1}$   
112 and 2918  $\text{cm}^{-1}$  and higher resolution in the region ca. 1500–1700  $\text{cm}^{-1}$  than those  
113 from eumelanin-rich black human hair and the ink sac of cuttlefish<sup>24</sup>. This, together  
114 with the SEM results, suggests that the densely packed microbodies in the pterosaur  
115 filaments are preserved melanosomes. The amide I peak at 1650  $\text{cm}^{-1}$  is more  
116 consistent with  $\alpha$ -keratin (characteristic of extant mammal hair<sup>25</sup>) than  $\beta$ -keratin (the  
117 primary keratin in extant avian feathers<sup>22,26</sup>). This signal may be original or  
118 diagenetic; the molecular configuration of keratin<sup>26</sup> and other proteins<sup>27</sup> can alter  
119 under mechanical stress and changes in hydration levels.

120 The ultrastructural and chemical features of the pterosaur filaments confirm that  
121 they are hair-like or feather-like integumentary structures. The four types of filaments  
122 described here show distinct distributions and morphologies. They are separated  
123 clearly from the sedimentary matrix by sharp boundaries (Supplementary Fig. 4g–i).  
124 There is no evidence that one or more filament type(s) were generated  
125 taphonomically, e.g. through selective degradation or fossilization, or superimposition  
126 of filaments. For instance, although Type 1 and 4 filaments occur widely in both  
127 specimens, Type 4 occurs only in the wings, while Type 1 occupies the remaining  
128 body regions. Type 1 filaments are thus not degraded products of Type 4, and Type 4  
129 filaments do not represent superimposed clusters of Type 1 filaments. Filament types

130 2 and 3 occur only in CAGS–Z070. Type 3 occurs only in the facial area and is  
131 associated with Type 1, where Types 2 and 4 are not evident. Type 3 filaments are  
132 thus not degraded Type 2 or 4 filaments. Central filaments of Type 3 are  
133 morphologically identical to the short, distally tapering filaments of Type 1, but the  
134 branching filaments are much thinner ( $< 40 \mu\text{m}$  (Type 3) versus  $>70 \mu\text{m}$  (Type 1)  
135 wide) and shorter ( $< 0.6 \text{ mm}$  vs.  $> 3.5 \text{ mm}$  long) than the latter. The branching  
136 filaments are thus unlikely to reflect superimposition of clusters of Type 1 filaments.  
137 In contrast, the distal ends of Type 2 filaments are similar, and have a similar  
138 distribution pattern to, Type 1 filaments. An alternative interpretation, that Type 2  
139 filaments might represent superimposition of Type 1 filaments at their proximal ends,  
140 is unlikely (see detailed discussion in Supplementary text). Feathers and feather-like  
141 integumentary structures have been reported in non-avian dinosaurs, although debate  
142 continues about their true nature<sup>2</sup>. These structures have been ascribed to several  
143 morphotypes, some absent in living birds<sup>3,5</sup>, and provide a basis to analyse the  
144 evolutionary significance of pterosaur pycnofibres. The pterosaur Type 1 filaments  
145 resemble monofilaments in the ornithischian dinosaurs *Tianyulong* and *Psittacosaurus*  
146 and the coelurosaur *Beipiaosaurus*: unbranched, cylindrical structures with a midline  
147 groove that widens towards the base (presumed in *Beipiaosaurus*)<sup>3,5</sup>. The pterosaur  
148 Type 2 filaments resemble the brush-like bundles of filaments in the coelurosaurs  
149 *Epidexipteryx* and *Yi*<sup>3,5,28</sup>: both comprise parallel filaments that unite proximally. The  
150 morphology and circum-cranial distribution of pterosaur Type 3 filaments resemble  
151 bristles in modern birds<sup>1</sup>, but surprisingly do not correspond to any reported



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152 morphotype in non-avian dinosaurs. The Type 3 filaments recall bilaterally branched  
153 filaments in *Sinornithosaurus*, *Anchiornis*, and *Dilong*, but the latter filaments branch  
154 throughout their length rather than halfway along the central filament(s), as in the  
155 pterosaur structure<sup>3,5</sup>. The pterosaur Type 4 filaments are identical to the radially  
156 branched, downy feather-like morphotype found widely in coelurosaurs such as  
157 *Sinornithosaurus*, *Beipiaosaurus*, *Protarchaeopteryx*, *Caudipteryx*, and *Dilong*<sup>3,5</sup>.

