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New occurrences of fossilized feathers: systematics, taphonomy, and paleoecology of the Santana Formation of the Araripe Basin (Cretaceous), NE, Brazil

Gustavo M. E. M. Prado, Guilherme Raffaelli Romero, Luiz Eduardo Anelli

Feathers are the most complex and diversified integuments in vertebrates. Their complexity are provided by the different forms and functions, and they occur both in non-avian and avian-dinosaurs. Despite their rareness, feathers are found throughout the world, and the Santana Formation (comprised by Crato and Romualdo formations) of the Araripe Basin is responsible for the majority of these records in Brazil. Most occurrences is consisted by isolated feathers, where downy-feathers is the recurrent morphotype, two coelurosaurs and one enantiornithe bird. The sedimentary deposition of this unit is consisted by a lacustrine (Crato Fm) and lagoonal (Romualdo Fm) environments, where reducing conditions prevailed, precluding the activity of bottom dwelling organisms that favored the exquisite preservation. Despite the arid and hot conditions during the Cretaceous, life teemed in the adjacency of both paleolakes, however, feathered non-avian dinosaurs were not found yet in the Crato Member. By the great diversity of life that existed in the paleolake surroundings, is possible to recognize, through the fossil record, that a complex and diversified trophic chain was well established during the time period of sedimentation of this unit. When the remains reached the bottom of the paleolakes, the subsequent isolation from the environment allowed their preservation. In this work, three fossilized feathers, consisted of two downy and one contour feather, extracted from the laminated limestone of the Crato Member of the Santana Formation, were described and identified according to morphological and evolutionary models. We also used the terminology commonly applied to extant organisms. Relying on the fossil record of this unit and the adjacencies formations and basins (by autochthonous condition), taxonomic inferences can be made when the lowest hierarchy level is considered, and hence, is possible to propose the plausible taxa that could bear these elements. Taphonomic and paleoecological aspects, such as the preservation of these structures, and the presence of dinosaurs, were also reviewed, as well as the future perspectives about the study of these elements. Despite the virtual low significance, the pragmatcal study of fossilized feathers, can help with the understanding of the evolution and paleobiology of dinosaurs, especially on the South Hemisphere.

48 INTRODUCTION

49

50 Feathers are the most complex integuments of vertebrates, due to their variety of forms and
51 roles. This structure is responsible in the thermoregulation, display, protection against radiation,
52 toxicity, buoyancy and even to produce sound (Lucas & Stettenheim, 1972; Dumbacher *et al.*,
53 2004; Bostwick & Prum, 2005; Clark *et al.*, 2011; Dimond *et al.*, 2011).

54 Recent studies of molecular data of feathers, suggest the possible phylogenetic hierarchy in
55 the emergence of these elements, tying with the genesis of the tetrapod integuments. During the
56 period of land transition, which was marked by the aerial exposure and its consequences (*e.g.*, the
57 radiation and free O₂), many amphibians shared the same toolkit for the development of this
58 novelty. Because of this, the integumentary filaments can now be considered a symplesiomorphy,
59 once it is also found in mammals, pterosaurs, non-avian and avian dinosaurs (Greenwold & Sawyer,
60 2013; Lowe *et al.*, 2014). Even though, they are distinct between these groups, where α -keratin is
61 synthesized by mammals and β -keratin by reptiles. As evidences indicate a plausible multiple origin
62 of these structures within Dinosauria (Clarke, 2013), is possible that the first feathers were present
63 even in the base of the superorder (Xu, 2006; Norell, 2011). Nevertheless, the presence of these
64 elements in basal dinosaurs remains uncertain (Barret, 2013).

65 Since filaments were reported in a basal ornithischian (Godefroit *et al.*, 2014), a possible
66 occurrence of filament-feathers in dinosauromorphs, or even, in early saurischians, may fills the gap
67 between dinosaurs and other archosaurs (*e.g.*, pterosaurs). However, remains of these animals are
68 often fragmented or unearthed in coarse grain sediments (Langer *et al.*, 2014; Nesbitt *et al.*, 2013;
69 Benton *et al.*, 2014) that precludes the preservation of this fragile structures. Nevertheless, both
70 filament and true feathers were reported in Jurassic theropods (megalosauroids and coelurosaurs),
71 suggesting that this character maybe present early in early theropods (Rauhut *et al.*, 2012; Foth *et*
72 *al.*, 2014; Xu *et al.*, 2014).

73 Despite the broad distribution within this clade, true feathers (*i.e.* modern morphotypes) of
74 β -keratin, are only synthesized by more derived theropod dinosaurs (Prum & Brush, 2002; Xu,
75 2006; Zhang *et al.*, 2006; Xu & Guo, 2009; Norell, 2011; Clarke, 2013). One remarkable finding of
76 these elements in Mesozoic dinosaurs, is an imprintation of wing and tail feathers in a
77 enantiornithine embryo of Liaoning province in China, suggesting that precocity is indeed, an
78 ancient characteristic of birds (Zhou & Zhang, 2004).

79 In the past, the genesis of feathers were related with the advent of flight (Feduccia, 1993;
80 Martin, 1998), but recent studies indicate that this function originated in a different way, which
81 required the fully formation of these elements (Dial, 2003; Dial *et al.*, 2008; Heers & Dial, 2012).

82 In addition, evidences of simple morphotypes in non-avian dinosaurs, such as *Psittacosaurus* (Mayr
83 *et al.*, 2002), *Tyaniulong* (Zheng *et al.*, 2009) and *Kulindadromeus* (Godefroit *et al.*, 2014), makes
84 this hypothesis even more unlikely. Other interpretations, consider that feathers originated to
85 perform the thermoregulation functions, nevertheless, recent studies indicate that dinosaurs were
86 mesothermic, suggesting that their origin do not have any relation with the advent of homeothermy
87 (Grady *et al.*, 2014). Furthermore, the endothermy may have only originated during or briefly after
88 the advent of the flight, since this activity require a high metabolism, with high consumption of O₂
89 and a low accumulation of C₃H₆O₃ (lactic acid). To have an efficient thermoregulation control, is
90 possible that this condition evolved with the help of the feathers (Ruben & Jones, 2000) since the
91 non-avian theropods already were covered with them.

92 A tactile function, as the possible cause of the origin of these elements, was recently
93 proposed by Persons & Currie (2015). This hypothesis explains satisfactorily the origin of
94 filamentous-type integuments, that could be located in the face of its owners for semi-fossorial
95 habits. Despite the difficulty of these elements to be preserved in the fossil record, their proposal
96 require further evidences, once they are inexistent up to the present date.

97 Suggested by their distribution throughout the dinosauria clade, the possible reason for this
98 integumentary novelty can be assigned to the ability in maintain social interactions (by visual
99 communications or physiological features), where feathers were important elements in this activity.
100 Despite being a theoretical concept, this model also explains the evolution of the morphotypes, as
101 well as its wide range of color patterns that arisen in avian-dinosaurs, once the sexual selection
102 could be the main driver for their evolution (Dimond *et al.*, 2011; Koschowitz *et al.*, 2014)

103 Because feathers are delicate, their presence in the fossil record, can be associated with soft-
104 tissue preservation, and by so, they can be related to *konservat-lagerstätten* deposits. These
105 elements rarely survive the physicochemical processes that follows the burial, thus, they are usually
106 found as carbonized and iron traces, inclusions in ambers and coprolites, and as imprints (Wetmore,
107 1943; Martins-Neto & Kellner, 1989; Davis & Briggs, 1995; Perrichot, 2004; Perrichot *et al.*, 2008;
108 Vinther *et al.*, 2008; McKellar *et al.*, 2011; Vitek *et al.*, 2013).

