Foot scales in the Early Cretaceous bird *Gansus yumenensis* from China

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22 **Abstract**

23

24 Most modern birds have scales covering the foot and feathers elsewhere. Discoveries
 25 of fossil feathers attached to the metatarsus in non-avian dinosaurs and basal birds
 26 suggests that the avian scales are secondarily derived from feathers. However, our
 27 knowledge of early avian scales and their taphonomy is still limited, due to the
 28 scarcity of fossil record. Here we employ multiple techniques to characterize the
 29 morphological and chemical details preserved and investigate how they are preserved
 30 in the skin of IVPP V15077, a referred specimen of the Early Cretaceous *Gansus*
 31 *yumenensis*. Results show that two types of scales, scutellate and interstitial scales,
 32 are preserved in IVPP V15077, which, in combination with previous discovery of
 33 scutate and reticulate scales in other Early Cretaceous birds, indicates that all four
 34 types of scales present in modern birds have appeared in the Early Cretaceous. SEM
 35 observations and Raman analysis suggest that the skin of *Gansus yumenensis* may be
 36 pigmented. Elemental mapping indicates that aluminosilicates and calcium phosphate
 37 are involved in the mineralization of the skin.

38

39 Key Words: *Gansus yumenensis*, skin, scale, melanosome, Raman spectroscopy

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42

43 **Introduction**

44

45 Most modern birds have scales covering the foot (tarsometatarsus and toes) and
 46 feathers covering most of the rest of the body, with several wild species and some
 47 breeds of domestic pigeon and chicken display foot feathering (ptilopody) [1–3]. The
 48 scales can be categorized into four types: scutate scales that are large and somewhat
 49 overlapping on the anterior surface of the tarsometatarsus and dorsal surface of toes,
 50 scutellate scales that are somewhat smaller than scutate scales and located on the
 51 caudal surface of the tarsometatarsus, reticulate scales that are located on the plantar
 52 surface of toes, and interstitial scales that are morphologically similar to reticulate
 53 scales but are located on the tarsometatarsus [4]. The scutate, scutellate, and
 54 interstitial scales have similar patterns of keratinization, containing both α -keratins
 55 and β -keratins; the reticulate scales, by contrast, contain α -keratins but no β -keratins
 56 [4]. The interstitial scales are also referred to as reticulate scales in some studies [e.g.,
 57 5–7].

58

59 Fossil discoveries of non-avian dinosaurs and basal birds with feathers attached to the
 60 metatarsi suggest that foot feathering is the primitive state for birds [8–11], which is
 61 consistent with the view that avian scales are secondarily derived from feathers
 62 [12–14]. The foot feathering in modern birds might represent a reversion to the
 63 ancestral state [15]. Another view concerning the origin of avian scales is that they are

64 homologues of reptilian scales [5,16]. To date, our knowledge of the foot scales in
65 early birds is limited, due to the scarcity of fossil record [11,17–19].

66

67 IVPP V15077 (Institute of Vertebrate Paleontology and Paleoanthropology) is a
68 referred specimen of *Gansus yumenensis* with scales well preserved *in situ* around the
69 joint of the tibiotarsus and the tarsometatarsus [17]. To date, all reported specimens of
70 *Gansus yumenensis* are from Xiagou Formation, Changma basin, China [17,20,21].

71 Stable isotope chemostratigraphy places the age of the bird quarries in the early
72 Aptian [22]. Despite the well preservation of the skin in IVPP V15077, no
73 investigation on the ultrastructure and the chemistry of the skin has been performed.

74 The aim of the present study is to investigate what morphological and chemical
75 details are preserved in the skin and how they are preserved by employing multiple
76 techniques, including scanning electron microscopy (SEM), scanning electron
77 microscopy-energy dispersive X-ray spectrometry (SEM-EDS), Raman spectroscopy,
78 and X-ray powder diffraction (XRPD).

79

80 **Material and Methods**

81

82 One skin sample was removed from IVPP V15077 using a sterile blade and directly
83 analyzed using scanning electron microscopy (SEM), scanning electron
84 microscopy-energy dispersive X-ray spectrometry energy dispersive X-ray

85 spectrometry (SEM-EDS), and Raman spectroscopy. One sediment sample was
86 scraped from the bedding plane surface where the fossil is preserved, and powered for
87 X-ray powder diffraction (XRPD) analysis.

88

89 SEM observations were performed using a Sigma 500 Field Emission Scanning
90 Electron Microscope (FE-SEM) at 1.5 keV. Elemental mappings of the skin sample
91 were performed using a Tescan MAIA3 FE-SEM equipped with an Energy Dispersive
92 X-ray Spectrometry (EDS) at 8 keV and at 20 keV.