158       The filamentous integumentary structures in our anurognathid pterosaurs are thus  
159 remarkably similar to feathers and feather-like structures in non-avian dinosaurs.  
160 Intriguingly, cylindrical (Type 1), radially symmetrical branched (Types 2 and 4) and  
161 bilaterally symmetrical branched (Type 3) filaments clearly coexisted in individual  
162 animals; these structures may represent transitional forms in the evolution of feathers,  
163 as revealed by developmental studies<sup>3,5</sup>. These new findings warrant revision of the  
164 origin of complex feather-like branching integumentary structures from Dinosauria to  
165 Avemetatarsalia, the wider clade that includes dinosaurs, pterosaurs, and close  
166 relatives<sup>4,29</sup>. The early evolutionary history of bird feathers and homologous structures  
167 in dinosaurs, and the multiple complex pycnofibres of pterosaurs, is enigmatic. A  
168 previous study concluded that the common ancestor of these clades bore scales and  
169 not filamentous integumentary appendages<sup>2</sup>, but this result emerged only when the  
170 filaments of pterosaurs were coded as non-homologous with those of dinosaurs. There  
171 are no morphological criteria, however, for such a determination. The presence of  
172 multiple pycnofibre types and their morphological, ultrastructural and chemical  
173 similarity to feathers and feather-like structures in various dinosaurian clades,

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174 confirms their likely homology with filamentous structures in non-avian dinosaurs  
175 and birds. Comparative phylogenetic analysis produces equivocal results: maximum  
176 likelihood modelling of plausible ancestral states, against various combinations of  
177 branch length and character transition models (Supplementary text and  
178 Supplementary Fig. 9, Table 3), reveals various potential solutions. The statistically  
179 most likely result (Fig. 3 and Supplementary Table 3, highest log-likelihood value)  
180 shows that the avemetatarsalian ancestors of dinosaurs and pterosaurs possessed  
181 integumentary filaments, with highest likelihood of possessing monofilaments; tufts  
182 of filaments, and, especially, brush-type filaments, are less likely ancestral states. This  
183 confirms that feather-like structures arose in the Early or Middle Triassic. The  
184 alternative tree for Dinosauria, with Ornithischia and Theropoda paired as  
185 Ornithoscelida<sup>30</sup>, produces an identical result.

186 We present these modelling data with caution, however, for two reasons: (1) the  
187 tree rooting method can influence the result (Supplementary Table 3), favouring  
188 results in which either scales are the basal condition or where non-theropod feather-  
189 like structures and feathers evolved independently (Supplementary Figure 9, Table 3),  
190 and (2) there is no adequate way to model probabilities of evolution of all six feather  
191 types, or to model probabilities of transitions between the six different feather types.

192 The discovery of multiple types of feather-like structures in pterosaurs has broad  
193 implications for our understanding of pterosaur biology and the functional origin of  
194 feather-like structures in Avemetatarsalia<sup>31,32</sup>. Potential functions of these structures  
195 include insulation, tactile sensing, streamlining and coloration (primarily for

196 camouflage and signalling), as for bristles, down feathers and mammalian hairs<sup>31-34</sup>.  
197 Type 1, 2 and 4 filaments could shape a filamentous covering around the body and  
198 wings (Fig. 4) that might have functioned in streamlining the body surface in order to  
199 reduce drag during flight, as for modern bat fur or avian covert feathers<sup>33,35</sup>. Type 1  
200 and 2 filaments occur in considerably high densities, particularly around the neck,  
201 shoulder, hindlimb and tail regions where the high degree of superposition prevents  
202 easy discrimination of adjacent fibres. This, along with the wide distribution and  
203 frayed appearance, resembles mammalian underfur adapted for thermal insulation<sup>36,35</sup>.  
204 Despite the less dense packing of Type 4 filaments on the wings, the morphology of  
205 the structures is consistent with a thermoregulatory function: down feathers can  
206 achieve similar insulation as mammalian hair with only about half the mass, due to  
207 their air-trapping properties and high mechanical resilience, effective in retaining an  
208 insulating layer of still air<sup>38</sup>. This may optimize the encumbrance of the large wing  
209 area to wing locomotion<sup>18</sup>. Type 3 filaments around the jaw (Fig. 4) may have had  
210 tactile functions in e.g. prey handling, information gathering during flight, navigating  
211 in nest cavities and on the ground at night, similar to bristles in birds<sup>39</sup>.