109 Only a few deposits possess this kind of vestiges, not exceeding 50 around the world
110 (Kellner, 2002). Despite its rareness, there is a relatively cosmopolitan distribution of these
111 structures, that extends from the Middle Jurassic to the Neogene. Feathers were found in Mesozoic
112 and Cenozoic sedimentary rocks and ambers on the North Hemisphere, in countries such as Canada,
113 China, France, Germany, United States, Russia, Slovenia and Spain (Williston, 1896; Wetmore,
114 1943; Shufeldt, 1913; Kurochkin, 1985; Sanz *et al.*, 1988; Laybourne, 1994; Grimaldi & Case,
115 1995; Alonso *et al.*, 2000; Buffetaut *et al.*, 2002; Grimaldi *et al.*, 2002; Perrichot, 2004; Zhang *et*

116 *al.*, 2006; 2010; Perrichot *et al.*, 2008; Schweigert *et al.*, 2009; Knight *et al.*, 2011; McKellar *et al.*,
117 2011; Zelenitsky *et al.*, 2012; Thomas *et al.*, 2014). On the South Hemisphere, they were found in
118 Australia (Talent *et al.*, 1966; Waldman 1970), Brazil (Kellner, 2002), Peru (Clarke *et al.*, 2010),
119 and Antarctica (Mansilla *et al.*, 2013).

120 The first occurrence of fossil feathers in Brazil, was reported by Shufeldt (1916), in which a
121 primary remex was unearthed from the pelitic sediments of the Tremembé Formation, since then,
122 specimens with different morphotypes and from three geologic units. It consists of the Early
123 Cretaceous (Aptian-Albian) of the Santana Formation of the Araripe Basin (NE, Brazil); the
124 Paleogene (Oligocene) of the Tremembé Formation of the Taubaté Basin (SE, Brazil); and, from the
125 Neogene (Early Miocene) of the Pirabas Formation of the Barreirinhas Basin (N, Brazil) (Shufeldt,
126 1916; Santos, 1950; Ackerman, 1964; Kellner, 2002; Sayão *et al.*, 2011). While the Pirabas
127 Formation exhibited a single occurrence of feathers since 1964, both Santana and Tremembé
128 formations are responsible for the major records of this type of fossil (Kellner, 2002; Sayão *et al.*,
129 2011). The occurrences of fossilized feathers in Brazil can be seen in Table 1.

130 On this paper, we report three new occurrences of fossil feathers, from Cretaceous of Crato
131 Formation of the Araripe Basin. Here, we propose the systematic approach to these fossils,
132 according to the available data. Preliminary discussions about the taphonomy and paleoecology are
133 presented; the presence of avian dinosaurs and their paleoecology are also discussed.

134

135 **Geologic Setting**

136

137 The Araripe Basin (Fig. 1) is located in the northeast of Brazil, and its extension is in the
138 order of the approximately 5.500 to 8.000 Km², extending through three states (Ceará, Pernambuco
139 and Piauí), and is situated between 38° 30' to 40° 50' W of longitude, and 7° 05' to 7° 50' S of
140 latitude (Coimbra *et al.*, 2002; Vianna & Neumann, 2002). By the exceptional fossil preservation,
141 this sedimentary unit is described as a *Konservat-Lagerstätte* (Martill *et al.*, 2007). The geology of
142 this basin has been studied since the XIX century (Carvalho & Santos, 2005), with different
143 interpretations that depend of each authors approaches (Maisey, 1991; Assine, 1992; Martill, 1993;
144 Carvalho & Santos, 2005; Assine, 2007; Martill *et al.*, 2007a).

145 Because Assine (1992; 1994; 2007) have been working with the entire basin, in a detailed
146 level and in accordance with Brazilian Code of Stratigraphy, we prefer to adopt his descriptions in
147 this paper. The Santana Formation, is comprised by the Crato Member (in the bottom), and the
148 Romualdo Member (in the atop). Both units have different lithologies that reflect their distinct
149 deposition environment. Many of the exquisitely preserved fossils of the Araripe Basin, come from

150 the Crato Member strata, which is characterized by micritic laminated limestones intercalated with
151 shales and mudstones of varied thickness. This unit was formed in a lacustrine environment, with
152 brackish water, and reducing conditions in the bottom strata of the controversially depth water
153 column (Assine, 1992; 1994; 2007; Martill, 2007; Heimhofer *et al.*, 2010).

154 Through the occurrences of ostracods and palynomorphs, Coimbra *et al.* (2002) correlated
155 the Araripe Basin with other deposits that was suggested with same age. However, to Barbalha and
156 Santana formations, ostracodes could not assign to any biozone. The assignment was made by the
157 study of palynomorphs, that indicated an Albian age (~120 Ma) to Crato Member of the Santana
158 Formation (Coimbra *et al.*, 2002).

159

160 **MATERIALS AND METHODS**

161

162 Three specimens were studied and described following the terminology of Lucas &
163 Stettemhein (1972); Sick (1984) and Proctor & Lynch (1993). These fossils were apprehended by
164 the Brazilian Federal Police and the IPHAN (Institute of National Historical and Artistic Heritage)
165 and are deposited in the Paleontological Collection of the Laboratory of Systematic Paleontology
166 from the Geosciences Institute, of the University of São Paulo, in the city of São Paulo. The
167 specimens received the registered numbers: GP/2E-7853, GP/2E-7854 and GP/2E- 8771. The
168 acronyms used in the collection assign the “GP” to Geology and Paleontology sets, and '2E', to the
169 vertebrate set.

170 All specimens were photographed using a millimeter-scale stand with Canon EOS REBEL
171 T3 with aperture of 100 mm and under a stereomicroscope Carl Zeiss with a capture system
172 AxioCam ICC3 and using the AxioVision LE software. The specimens were measured with a
173 caliper and the AxioVision LE software. We measured specific portions of the feathers such as
174 barbs and rachis. The difference between each portion that was compared with the total size of the
175 length. These measurements were used to infer the morphology to classify them according to the
176 literature of extant feathers (Lucas & Stettemheim, 1972; Sick, 1984; Proctor & Lynch, 1994).

177

178 **RESULTS**

179

180 **Systematic Palaeontology**

181

182 Order Saurischia Seeley 1888

183 Suborder Therapoda Marsh 1881

184 Division Coelurosauria Von Huene 1914 *sensu* Gauthier 1986

185 Family *Incertae sedis*

186 (Figure 2, A - B)

187

188 **Material:** GP/2E-7853 (fig. 2, A).

189 **Horizon:** Crato Member, Santana Formation, Araripe Basin.

190 **Lithology:** Weathered (beige) micritic laminated limestone.

191 **Age:** Lower Cretaceous (Aptian/Albian).

192 **Description:** This specimen is a complete feather with reduced dimensions compared to other
193 morphotypes (*i.e.*, contour feathers and pennaceous feathers) and orange coloration. Barbules are
194 not clearly visible and are presented only in some regions of the barbs. The rachis consists of a
195 slight line. The distal extremity presents ramifications where barbs with a diverse length originates.
196 The calamus is not present.

197 **Measures:** See table 2, first row. Dimensions are in mm.

198 **Taphonomy:** The color of this specimen (orange/reddish), indicate that the fossil may be preserved
199 as an iron oxide. The matrix presents features such as a light beige coloration due slight weathering,
200 calcified filaments, crystals of sphalerite, etc. (Martill & Briggs, 2001; Heimhofer *et al.*, 2010).

201 **Diagnosis:** Despite having a fairly generic morphotype, this specimen has a typical morphology of
202 the plumulaceous feathers due to the presence of rachis very well delineated and barbs of varying
203 sizes, this feather is interpreted as a downy feather (Lucas & Stettenheim, 1972; Sick, 1984; Proctor
204 & Lynch, 1994). It is not possible to observe the presence of the calamus. Generally, because of
205 their fragility and their small size (in life it could represented only 1.5% of the total length of the
206 feather), this portion does not preserve widely in the fossil record (Lucas & Stettenheim, 1972;
207 Kellner, 2002). Also, in the matrix, a nearly complete skeleton of a small fish is associated (Fig. 2,
208 D), that here we interpreted belonging to the *Dastilbe* genus (Maisey, 1991; Dietze, 2007; Martill *et*
209 *al.*, 2007a).

210

211 Family *Incertae sedis*

212

213 **Material:** GP/2E-7854 (fig. 2, B).

214 **Horizon:** Crato Member, Santana Formation, Araripe Basin.

215 **Lithology:** Weathered (beige) micritic laminated limestone.

216 **Age:** Lower Cretaceous (Aptian/Albian).

217 **Description:** The proximal portion is degraded, although, the rachis are visible. Several barbs with

218 different length originate from them. Also, it is possible to notice the presence of vestigial barbules.
219 As the GP/2E-7853, the calamus is a slight line.