93

94 Raman analysis of the skin sample was performed using a LabRAM HR Evolution
95 Raman spectrometer with a 532.11 nm laser and a 50 × Olympus objective with a
96 long working distance. A 600 groove/mm grating was used with the spectral
97 resolution better than 2 cm⁻¹. Spectra were acquired with four accumulations and
98 accumulation time of 4s to 8s. Raman analysis was also performed a black chicken
99 feather to obtain spectra of eumelanin [23] for comparison.

100

101 XRPD analysis of the sediment sample was performed using a Bruker D8 ADVANCE
102 diffractometer with Cu Kα radiation and the scanning angel ranged from 3° to 90° of
103 2θ.

104

105 **Results**

106

107 The skin preserved around the joint of the right tibiotarsus and tarsometatarsus is
 108 exposed in the inner view (Figure 1). The scales are non-overlapping. The proximal
 109 scales are large and elongate, and correspond to the scutellate scales. The distal and
 110 medial scales are small and rounder than the proximal scales, and correspond to the
 111 interstitial scales. The regions between scales, referred to as sulci in extant birds, are
 112 lighter in color than the scales, as seen from where the sulci are exposed (Figure 2A).
 113 Most part of the sulci is covered by a layer of sediment.

114

115 SEM reveals impressions of ovoid and rod-like microbodies on some scattered
 116 fragments in the skin (Figure 2). Such microbodies likely represent melanosomes
 117 following recent studies on fossil feathers and reptile skin [24–30]. The dimensions of
 118 these microbodies fall within the range of melanosomes from feathers, more
 119 specifically, the overlapping region of melanosomes from black feathers, gray
 120 feathers, brown feathers, and feathers with non-iridescent structural colors [31].

121

122 The elemental mapping was performed with two accelerating voltages of 8 keV and
 123 20 keV to detect the vertical variation of the elemental distribution. The elemental
 124 mapping at 8 keV show that the scales have an elevated concentration of C than the
 125 sulci. This discrepancy is less distinct in the elemental mapping at 20 keV, indicating
 126 the C is distributed near the surface. The layer of sediment covering the sulci has an

127 elevated concentration of Ca and P, indicating the presence of calcium phosphate.

128 Where this layer of sediment was removed (arrows in Figure 4), the elements Si, Al,

129 Fe, Na, S, Mg, and K show no spatial partitioning between scales and sulci.

130

131 Raman spectroscopy confirms the presence of carbonaceous material in the fossil skin.

132 The Raman spectra of the sulcus and the sediment are similar; both exhibit two broad

133 bands near 1350 cm^{-1} and 1600 cm^{-1} , which are characteristic of carbonaceous

134 materials and referred to as the D-band and the G-band. By contrast, the G-band in the

135 Raman spectrum of the scale has a lower wavenumber (1585 cm^{-1}), resembling that in

136 eumelanin.

137

138 XRPD shows that the sediment consists mainly of analcime, apatite, quartz, calcite,

139 and illite (Figure 6).

140

141 **Discussion**

142

143 *Foot scales in early birds*

144

145 Fossil record is key to determining when modern taxa acquire their morphological

146 characters. Among the four types of scales in modern birds, reticulate scales on the

147 plantar surface of toes appeared earliest in the lineage leading to modern birds, and

148 have been found in basal birds *Sapeornis* [32] and *Confuciusornis* [18]. Discoveries
149 of metatarsal feathers in basal birds *Sapeornis* and *Confuciusornis* and non-avian
150 dinosaurs imply that scales on the tarsometatarsus in modern birds evolved
151 secondarily from feathers in the Ornithuromorpha [11], the most inclusive avian clade
152 that contains all modern birds but not Enantiornithes [33]. In the basal
153 ornithuromorph *Yanornis* from the Early Cretaceous Jehol Biota, scutate scales
154 covering the anterior surface of the tarsometatarsus and dorsal surface of toes have
155 been previously found [11]. Reexamination of IVPP V15077 here reveals the
156 presence of scutellate scales and interstitial scales in the Early Cretaceous
157 ornithuromorph *Gansus yumenensis*. These results show that all the four types of
158 scales in modern birds [4] have appeared in the Early Cretaceous.

159

160 *Pigmentation of the preserved skin*

161

162 SEM observations and Raman spectroscopy suggest that the preserved skin of *Gansus*
163 *yumenensis* is likely pigmented. The dimensions of the melanosome-like structures
164 fall within the range of melanosomes from feathers [31]. It has been noted that the
165 Raman spectra of eumelanin resemble that of disordered graphite [23,34]. Raman
166 spectroscopy was thus cautioned to be used alone as a definitive test for the presence
167 of eumelanin in fossils [35], as organic matter can be progressively transformed into
168 graphite when heated [36]. Nevertheless, the assignment of the 1585 cm⁻¹ band in the

169 Raman spectrum of the scale to eumelanin here is supported by its wavenumber
 170 difference from the G-band in the spectrum of the sulcus. Raman spectral parameters
 171 of organic matter is indicative of the temperature experienced by host rocks and the
 172 thermal maturity of organic matter [37,38]. A G-band at 1585 cm^{-1} indicates a higher
 173 maturity level than a G-band at 1600 cm^{-1} band. As the scales and the sulci have the
 174 same geological history, their difference in Raman spectra supports an original
 175 compositional difference.