212

## 213 **Methods**

214 **Sampling.** The specimen NJU-57003 is represented by two fragmented slabs, both  
215 containing original bone, fossilized soft tissues, and natural moulds of bones. Each  
216 slab was glued together along the fissures by fossil dealers with the fossil on the

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217 surfaces untouched. The specimen CAGS–Z070 is represented by a single unbroken  
218 slab. Small flakes (1–3 mm wide) of samples with preserved integument and/or  
219 enclosing sediments were carefully removed from the inferred integumentary  
220 filaments from different parts of NJU–57003 (Supplementary Figs. 1a and 4a–c)  
221 using a dissecting scalpel. This method was used to avoid sampling from degraded  
222 products of other tissues, such as dermis, epidermis, or even internal organs. Most  
223 samples were not treated further; the remainder were sputter-coated with Au to  
224 enhance SEM resolution (Fig. 2g–h and Supplementary Figs. 4a–f and 6). All  
225 experiments described below were repeated in order to validate the results.

226

227 **SEM.** Samples were examined using a JEOL 8530F Hyperprobe at the School of  
228 Earth Sciences, University of Bristol, and a LEO 1530VP scanning electron  
229 microscope at the Technical Services Centre, Nanjing Institute of Geology and  
230 Palaeontology, Chinese Academy of Sciences. Both instruments were equipped with a  
231 secondary electron (SE) detector, a back-scattered electron (BSE) detector and an  
232 energy dispersive X-ray spectrometer (EDS).

233

234 **Measurements of melanosomes.** The geometry of melanosomes was measured from  
235 SEM images using the image-processing program ImageJ (available for download at  
236 <http://rsbweb.nih.gov/ij/>). We measured maximum short and long axis length of  
237 melanosomes that were oriented perpendicular to line of sight, and from these data we  
238 calculated mean and coefficient of variation (CV) of the long and short axis, and mean

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239 aspect ratio (long:short axis). Based on the proposed taphonomic alteration of fossil  
240 melanosome size (shrinkage up to ~20% in both length and diameter)<sup>40,41</sup>, we  
241 modelled potential diagenetic alteration by enlarging original measurements by 20%.

242

243 **FTIR microspectroscopy.** Samples of the filamentous tissues and the associated  
244 sediments were removed separately from NJU-57003 and placed on a BaF<sub>2</sub> plate  
245 without further treatment. The IR absorbance spectra were collected using a Thermo  
246 iN10MX infrared microscope with a cooled MCT detector, at the School of Earth  
247 Sciences, University of Bristol. The microscope was operated in transmission mode  
248 with a 15x15 micron aperture. 10 spectra were obtained from the filamentous tissues.  
249 The spectra show consistent results and the example presented in Fig. 2 shows the  
250 highest signal to noise ratio and was obtained with 2 cm<sup>-1</sup> resolution and 2000 scans.

251

252 **Fluorescence microscopy.** Selected areas with extensive soft tissue preservation in  
253 NJU-57003 were investigated and photographed using a Zeiss Axio Imager Z2  
254 microscope with a digital camera (AxioCam HRc) and a fluorescence illuminator  
255 (514 nm LED) attached, at the Technical Services Centre, Nanjing Institute of  
256 Geology and Palaeontology, Chinese Academy of Sciences.

257

258 **Laser-stimulated fluorescence (LSF) imaging and data reduction protocol.** LSF  
259 images were collected using the protocol of Kaye et al.<sup>15,16</sup>. NJU-57003 was imaged  
260 with a 405 nm 500 mw laser that was projected into a vertical line by a Laserline

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261 Optics Canada lens. The laser line was swept repeatedly over the specimen during the  
262 exposure time for each image in a dark room. Images were captured with a Nikon  
263 D610 DSLR camera fitted with an appropriate long pass blocking filter in front of the  
264 lens to prevent image saturation by the laser. Standard laser safety protocols were  
265 followed during laser usage. The images were post processed in Photoshop CS6 for  
266 sharpness, colour balance and saturation.

267

268 **Phylogenetic macroevolutionary analysis.** In order to analyse the evolution of  
269 feather characters, data were compiled on known integumentary characters across  
270 dinosaurs and pterosaurs. The basic data were taken from the Supplementary data of  
271 Barrett et al. <sup>2</sup>, comprising 74 dinosaurs (33 ornithischians, seven sauropods and 44  
272 theropods (including four Mesozoic birds)); to this dataset we added four pterosaurs.  
273 Barrett et al. <sup>2</sup> scored taxa for three integumentary states (scales, filaments, feathers)  
274 in their macroevolutionary analyses. We checked and followed these basic categories  
275 and added three more; we then cross-referenced these six categories against the  
276 feather morphotypes defined by Xu et al. <sup>42</sup>. The categories used herein are: scales (1;  
277 not included in Xu et al. <sup>42</sup>), monofilaments (2; morphotypes 1 and 2 in Xu et al. <sup>42</sup>),  
278 brush-like filaments associated with a planar basal feature (3; morphotypes 4 and 6 in  
279 Xu et al. <sup>42</sup>), tufts of filaments joined basally (4; morphotype 3 in Xu et al. <sup>42</sup>), open  
280 pennaceous vane, lacking secondary branching (5; morphotype 5 in Xu et al., <sup>42</sup>), and  
281 closed pennaceous feathers comprising a rachis-like structure associated with lateral  
282 branches (barbs and barbules) (6). There was some uncertainty over feathers coded