220 **Measures:** See table 2, second row. Dimensions in mm.

221 **Taphonomy:** Similar to GP/2E-7853, this feather possesses a small dimension and it is complete. It
222 is possible to notice that there is color variation between the proximal to distal portion of the vanes,
223 with light to darker brownish tones that represents the preservation by carbonaceous traces (Davis
224 & Briggs, 1995).

225 **Diagnosis:** This specimen also presents the typical morphotype of the plumulaceous feathers,
226 classified as downy feathers. On the umbilicus proximallis portion (Fig. 2, E), the slight line
227 structure is consisted of an external molt that is interpreted as the vestige of the calamus. By the
228 preservational characteristics (*e.g.*, external mould, lack of organic remains), the evidence suggests
229 that this portion was degraded during the taphocenosis, or geochemical processes that followed the
230 burial (diagenesis).

231

232 Order Saurischia Seeley 1888

233 Suborder Therapoda Marsh 1881

234 Division Coelurosauria Von Huene 1914 *sensu* Gauthier 1986

235 Subdivision Maniraptoriformes Holtz 1995

236 *Family Incertae sedis*

237 (Figure 2, C)

238

239 **Material:** GP/2E-8771 (fig. 2, C).

240 **Horizon:** Crato Member, Santana Formation, Araripe Basin.

241 **Lithology:** Grayish micritic laminated limestone.

242 **Age:** Lower Cretaceous (Aptian/Albian).

243 **Description:** This specimen it is a complete feather with a bigger dimension, compared with the
244 two previously described (tables 4 and 5). A diverse barbs with variable lengths originates from a
245 slight rachis. The barbules are clearly visible, and they also vary in size. In extant feathers, vanes
246 are united by the 'hooklets' (structures similar to hooks) (Lucas & Stettenheim, 1972; Sick, 1984),
247 however they are not preserved in this fossil.

248 **Measures:** See table 2, third row. Dimensions are in mm.

249 **Taphonomy:** As well as GP/2E-7853 and GP/2E-7854, this specimen is also occurs in a limestone
250 matrix. Due to the blackish color of the fossil, this feather may be preserved as carbonized trace,
251 since it is the common type of preservation of feathers in rocks (Davis & Briggs 1995).

252 **Diagnosis:** According to morphology, GP/2E-8771 is associated to the typical extant contour
253 feathers or semiplumes. Attached to the basal part (the *umbilicus*), an structure similar to
254 afterfeather emerged forming an V shape. This element is larger than the vanes (Lucas &
255 Stettenheim, 1972). Nevertheless, it is unlikely that this element represent an afterfeather once it
256 does not show any diagnose feature, such as a “slight rachis” or umbilical origin. The barbules are
257 present and they suggest some degree of cohesion between barbs, however, there are no ‘hooklets’
258 preserved on this specimen. The characteristic that distinguish this specimen to the other two
259 described previously, is the color hue of the matrix. This feature is an indicative that this sediment
260 may not be exposed to weathering processes that usually changes the rock color (Martill & Frey,
261 1995). In an attempt to make more attractive to the illegal sale, some portions of the feather were
262 degraded with a scraper tool, especially on the portion where the calamus was supposed to be
263 found. The GP/2E-8771 sample is the only Mesozoic feather described here, that is truly secure to
264 be assigned to the crown group Aves, since all of its characteristics are very similar to modern
265 morphotypes.

267 Systematic analysis

268
269 Two specimens (GP/2E-7853 and GP/2E-7854) possess a simplest and generic morphotype.
270 They resembled the 'IIIb' evolutionary-developmental stage (Prum & Brush, 2002) and the '4th'
271 specimen of the morphological models reported in the fossil record (Xu & Guo, 2009). We have
272 tried to classify the other feather, by the same process. Based on the morphology, we compared
273 specific portions (table 3) that enabled us to classify to the plumulaceous morphotype (table 4).

274 Both feathers GP/2E-7853 and GP/2E-7854 have a plumulaceous appearance that is similar
275 to downy feathers that main character is its dimension, where the rachis is shorter than the longest
276 barb. The difference between the rachis and the longest barbs of GP/2E-7854 is 48,21%, although,
277 the rachis of GP/2E-7853 is 8,27% longest than the larger barb. Despite the fact that GP/2E-7853
278 have a longest rachis than the larger barbs, by the fluffy aspect, dimension, and morphology, we
279 prefer to assign this feather (together with GP/2E-7854) as a downy feather. The occurrence of this
280 morphotype is wide in the extant class Aves, once they are present beyond the semiplumes and are
281 located in the apterium portions of most birds. According to the fossil record, these structures could
282 also belong to non-avian dinosaurs, making the taxonomic assignment even hard to be inferred
283 (Lucas & Stettenheim, 1972; Prum & Brush, 2002; Zhang *et al.*, 2006; Xu & Guo, 2009).

284 The specimen GP/2E-8771, possess a morphotype similar to semiplumes, with a apparent
285 aftershaft on the proximallis portion. However, this structure may not represent this element. The

286 rachis is 43,95% shorter than the longest barb. The morphology of this feather is similar to the type
287 of afterfeathers, that possess a long, narrow with shorter vanes. The hyporachis is almost with the
288 same length of the afterfeather. In extant cases, these feathers are related mainly to birds of the
289 order of Galliformes and Trogoniformes, but also to Tinamiformes birds (Lucas & Stettenheim,
290 1972).

291

292 **DISCUSSION**

293

294 Isolated feathers have been described formally in many works (Kellner, 2002), however,
295 differently from fish scales, mollusks shells or plant trunks and leaves, none of them received a
296 proper taxonomic treatment until the present date. The mainly reason for the lack systematic
297 procedure, may be caused by its rareness in the fossil record, that hampers the exact taxonomic
298 determination. Despite the taphonomic significance, this inappropriate treatment, can also be an
299 issue that systematists simply ignores once these elements demonstrate low taxonomic interest (*i.e.*,
300 low potential to assign a new taxon). Nevertheless, Rautian (1978) applied a different taxonomic
301 approach to these elements, once their existence represented a diagnose of new bird taxon.
302 Nowadays, this method prove to be problematic, since non-avian dinosaurs also possessed them,
303 demanding a different way to assess their taxonomic value. Here, we propose a simple and
304 parsimonious approach to describe fossilized feathers, assigning their morphotypes to the basal
305 animals that possessed them according to the fossil record of non-avian and avian dinosaurs.

306 Because the specimens studied here were product of apprehension (illegal fossil trade), the
307 exactly stratigraphic position cannot be determined. However, the laminated limestones (LL) of the
308 Crato Member, possess many characteristics that is well known by worldwide geologists and
309 paleontologists. Since the LL only occur in this unit, it is plausible to assign these fossils to this
310 specific strata.

311 Two specimens (GP/2E-7853 and GP/2E7854) deserved more attention, since they are from
312 the Mesozoic Era (period marked by “evolutionary experiments”), and possess a generic
313 morphotype that resembles early, and then, basal feathers. Despite the controversy about the
314 morphotype diversity provided by the squeeze during diagenesis (Foth, 2012), an apparent decrease
315 is suggested by the fossil record (Zhang *et al.*, 2006; Xu & Guo, 2009; Xu *et al.*, 2010).
316 Nevertheless, it was possible to associate both specimens aforementioned, to the evolutionary stages
317 as it is proposed by the literature (Prum and Brush, 2002; Zhang *et al.*, 2006, Xu & Guo, 2009).
318 Features such as presence of barbs that originates from a scanty rachis, absence of barbules, small
319 dimension between morphotypes, bigger length of the barb than the rachis, and fluffy aspect, are

320 present in both feathers. By these characteristics, they represent a basal morphotype and we
321 classified them belonging to the 'IIIb' stage of the evolutionary model (Prum and Brush, 2002) and
322 to '4th morphotype' commonly found on the fossil record (Xu and Guo, 2009).