176

177 *Taphonomy*

178

179 Usually, the skin decays quickly after the death of birds [39]. The preserved
 180 carbonaceous matter in the fossil suggests that the skin was stabilized from enzymatic
 181 and other postmortem changes soon after the death of the bird [40].

182

183 Sedimentary facies analysis indicated that the Xiagou formation in Changma Basin in
 184 dominated by lacustrine deposits [41]. The primary to early diagenetic dolomites in
 185 this Formation suggests that the lake is closed, alkaline to saline [42]. The
 186 identification of analcime in the sediment is consistent with this interpretation of the
 187 lake. Reaction of alkaline lake water and detrital clay and perhaps other materials can
 188 result in the formation of analcime [43].

189

190 The pattern of elemental distribution suggests two mineralization modes are
 191 responsible for the preservation of the skin in IVPP V15077. The epidermis, including
 192 the scales and sulci, is mineralized in aluminosilicates. As the skin of IVPP V15077 is
 193 exposed in the inner view, the layer of carbonate phosphate covering the sulci is
 194 supposed to correspond to the dermis. Preservation of soft tissues, including skin, in
 195 calcium phosphate is relatively common in fossil record [44,45]. To date, research
 196 into mineralization of soft tissues in aluminosilicates is mainly focused on marine
 197 settings, aiming to understanding the Burgess Shale-type fossilization [e.g., 46–49].
 198 Al is suggested to be a key factor in the stabilization of soft tissues [47,48,50]. It has
 199 been hypothesized that Al can induce taphonomic tanning, a concept borrowed from
 200 leather industry, involving secondary cross-linking of structural biomolecules that
 201 protects them from bacterial degradation [47]. The surrounding sediment can serve as
 202 the source of Al. Experimental work demonstrated that the decay of soft tissues can
 203 lower the pH values and lead to the acid hydrolysis of clay minerals in the
 204 surrounding environments both in marine settings [48] and in fresh water settings [50].
 205 The experimental work simulating marine environments demonstrated that kaolinite
 206 and chlorite sediment enhanced soft tissue preservation compared with sediment-free
 207 control and the effect of kaolinite is higher than that of chlorite [48]. Consistent with
 208 the hypothesis of taphonomic tanning of Al is that more Al was released during the
 209 acidic hydrolysis of kaolinite compared to chlorite [48]. Likewise, the experimental
 210 work simulating fresh water environments demonstrated that kaolinite and

211 montmorillonite sediment enhanced soft tissue preservation compared with
212 sediment-free control and the effect of kaolinite is higher than that of montmorillonite
213 [50]. Though recent studies focused on the role of kaolinite in the preservation of soft
214 tissues [48–50], kaolinite is by no means the only mineral that can produce Al through
215 acid hydrolysis. Both albite and analcime identified in the sediment from the bedding
216 plane of IVPP V15077 can be dissolved by organic acid [e.g., 51,52]. Analogously,
217 Fe-based tanning may also contribute to the inhibition of the decay of soft tissues
218 [47,53].

219

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235

236 **Competing Interest Statement**

237

238 The authors declare no competing interest.

239

240 **References**

241

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403 **Figure captions**

404

405 Figure 1. Photo of IVPP V15077, a referred specimen of *Gansus yumenensis* showing
406 the skin preserved around the joint of the right tibiotarsus and tarsometatarsus. Scale
407 bar in (A) equals to 1 cm.

408

409 Figure 2. Photo and SEM images of the skin preserved in IVPP V15077. Arrows in (A)
410 and (B) mark the same position. Scale bar equals to 200 μm in (A), 100 μm in (B), 20
411 μm in (C), 10 μm in (D), 1 μm in (E) and (F).

412

413 Figure 3. Comparison of the length and width of the microbodies in the skin of IVPP
414 V15077 with those of melanosomes from feathers. Data on melanosomes from
415 feathers are from ref. 31. Feathers are categorized into 6 color groups: black, brown,
416 grey, iridescent, non-iridescent structural color and penguin.

417

418 Figure 4. Elemental maps for the skin in IVPP V15077 at 8 keV (A) and 20 keV (B).
419 Arrows indicate where the layer of sediment covering the sulci was removed. Scale
420 bar equals to 500 μm in (A) and (B).

421

422 Figure 5. Raman spectra of the skin in IVPP V15077. Scale bar equals to 500 μm .

423

424 Figure 6. X-ray powder diffraction analysis of the sediment from the bedding plane

425 surface where IVPP V15077 is preserved.