---

283 herein as type 3, which could correspond to morphotype 6, or morphotypes 4 and 6 in  
284 Xu et al.<sup>42</sup>. However, the only taxa coded with these as the most derived feather type  
285 are *Sordes pilosus* and *Beipiaosaurus inexpectus*. These taxa belong to separate clades  
286 and thus the calculation of ancestral states is not affected by how our feather type 3 is  
287 coded (i.e. whether treating morphotypes 4 and 6 of Xu et al.<sup>42</sup> in combination or  
288 separately).

289 As in previous studies<sup>2</sup>, we used maximum-likelihood (ML) approaches to  
290 explore trait evolution. There are many methods to estimate ancestral states for  
291 continuous characters, but choices are more limited for discrete characters, such as  
292 here, where only ML estimation of ancestral states is appropriate<sup>43</sup>. We calculated ML  
293 reconstructions of ancestral character states using the ‘ace’ function of the ape R  
294 package<sup>44</sup>, with tree branch lengths estimated in terms of time, derived using the  
295 ‘timePaleoPhy’ function in the paleotree package<sup>45</sup> and the ‘DatePhylo’ function in  
296 the strap R package<sup>46</sup>. These enabled us to assess results according to three methods  
297 of estimating branch lengths, the ‘basic’ method, which makes each internal node in a  
298 tree the age of its oldest descendant, the ‘equal branch length’ (equal) method, which  
299 adds a pre-determined branch length (often 1 Myr) to the tree root and then evenly  
300 distributes zero-length branches at the base of the tree, and the ‘minimum branch  
301 length’ (mbl) method, which minimizes inferred branching times and closely  
302 resembles the raw, time-calibrated tree. A problem with the ‘basic’ branch length  
303 estimation is that it results in many branch lengths of length zero, in cases where  
304 many related taxa are of the same age; in these cases, we added a line of code to make

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305 such zero branch lengths equal to 1/1000000 of the total tree length. A criticism of the  
306 mbl method is that it tends to extend terminal branching events back in time,  
307 especially when internal ghost lineages are extensive<sup>2</sup>, but this is not the case here,  
308 and the base of the tree barely extends to the Triassic / Jurassic boundary.

309 We ran our analyses using three evolutionary models with different rates of  
310 transition between the specified number of character states (six here), namely “ER”,  
311 an equal-rates model, "ARD", an all-rates-different model and "SYM", a symmetrical  
312 model. These were calculated using the ‘ace’ function in ape<sup>2</sup> and the  
313 ‘add.simmap.legend’ function of the R package ‘phytools’<sup>47</sup>.

314 In a further series of analyses, we attempted to model the macroevolution of all  
315 traits, as coded (see Supplementary results), so coding multiple trait values for taxa  
316 that preserve multiple feather types. This did not shed much light on patterns of  
317 evolution of feather types because the multiple trait codings (e.g. 1,2 or 2,5,6) were  
318 each made into a new state, making 14 in all, and these were not linked. Therefore,  
319 the six multiply coded taxa that each had feather type 6 were represented as six  
320 independent states and their evolution tracked in those terms. Further, we attempted to  
321 separate the six characters, so they would track through the tree, whether recorded as  
322 singles or multiples in different taxa; however, we did not have the information to  
323 enable us to do this with confidence because of gaps in coding. In terms of reality,  
324 these multiply coded taxa still represent an incomplete sample of the true presence  
325 and absence of character states - by chance, many coelurosaurs are not coded for  
326 scales (1) or monofilaments (1), and yet it is likely they all had these epidermal



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327 appendages. Therefore, attempting to run such multiple codings, with characters  
328 either as groups or coded independently, encounters so many gaps that the result is  
329 hard to interpret. Our approach is to code the most derived feather in each taxon, and  
330 that too is incomplete because of fossilization gaps, but at least it represents a  
331 minimal, or conservative, approach to trait coding and hence to the discoveries of  
332 macroevolutionary patterns of feather evolution; complete fossil data might show  
333 wider distributions of each feather type and hence deeper hypothesized points of  
334 origin. Complete coding of feather types would of course allow each trait to be  
335 tracked in a multiple-traits analysis.