323 The preservation of the macro-structures, identification of morphotype, and size, allow us to
324 suggest the possible roles during life, their placement throughout their body, and proportion of the
325 owners (Lucas & Stettenheim, 1972; Sick, 1984; Proctor & Lynch, 1993). Considering that these
326 two feathers (GP/2E-7853 and GP/2E-7854) were identified as auricular feathers (length between
327 2.5 to 17 mm), the animal that possessed these elements may not have a big dimension, *i.e.*, not
328 exceeding the domestic chicken size. Thus, it must had a role similar to the extant birds, where the
329 mainly function is in ear protection (Lucas & Stettenheim, 1972). The other feather (GP/2E-8771),
330 a contour feather, we suggest that it may have also taken the same protective function. However, it
331 might functioned in the thermoregulation of its owners. Nevertheless, even in basal coelurosaurs,
332 they may had other roles such as in display, shielding nests, etc. (Turner *et al.*, 2007). Other lines of
333 evidences suggests that dinosaurs already possessed visual acuity, with nocturnal or crepuscular
334 behavior, and abilities to communicate visually may have been present in the Mesozoic (Varrichio,
335 *et al.*, 2007; Xu *et al.*, 2009; Schmitz & Motani, 2011; Koschowitz *et al.*, 2014).

336 The morphotype of GP/2E-8771, and its position throughout the body, indicate that this
337 feather may favored the camouflage and communication between the owners, as seen in modern
338 birds (Gluckman & Cardoso, 2010). In addition, it could have also assumed -- hypothetically -- a
339 sexual role, similar to extant birds with iridescent and colorful feathers, such as peacocks (Zi *et al.*,
340 2003) and birds-of-paradise (Irestedt *et al.*, 2009).

341 The process of preservation explains the absence of hooklets in all specimens, since these
342 structures are very delicate, their presence is not expected. Because of this feature, they are not
343 common in feathers preserved in rock matrix, only present in feathers included in amber (Davis &
344 Briggs, 1995; Laybourne, 1994; Perrichot *et al.*, 2008; Mckellar *et al.*, 2011; Thomas *et al.*, 2014).

345

346 **Sedimentary Deposition, Paleoenvironment, and Taphonomy**

347

348 Over the Aptian-Albian, the Santana Formation had two different depositional systems that
349 followed the evolution of the basin throughout the late Mesozoic. The Crato Member is represented
350 by a restricted lacustrine environment with brackish waters; and the Romualdo Member is
351 suggested to be formed by a lagoonal, with seasonally contact with marine waters, or even to a
352 moments of marine regression-transgressions (Assine, 1994; 2007; Martill *et al.*, 2007a). The Crato
353 and Romualdo formations, are separated by an unconformity marked at the top of the Crato

354 Member. A fossiliferous strata of shales and evaporites that characterizes the 'Ipubi Layers'. This
355 layer occur with varied thickness and lateral continuum, suggesting the possible shallowing of the
356 water column (Assine, 2007; Martill *et al.*, 2007b). The shales of this unit is responsible for the
357 single occurrence of an ichonofossil in the entire Santana Formation, where it was assigned to a
358 turtle (Dentzien-Dias *et al.*, 2010). Fielding *et al.* (2005) mentioned a turtle remains from this layer.
359 Despite her inaccurate taxonomic assignment (as *Araripemys*), Oliveira *et al.* (2011) described this
360 fossil correctly, noting the affinity with a undetermined pleurodiran.

361 According to paleontological and sedimentary evidences, such as palynomorphs and
362 evaporites, the Crato Member was formed in a clear and relatively shallow waters during an arid
363 and dry climate, where the calcium carbonate sediments were deposited in a low energetic input
364 with formation of halite and anhydrite minerals (Assine, 1994; Silva *et al.*, 2003; Assine, 2007;
365 Martill *et al.*, 2007). As suggested elsewhere (Martill *et al.*, 2007a), this anoxic and hypersaline
366 environment prevented the presence of the bottom-dwelling organisms, once the salinity level might
367 have be higher to the osmotic toleration (Martill, 1993; Martill *et al.*, 2007ab; Martill *et al.*, 2008b).

368 Despite the controversy, the source of the sediment may be due the events of algal blooms,
369 where the carbonate, was organically precipitated by pico- and phytoplankton (Martill *et al.*,
370 2007a). However, but albeit meager, evidences of microbial mats may also indicate the origin of
371 this sediment, *i.e.*, precipitated by these microorganisms (Martill *et al.*, 2007a; Martill *et al.*,
372 2008b). The presence of articulated, undisturbed fossils, and pseudomorphs of pyrite and marcasite,
373 indicate that the reducing condition prevailed in the bottom of the paleolake, enabling the exquisite
374 preservation, allowing the presence of non-resistant tissues in the fossil record (Fielding *et al.*,
375 2005; Martill *et al.*, 2007a; Pinheiro *et al.*, 2012; Simões *et al.*, 2014; Barling *et al.*, 2015). The high
376 degree of articulation and the exquisite preservation, suggests that a low energy environment
377 prevailed, without any or significant carcass transportation, as well as disturbance by scavenging
378 organisms (Fielding *et al.*, 2005; Martill *et al.*, 2007a; Bráez *et al.*, 2009; Figueiredo & Kellner,
379 2009; Pinheiro *et al.*, 2012; Barling *et al.*, 2015).

380 Despite this “harsh” environment, this sedimentary unit is remarkably noted by the abundant
381 biota that is preserved with a high degree of fidelity. The vertebrate fauna is composed primarily by
382 crocodiles, turtles, frogs, birds, pterosaurs, and numerous fishes (Maisey, 1991; Martill, 1993; 1997;
383 Fielding *et al.*, 2005; Martill *et al.*, 2007a; Martill *et al.*, 2008a; Figueiredo & Kellner, 2009;
384 Pinheiro *et al.*, 2012; Simões *et al.*, 2014; Oliveira & Kellner, 2015). The invertebrate animals was
385 also abundant, with the mainly occurrences of arthropods and mollusks (Maisey, 1991; Martill,
386 1993; Grimaldi & Engel, 2005; Martill *et al.*, 2007a; Barling *et al.*, 2015). Despite this faunal
387 richness, the flora was also exuberant (Martill *et al.*, 2007; 2012; Mohr *et al.*, 2015), with a

388 diversity characterized by the presence of macro and microfossils of pteridophytes, gymnosperms,
389 angiosperms, palynomorphs, pollens, seeds, etc. (cf. Maisey, 1991; Martill, 1993; Martill *et al.*,
390 2007a; 2012).

391 The fauna of the Crato Member may have been autochthonous (Naish *et al.*, 2004), however,
392 the terrestrial vertebrates of the Santana Formation may had a different geographical origin through
393 time, indicated by evidences in other adjacent basins (Carvalho & Gonçalves, 1994; Carvalho,
394 1995; Carvalho & Araújo, 1995; Carvalho *et al.*, 1995; Carvalho & Pedrão, 1998). Nevertheless, in
395 both *lagerstätten* units (Crato and Romualdo members), animals may have be well adapted to the
396 arid and dry climate (Naish *et al.*, 2004; Martill *et al.*, 2007a; Heimhofer *et al.*, 2010). Many of the
397 animals may lived in the surroundings of the paleolake, that could bear a high diversity of plants,
398 especially angiosperms. By these singular taphonomic features, we suggest that, the presence of
399 larger vertebrates in this unit, is derived by the occasional incursions into shallow waters, in order to
400 prey fishes, insects, and other land animals, preserving these animals *in situ*.

401 On the other hand, it can be also speculated that the Romualdo fauna may have been
402 allochthonous. The presence of a very diversified animals, indicate that they lived in the nearby
403 shorelines, since they was also well established to this environment (Naish *et al.*, 2004). Especially
404 to the vertebrate remains, their presence can be explained by the drifting hypothesis. As proposed
405 by Naish *et al.* (2004), the carcasses of the animals who lived in the nearby regions, may have been
406 transported by rivers through tens of kilometers (or less), before it reached the paleolake. Although,
407 as Assine (1994) noted, during the Romualdo Member deposition, the environment was
408 characterized by the maximum marine transgression, where the salty waters entered this basin with
409 N-NW direction. Therefore, the carcass of these animals may have been dragged by these moments
410 of water incursions, not having any relationship with perennial rivers.

411 Nevertheless, their presence can be also explained by the attraction of the dead fish, that
412 could be exposed on the shores of the paleolake during the mass mortality events, caused by
413 chemoclinal alterations or by the remobilization of the anoxic layers to upper strata. Once in the
414 shoreline, these large vertebrates may have stuck on the soft and deep sediments, where they died
415 by natural means (Olson & Alvarenga, 2002, Varricchio *et al.*, 2008). After death and despite the
416 scavenger activity that might followed, the carcass of these vertebrates could be finally transported
417 into the paleolake. Once there, they were preserved by the process of 'encapsulation', also known as
418 “*The Medusa effect*” (Martill, 1989), that is a characteristic mode of preservation of the Romualdo
419 Member nodules. This hypothesis could also explain the preservation of the isolated and often
420 disarticulated bones of pterosaurs, dinosaurs and other aerial and terrestrial vertebrates.
421 Nonetheless, the absence of ichnofossils in the rocks of this unit, makes this hypothesis difficult to

422 be established. However, further works might concentrate in these evidences.

423 Besides the previous 'trapping hypothesis', Duncan & Jensen (1976) presented evidence of
424 mass mortality of modern aquatic birds by toxins, consisted mainly by *Clostridium botulinum*. As
425 pointed by these authors, *C. botulinum* can colonize similar environments, and evidences of these
426 microorganisms in other fossil sites suggests their responsibility to the mass mortality events
427 (Varrichio, 1995; Lingham-Soliar, 2012). In the Santana Formation, the activity of these organisms
428 could also be responsible for the presence of the vertebrates in the fossil record (Duncan & Jensen,
429 1976; Varrichio, 1995). However, only the mass mortality of fishes is commonly observed, and
430 further evidences of this phenomenon is needed, such as, a high bone concentration of different
431 vertebrates in the same strata (Varrichio, 1995; Martill, 1997; Martill *et al.*, 2008a).

432 From the three specimens studied, only GP/2E-7853 shows a coloration (reddish/orange)
433 that is typical of the iron oxides-hydroxides, possibly limonite. This type of preservation was also
434 observed in others feathers from the same provenance (Maisey, 1991; Martins-Neto & Kellner,
435 1988; Martill & Frey, 1995; Martill & Davis, 2001). The remaining specimens, may be preserved as
436 incarbonization, once it is one of the most common type of preservation of organic molecules, as it
437 presents the characteristic dark black hue (Tegelaar *et al.*, 1989; Davis & Briggs, 1990; 1995;
438 Kellner, 2002; Briggs, 2003). Although, the explanation of their chemical composition, needs
439 further geochemical investigation.

440 The main hypothesis that explains the presence of the isolated feathers in the fossil record,
441 especially in the Santana Formation, assumes that these elements may have been blown into the
442 paleolake by events of strong winds. Once they have reached the waters of the lake, these feathers
443 may have sunk quickly, reaching the bottom in seconds to few minutes, where they were rapidly
444 buried (Martill & Davis, 2001). Despite the fact that this hypothesis satisfy this question, others
445 mechanisms (and educated guesses) may also be praised.

446 During their life, birds tend to lose feathers by ontogeny, breeding season, and under high
447 stress situations. This latter mechanism is called 'fright molt'. Generally, they tend to release
448 rectrices and semiplumes (Sick, 1984). It is possible that the animals that possessed these structures,
449 released them during similar conditions. The presence of the isolated feathers could occur by animal
450 hunting, *i.e.*, by fish, crocodiles, dinosaurs, or, pterosaurs. Some extant fishes occasionally include
451 birds on their diet by opportunism (Davenport, 1979; French, 1981; O'Brien, 2014; Perry *et al.*,
452 2013). A good prey-predator example in the Santana Formation, is indicated by the evidence of a
453 conical tooth assigned to a spinosaurid dinosaur, reported inserted in a cervical vertebrae of the
454 ornithocheirid pterosaur (Buffetaut *et al.*, 2004). But, despite the possibility that birds were also
455 prey, the fossil record of the established trophic chain, do not show yet, these animals as a food

456 source of the other organisms, in a way that coprolites did not provide yet, evidence of this diet
457 (Maisey, 1991; Martill, 1993; Lima *et al.*, 2007).

458 Other hypothesis may also explain satisfactorily the occurrence of isolated feathers and the
459 absence of bones associated with them. Nevertheless, the “wind hypothesis” remain the most valid
460 and satisfactory.

461 The carbonate concretions of the Romualdo Member, provided a record of at least four non-
462 avian dinosaurs, although, only theropods were found in this unit. The review of the previously
463 considered an ornithischian ischium, is now interpreted as a rib of a unknown theropod dinosaur
464 (Machado & Kellner, 2007). Thus, the dinosaur fauna of the Araripe Basin consists of two
465 spinosaurids, *Irritator challengeri* (Martill *et al.*, 1996) and its possible synonym, *Angaturama*
466 *limai* (Kellner & Campos, 1996); and two coelurosaurs, *Santanaraptor placidus* (Kellner, 1999) and
467 *Mirischia asymmetrica* (Naish *et al.*, 2004). The latter dinosaur, possess at least at the family level,
468 two feathered species (Ji & Ji, 1996; Ji *et al.*, 2007). It is speculated, that filament feathers were
469 present even in megalosauroid dinosaurs (Rauhut *et al.*, 2012). But according to previous reports,
470 evidences of feathers were not detected in any taxa of non-avian dinosaurs of the Araripe Basin
471 (Kellner, 1999; Naish *et al.*, 2004). This absence is odd, by the vast record of soft tissues in both
472 members (Crato and Romualdo members). They include insect muscle fibers (Grimaldi & Engel,
473 2005; Barling *et al.*, 2015), dinosaurs blood vessels (Kellner, 1996a), pterosaur wing membranes,
474 muscle fibers, and headcrest (Martill & Unwin, 1989; Kellner, 1996b; Pinheiro *et al.*, 2012), fish
475 muscle tissue and stomach contents (Martill, 1989; 1990; Wilby & Martill, 1992), skin impressions
476 of turtle (Fielding *et al.*, 2005), fossilized microbodies related to pigmentation (Vinther *et al.*,
477 2008), among others (cf. Martill, 1993; Martill *et al.*, 2007a).

478 The first record of Mesozoic avian dinosaur in Brazil, was only described recently with a
479 fossil unearthed from the Crato Member of the Santana Formation (Carvalho *et al.*, 2015). The
480 feathers of this fossil, an enantiornithine undetermined, possess interesting features, showing an
481 extremely long rectrices, secondary remiges, alular feathers, and filamentous feathers. Regarding to
482 the remex and rectrices, there is no doubt that they were pennaceous feathers. Nevertheless, the
483 filamentous aspect may be a taphonomic artifact (Foth, 2013), indicating that these structures most
484 likely were, contour feathers or downy feathers. It is possible to note that in rectrices, patches with
485 granulate spots may be associated with color patterns. However, no other evidence of its hue is
486 given by the authors. Two other possible specimens of enantiornithine, from the same provenance,
487 are briefly mentioned elsewhere (Fielding *et al.*, 2005; Naish, 2007). These specimens are not
488 accessible, and so, they are not formally described, since these specimens seemingly were lost to
489 private collectors that they acquired through the illegal fossil trade.

490 The presence of this undetermined enantiornithine, suggests doubtless, that birds were
491 present in the Araripe Basin landscape. Even though, non-avian dinosaurs with feathers, still
492 remains unknown to this deposit. Since the absence of feathers associated with bones of non-avian
493 dinosaurs makes an unusual event in both *Lagerstätten* (Crato and Romualdo members), some
494 possibilities emerges: (i) the non-avian dinosaurs found in this deposit were glabrous (*i.e.*, they did
495 not possessed feathers) or were low in coverings; (ii) a selective taphonomic or geological process
496 acted obliterating their preservation; (iii) during the time of deposition, taphonomic conditions were
497 very different between both members or even to the same unit, disallowing their preservation; (iv)
498 all possibilities may have happened simultaneously, or consecutively for the case of taphonomical
499 and diagenetical processes; (v) feathered non-avian dinosaurs (and most birds) were lost by
500 geological processes (diagenesis, erosion, and weathering); or, (vi) these animals were not
501 discovered yet. With the exception of the two latter, we consider these possibilities to be very
502 problematic because the process of fossilization preserved tissues that is more prone to degradation,
503 but did not allowed feathers that is relatively more resistant. This can wrongly suggests, that a
504 differential preservation may have occurred. But, the considerable numbers of non-resistant tissues
505 reported in both members, makes this hypothesis very unlikely. It is important to state, that
506 analogous deposits with similar lithology (limestone rocks) and depositional settings, *e.g.*, the Las
507 Hoyas Formation in Spain (Sanz *et al.*, 1988; 1996) and the Solnhofen Formation in Germany
508 (Barthel *et al.*, 1994); hold records of dinosaurs preserved similarly to the Araripe Basin. Especially
509 in Solnhofen, feathers are present in the *Archaeopteryx* specimens, but they are not in the
510 *Compsognathus longipes* (Barthel *et al.*, 1994). This suggests that the third hypothesis may be true,
511 once the selective taphonomic/geological events can determinate the differential preservation of
512 carcasses in the same depositional conditions. Especially to Santana fossils, the formation of
513 concretions of the Romualdo Member, may be the responsible for obliterating these integumentary
514 tissues, differently from the Crato Member that preserved the enantiornithine with feathers.