336

### 337 **Data availability**

338 The data that support the findings of this study are available from the corresponding  
339 authors upon reasonable request.

340

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454

455 **Supplementary Information** is available in the online version of the paper.

456

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466

## 467 **Author Contributions**

468 B.Y.J. and M.J.B. designed the research, Z.X.Y., B.Y.J. and X.X. systematically  
469 studied the specimens, Z.X.Y., S.L.K., M.E.M, and P.J.O. did the SEM analysis,  
470 Z.X.Y. and B.Y.J. did the FTIR analysis, M.P. and T.G.K. did the LSF imaging, data  
471 reduction and interpretation, M.J.B. did the maximum likelihood analyses, and  
472 Z.X.Y., B.Y.J., M.J.B., M.E.M, X.X. and P.J.O. wrote the paper; all authors approved  
473 the final draft of the paper.

474

## 475 **Author Information**

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480

481 **Figure 1 | Integumentary filamentous structures in CAGS–Z070.** **a**, Overview  
482 shows extensive preservation of soft tissues. **b–p**, Details of the integumentary  
483 filaments in the regions indicated in **a** on the head and neck (**b–d**, **i–j**), forelimb (**f–g**),  
484 wing (**l–m**) and tail (**o–p**), and illustrated reconstructions of the filaments (**e**: Type 1  
485 filament; **h**: Type 2 filament; **k**: Type 3 filament; **n**: Type 4 filament). Scale bars: 20  
486 mm in **a**; 10 mm in **b**; 500  $\mu\text{m}$  in **c** and **i**; 100  $\mu\text{m}$  in **d**; 1 mm in **f**, **l**, **m** and **p**; 200  $\mu\text{m}$   
487 in **g** and **j**; 5 mm in **o**.

488

489 **Figure 2 | Preservation, microstructure and chemistry of the integumentary**  
490 **filamentous structures in NJU–57003.** **a**, Laser-stimulated fluorescence<sup>6,15,16</sup> image  
491 highlights extensive preservation of soft tissues (black areas). **b–f**, Details of the  
492 integumentary filaments in the regions indicated in **A** on the head and neck (**b–c**),  
493 wing (**d–e**) and tail (**f**). **g–h**, Scanning electron micrographs of the monofilaments on  
494 the neck and hindlimb of NJU–57003 (samples 10 and 39, respectively,  
495 Supplementary Fig. 1**a**) show densely packed, elongate and oblate melanosomes. **i**,  
496 FTIR absorbance spectra of the monofilaments, monofilaments with sediment matrix,  
497 and sediment matrix in NJU–57003 (Sample 15, Supplementary Fig. 1**a**) compared  
498 with spectra from a feather of *Anchiornis* (from ref. <sup>20</sup>), extant Marabou stork feather



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499 (from ref. <sup>21</sup>) and black and red human hair melanosomes (from ref. <sup>24</sup>). Scale bars: 20  
500 mm in **a**; 1 mm in **b**, **c** and **e**; 5 mm in **d** and **f**; 1  $\mu$ m in **g** and **h**.

501

502 **Figure 3 | Phylogenetic comparative analysis of integumentary filament and**  
503 **feather evolution in pterosaurs and archosaurs.** The phylogeny is scaled to  
504 geological time, with recorded terminal character states for each species, and  
505 estimated ancestral character states at the lower nodes. The model is the most likely of  
506 the maximum likelihood models, based on minimum-branch lengths (mbl) and  
507 transitions occurring as all-rates-different (ARD), but other results with lower  
508 likelihoods show scales as ancestral. The ancestral state reconstruction shows a  
509 combination of monofilaments, tuft-like filaments, and brush-type filaments as the  
510 ancestral state for Avemetatarsalia and for Dinosauria. The estimated ancestral state  
511 for Theropoda comprises all five feather states. Numbered small vertical arrows  
512 indicate earliest occurrences of feather types 2–6. Two hypotheses for timing of avian  
513 feather origins are indicated: A, early origin, at the base of Avemetatarsalia in the  
514 Early Triassic, or B, late origin, at the base of Maniraptora in the Early–Middle  
515 Jurassic.

516

517 **Figure 4 | Reconstruction of one of the studied anurognathid pterosaurs, exhibiting**  
518 **diverse types of pycnofibres distributed in different body parts.**