515 By their localization throughout the body, it is possible that these elements were more
516 exposed to geochemical reactions during the initial phase of decay that followed the burial, being
517 degraded early in diagenesis or by the weathering that succeeded their exposure. However, to
518 nodules, the geochemical alteration by weathering may not be the responsible for the absence of
519 these elements, since the dinosaur tissues remained relatively isolated from the surrounding
520 environment throughout the geological time. Is expected that further studies may enlighten this odd
521 feature.

522 Until the present day, only a few records of feathers, or filaments considered as
523 'protofeathers', were found associated with ornithischians dinosaurs (Mayr *et al.*, 2002; Xu *et al.*,

524 2009; Zheng *et al.*, 2009; Sevaliev & Alifanov, 2014; Godefroit *et al.*, 2014). Evidences of sauropod
525 integuments, indicate that they were consisted mainly by scales and osteoderms (Czerkas, 1992).
526 Although, the poor record of feathers in individuals of ornithischia, and the absence in sauropoda,
527 may be also a taphonomic artifact. Despite the occasional events of great sediment deposition, the
528 preservation of the carcass of these animals (often huge), required more time to be completely
529 buried, and so, preserved. This slow process opposes to the rapid burial of feathers as suggested
530 elsewhere (Martill & Davis, 2001), explaining their absence alongside sauropods and great
531 ornithischians bones.

532 Another taphonomic feature, is the type and grain size of the sediment that buried these
533 animals. Siliciclastic coarse grains, tend to preserve only larger hard parts of the animals (*i.e.*,
534 bones, keratinous beaks, teeth, and claws). Generally, these sediments are related to high energetic
535 depositional systems, with unidirectional flows, such as rivers and streams (Holz & Simões, 2002).
536 Even though, fine-grained sandstones, such as found in the Ediacara Hills in Australia (Gehling,
537 1999) and in Horseshoe Canyon Formation in Canada (Quinney *et al.*, 2013), preserved soft tissues
538 such as the Ediacara organisms and feathers, respectively. Nevertheless, the lack of recognition
539 during the bone extraction, or a careless excavation also represents a destructive potential of these
540 elements (Zelenitsky *et al.*, 2012).

541 Despite their scarcity, evidences of enanthionithines and maniraptorans were found in
542 Cretaceous deposits of Brazil, emphasizing their presence in the Brazilian landscapes (Chiappe &
543 Calvo, 1994; Carvalho & Pedrão, 1998; Alvarenga & Nava, 2005; Novas *et al.*, 2005; Naish, 2007;
544 Machado *et al.*, 2008; Candeiro *et al.*, 2012a; Candeiro *et al.*, 2012b; Marsola *et al.*, 2014; Tavares
545 *et al.*, 2014; Carvalho *et al.*, 2015; Delcourt & Grillo, 2015). Even though, the poor record of
546 Mesozoic birds, added to the absence of feathered dinosaurs, makes the taxonomic assignment even
547 harder to infer (Naish, 2007; Sayão *et al.*, 2011). It is unlikely that these feathers belonged to non-
548 theropod dinosaurs, such as sauropods or ornithischians, once they are also absent in the Araripe
549 Basin (Naish, 2004). On the other hand, a large numbers of evidences indicate that only non-avian
550 theropods possessed these structures (Unwin, 1998; Chiappe & Witmer, 2002; Prum & Brush, 2002;
551 Norell & Xu, 2005; Xu, 2006; Zhang *et al.*, 2006; Xu & Guo, 2009; Norell, 2011; Mckellar, 2011).

552 Because modern-type of feathers was already present in the Middle Jurassic basal and
553 derived animals (Foth *et al.*, 2012; 2014b), it hinders the taxa assignment of these isolated feathers
554 at the genus level. The occurrence of these elements attached to bones of known feathered
555 dinosaurs, is very important to determine the possible taxon and morphotype. But despite this
556 difficulty, the taxonomic attribution can be made at least at the division and subdivision levels. As
557 filament-feathers were found in basal theropods; *e.g.*, *Sinocalliopteryx prima* (Ji & Ji, 1996);

558 *Sinocalliopteryx gigas* (Ji *et al.*, 2007); *Sciurumimus albersdoerferi* (Rauhut *et al.*, 2012), and
559 *Yutyrannus huali* (Xu *et al.*, 2012); we consider that the Araripe Basin non-avian dinosaurs were
560 also covered with these elements. However, their were restricted in distribution throughout the body
561 as suggested by evidences in the other specimens. We consider more parsimonious to assign both
562 feathers, GP/2E-7853 and GP/2E-7854, to the Coelurosauria clade. Because true pennaceous
563 feathers were found in *Ornithomimus edmontonicus* (Zelenitsky *et al.*, 2012), we assign
564 GP/2E-8771 to the Maniraptoriformes clade. As pointed by the large numbers of evidences, both
565 groups (Fig. 3) are responsible for these integuments in dinosaurs (Clarke, 2013).

566

567 **Future perspectives**

568

569 In a striped contour feather from the Araripe Basin described by Martill & Frey (1995),
570 Vinther *et al.* (2008) have found oblate microbodies restricted only to the dark portions of the
571 specimen. The light portions, were markedly preserved as imprintation. Those structures were
572 previously interpreted as autolithified bacteria (Wuttke, 1983; Davis & Briggs, 1995), but
573 subsequent studies revealed them as evidence of fossilized melanosomes (Vinther *et al.* 2008;
574 Zhang *et al.*, 2010; Barden *et al.*, 2011; Glass *et al.*, 2012; 2013; McNamara *et al.*, 2013; Vitek *et*
575 *al.*, 2013; Barden *et al.*, 2014; Li *et al.*, 2014; Egerton *et al.*, 2015; Vinther, 2015). This
576 interpretation, enabled reconstructions of ancient color patterns of extinct animals, such as
577 dinosaurs, birds, reptiles and fishes. (Vinther *et al.*, 2008; 2010; Clarke *et al.*, 2010; Carney *et al.*,
578 2012; Field *et al.*, 2013; Li *et al.*, 2010, 2012, Lindgren *et al.*, 2012, 2014). Grueling evidence of
579 melanin in fossilized feathers still remains unknown, however, works on this subject has been focus
580 of investigations (Colleary & Vinther, 2013).

581 Further investigations using the Scanning Electron Microscopy equipped with Energy
582 Dispersive X-Ray Spectroscopy (SEM-EDS), will help on the identification of the presence of the
583 ultrastructures such as minerals, melanosomes, and other possible elements in this feathers. In
584 addition, other techniques, such as Raman Spectroscopy (RAMAN), X-Ray Fluorescence (XRF),
585 Gas Chromatography-Mass Spectrometry (GC-MS), among others, also can give information about
586 their chemistry (Wogelius *et al.*, 2011; Egerton *et al.*, 2015), indicating possible taphonomic
587 processes that occurred after the deposition (Davis & Briggs, 1995; Schweitzer *et al.*, 2008;
588 McNamara, 2013). Besides the study with ancient pigmentation, the application of these techniques
589 are important, once it provides more information about these fossils. Theses approaches not only
590 allow a better understand of the taphonomic and diagenetic processes, but it also enables
591 paleoenvironmental and paleoecological reconstructions.

592

593 CONCLUSION

594

595 Despite the difficulty on the systematic approach, it is possible to identify the isolated
596 feathers, basing on the lower taxonomic rank, relying on the fossil record of the unit. For the
597 Santana Formation of the Araripe Basin, the maximum taxonomic status reached, is the Division
598 (Coelurosauria) and Subdivision level (Maniraptoriformes). Based on the extinct and modern
599 morphotypes, and, on evolutionary model of feathers, the fossils were identified as, two downy
600 feathers (GP/2E-7853 and GP/2E-7854) and one semiplume (GP/2E-8771).

601 These feathers may be preserved as limonite (GP/2E-7853) and carbonized traces
602 (GP/2E-7854 and GP/2E-8771); and the mechanisms which allowed the preservation of these
603 elements was briefly discussed. As suggested by Martill & Davis (2001), we also consider that these
604 feathers have been transported into the paleolake by strong winds. Once in the waters, they sunk
605 and were buried rapidly in the anoxic bottom. The absence of oxygen, has an important role, once it
606 prevented the activity of scavenging organisms, allowing its preservation. Nevertheless, we also
607 considered other possible causes, *e.g.*, by predation (by fright molt).

608 While there are records of non-avian dinosaurs in the Araripe Basin, there is not yet formally
609 descriptions of avian dinosaurs. Nor, presence of feathers associated directly with bones. Even
610 though, soft tissues were found in many animals, including dinosaurs. Although unlikely, its
611 possible that a differential taphonomic process happened, preserving these non-resistant tissues
612 instead of feathers. Further geochemical investigations may reveal this process and how this
613 specimens were preserved. Future investigations may also focus on the identification of the
614 ultrastructures in addition to its chemical composition, offering the possible roles in life. Despite
615 their rareness and low taxonomic potential, fossilized feathers can offer insights about the
616 paleobiology of its owners and the paleoecology of the Araripe Basin.

617

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631

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636

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Table 1 (on next page)

Brazilian feather occurrences

Table 1. The Brazilian fossil record of feathers (formally described specimens).

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FEATHER	DEPOSIT	AGE	PRESERVATION	OBSERVATIONS	REFERENCE
One primary remex	Tremembé Fm	Paleogene (Oligocene)	Carbonized	First record in Brazil	Shufeldt (1916)
One contour feather	Tremembé Fm	Paleogene (Oligocene)	Carbonized	Feather assigned to a Turdidae (<i>Turdus rufiventris</i>)	Santos (1950)
Two pennaceous feathers	Pirabas Fm	Neogene (Miocene)	Carbonized	Possible semiplumes	Ackerman (1964)
One primary remex	Santana Fm	Cretaceous (Aptian/Albian)	Limonite/Imprint	Asymmetrical feather assigned to birds	Martins-Neto & Kellner (1988)
Contour feathers	Tremembé Fm	Paleogene (Oligocene)	Carbonized/Imprint	Several feathers associated with skeleton of the bird <i>Taubacrex granivora</i>	Alvarenga (1988)
Semiplume	Santana Fm	Cretaceous (Aptian/Albian)	Carbonized	Feather assigned to passerine birds	Martill & Filgueira (1994)
Down feather	Santana Fm	Cretaceous (Aptian/Albian)	Carbonized	Feather attributed to thermoregulation function of a bird	Kellner <i>et al.</i> (1994)
Contour feather	Santana Fm	Cretaceous (Aptian/Albian)	Carbonized (with melanosome preservation)	Feather with (banded) color pattern preserved.	Martill & Frey (1995)
One symmetrical feather	Santana Fm	Cretaceous (Aptian/Albian)	Carbonized	The biggest isolated feather associated with ectoparasite eggs. Assigned to a bird.	Martill & Davis, (1998; 2001)
Plumulaceous feathers	Santana Fm	Cretaceous (Aptian/Albian)	No data. Presumably carbonized	One plume and one semiplume	Sayão & Uejima (2009)
Down feather	Santana Fm	Cretaceous (Aptian/Albian)	Carbonized	Feather assigned to a bird	Sayão <i>et al.</i> (2011)
Several rectrices, remiges and filamentous feathers (possibly contour feathers)	Santana Fm	Cretaceous (Aptian/Albian)	Carbonized	Several feathers associated with a skeleton of an enantiornithe bird. First record of Mesozoic bird in Brazil.	Carvalho <i>et al.</i> (2015)

Figure 1 (on next page)

Araripe Basin locality and lithology

Figure 1. The Araripe Basin locality, the stratigraphic columns, units and chronology.

(Adapted and modified from Coimbra et al., 2002; Vianna & Neumann, 2002; Assine, 2007)

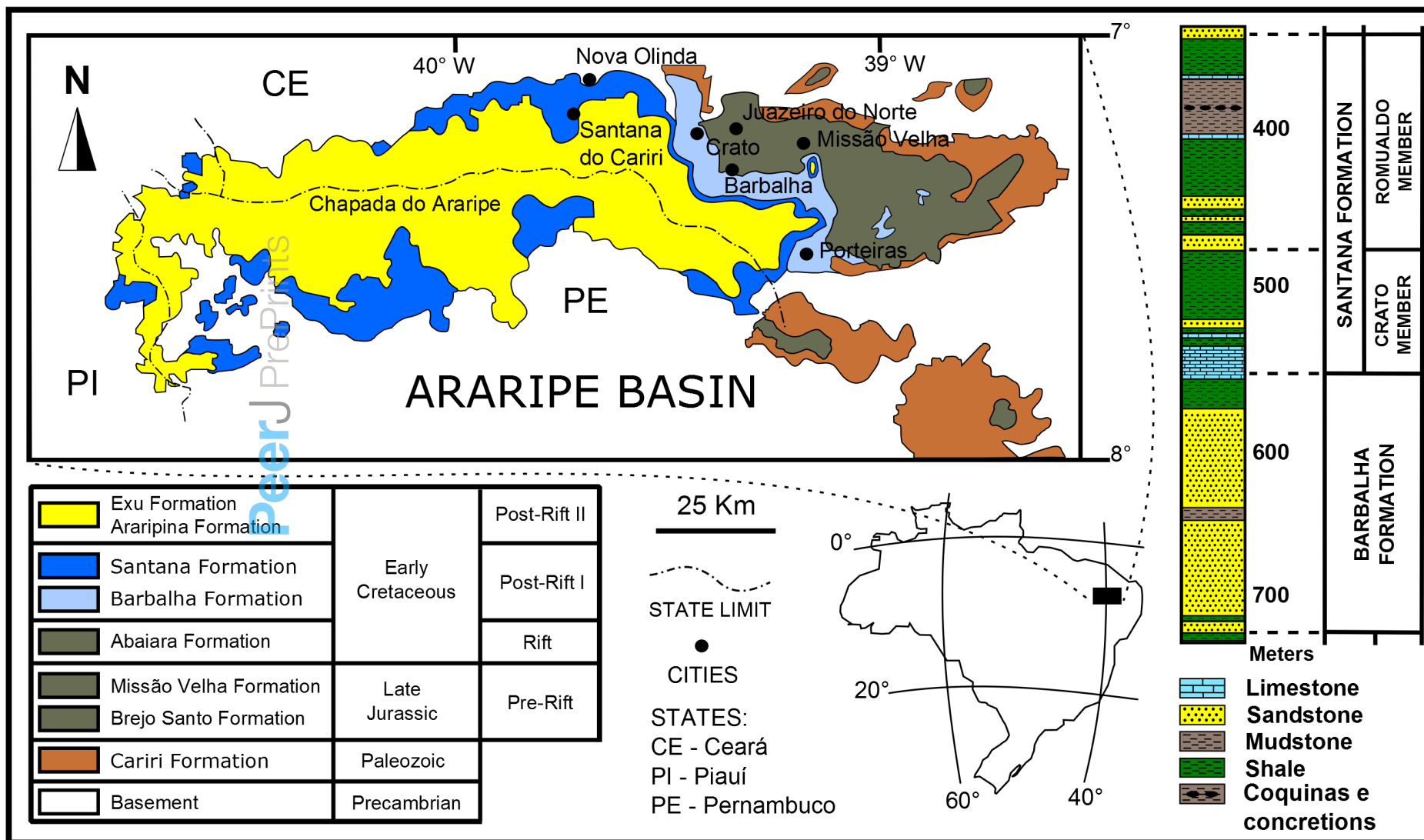


Figure 1. The Araripe Basin locality, the stratigraphic columns, units and chronology. (Adapted and modified from Coimbra *et al.*, 2002; Vianna & Neumann, 2002; Assine, 2007)

Table 2 (on next page)

Measures of the new specimens

Table 2. Values of the measures of the three specimens. Legend: NP - Not present.

Dimensions are in mm

Table 2. Values of the measures of the three specimens. Legend: NP - Not present. Dimensions are in mm

Specimen	Width	Length	Larger barb	Minor barb	Calamus	Rachis	Rachis thickness
GP/2E-7853	12,36	16,14	8,65	4,85	NP	9,43	0,49
GP/2E-7854	12,76	19,00	17,83	4,30	0,24	12,03	0,49
GP/2E-8771	15,63	33,50	16,45	4,12	NP	29,35	0,03

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Figure 2 (on next page)

Samples (Feathers and fish)

Figure 2. Fossilized feathers and fish of the Santana Formation. (A) GP/2E-7853; (B) GP/2E-7854; (C) GP/2E-8771. (D) The Dastilbe fossil fish of the GP/2E-7853 specimen; (E-F) External molt of the calamus of GP/2E-7854; (E) Photograph of the the umbilicus proximallis; (F) Interpretative drawing of the calamus. Legend: CL - Calamus; BI - Isolated Barbule; VX - Vexillum (vanes); RQ - Rachis. Scale bars: Scale bar: (A, E-F) 2 mm; (B-C) 5 mm; (D) 10 mm.

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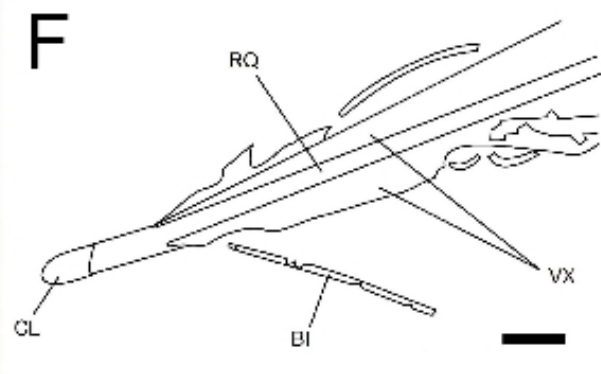
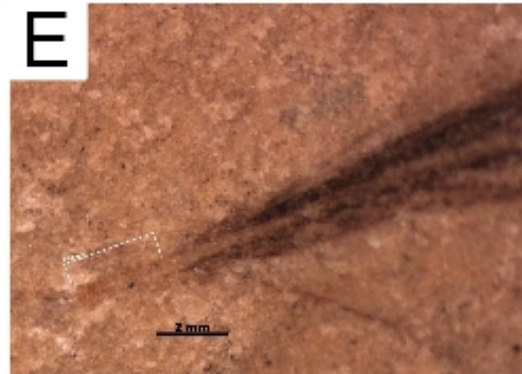


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Table 3 (on next page)

Feather portions calculation

Table 3. Difference in percentage between portions of the feathers compared to the maximum length. Legend: ND - No data available.

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STRUCTURE	PERCENTAGE		
	GP/2E-7853	GP/2E-7854	GP/2E-8771
Larger barb	46,41	6,16	50,90
Minor barb	69,95	77,37	87,70
Calamus	ND	1,26	ND
Rachis	41,57	36,68	12,39

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Table 4(on next page)

Taxonomic assignment

Table 4. Classification of the described feathers. PeerJ reviewing

Table 4. Classification of the described feathers.

SPECIMEN	MORPHOTYPE	EVOLUTIONARY- DEVELOPMENTAL MODEL	MORPHOTYPE MODEL PRESENT OF THE FOSSIL RECORD
GP/2E-7853 GP/2E-7854	Downy feathers	IIIb	Morphotype 4
GP/2E-8771	Semiplume (Contour feather)	IIIa+b	Morphotype 6

Figure 3 (on next page)

Simplified Cladogram of Dinosauria and feathers

Figure 3. Simplified cladogram of Dinosauria with the distribution of feathers according to the fossil record. Despite its more ancient origin, it was only in maniraptoriformes that modern type feathers (plumulaceous and pennaceous feathers) have arisen (Based in Xu & Guo, 2009; Clarke, 2013; Godefroit et al., 2013; Han et al., 2014; Koshchowitz et al., 2014).

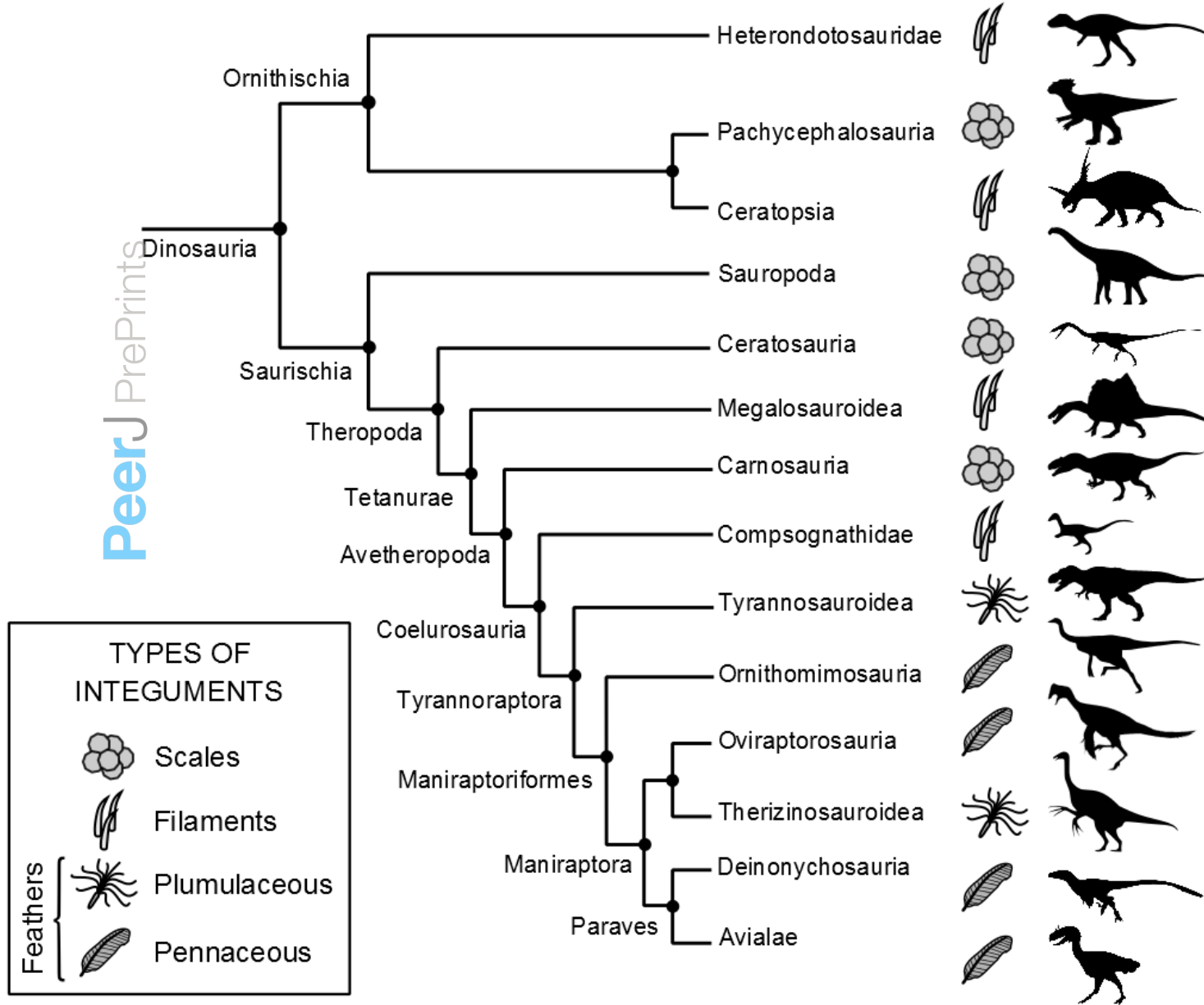


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