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

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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 pragmatical study of fossilized feathers, can help with the understanding of the evolution and paleobiology of dinosaurs, especially on the South Hemisphere.

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NEW OCCURRENCES OF FOSSILIZED FEATHERS: SYSTEMATICS, TAPHONOMY, AND PALEOECOLOGY OF THE SANTANA FORMATION OF THE ARARIPE BASIN (CRETACEOUS), NE, BRAZIL

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ABSTRACT

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 pragmatical study of fossilized feathers, can help with the understanding of the evolution and paleobiology of dinosaurs, especially on the South Hemisphere.

Keywords: Fossil Feathers, Santana Formation, Systematic Paleontology, Paleoecology

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INTRODUCTION

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

Recent studies of molecular data of feathers, suggest the possible phylogenetic hierarchy in the emergence of these elements, tying with the genesis of the tetrapod integuments. During the period of land transition, which was marked by the aerial exposure and its consequences (*e.g.*, the radiation and free O_2), many amphibians shared the same toolkit for the development of this novelty. Because of this, the integumentary filaments can now be considered a symplesiomorphy, once it is also found in mammals, pterosaurs, non-avian and avian dinosaurs (Greenwold & Sawyer, 2013; Lowe *et al*., 2014). Even though, they are distinct between these groups, where α-keratin is synthesized by mammals and β-keratin by reptiles. As evidences indicate a plausible multiple origin of these structures within Dinosauria (Clarke, 2013), is possible that the first feathers were present even in the base of the superorder (Xu, 2006; Norell, 2011). Nevertheless, the presence of these elements in basal dinosaurs remains uncertain (Barret, 2013).

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

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

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

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In addition, evidences of simple morphotypes in non-avian dinosaurs, such as *Psittacosaurus* (Mayr *et al.*, 2002), *Tyaniulong* (Zheng *et al.*, 2009) and *Kulindadromeus* (Godefroit *et al.*, 2014), makes this hypothesis even more unlikely. Other interpretations, consider that feathers originated to perform the thermoregulation functions, nevertheless, recent studies indicate that dinosaurs were mesothermic, suggesting that their origin do not have any relation with the advent of homeothermy (Grady *et al.*, 2014). Furthermore, the endothermy may have only originated during or briefly after the advent of the flight, since this activity require a high metabolism, with high consumption of O_2 and a low accumulation of $C_3H_6O_3$ (lactic acid). To have an efficient thermoregulation control, is possible that this condition evolved with the help of the feathers (Ruben & Jones, 2000) since the non-avian theropods already were covered with them.

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

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

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

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

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

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

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

Geologic Setting

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

Because Assine (1992; 1994; 2007) have been working with the entire basin, in a detailed level and in accordance with Brazilian Code of Stratigraphy, we prefer to adopt his descriptions in this paper. The Santana Formation, is comprised by the Crato Member (in the bottom), and the Romualdo Member (in the atop). Both units have different lithologies that reflect their distinct deposition environment. Many of the exquisitely preserved fossils of the Araripe Basin, come from the Crato Member strata, which is characterized by micritic laminated limestones intercalated with shales and mudstones of varied thickness. This unit was formed in a lacustrine environment, with brackish water, and reducing conditions in the bottom strata of the controversially depth water column (Assine, 1992; 1994; 2007; Martill, 2007; Heimhofer *et al*., 2010).

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

MATERIALS AND METHODS

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

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

RESULTS

Systematic Palaeontology

Order Saurischia Seeley 1888

Suborder Therapoda Marsh 1881

Division Coelurosauria Von Huene 1914 *sensu* Gauthier 1986

Family *Incertae sedis*

(Figure 2, A - B)

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

Horizon: Crato Member, Santana Formation, Araripe Basin.

Lithology: Weathered (beige) micritic laminated limestone.

Age: Lower Cretaceous (Aptian/Albian).

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

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

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

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

Family *Incertae sedis*

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

Horizon: Crato Member, Santana Formation, Araripe Basin.

Lithology: Weathered (beige) micritic laminated limestone.

Age: Lower Cretaceous (Aptian/Albian).

Description: The proximal portion is degraded, although, the rachis are visible. Several barbs with different length originate from them. Also, it is possible to notice the presence of vestigial barbules. As the GP/2E-7853, the calamus is a slight line.

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

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

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

Order Saurischia Seeley 1888
Suborder Therapoda Marsh 1881
Division Coelurosauria Von Huene 1914 *sensu* Gauthier 1986
Subdivision Maniraptoriformes Holtz 1995
Family Incertae sedis
(Figure 2, C)

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

Horizon: Crato Member, Santana Formation, Araripe Basin.

Lithology: Grayish micritic laminated limestone.

Age: Lower Cretaceous (Aptian/Albian).

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

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

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

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

Systematic analysis

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

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

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

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

DISCUSSION

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

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

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

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

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

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

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

Sedimentary Deposition, Paleoenvironment, and Taphonomy

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

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

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

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

Despite this “harsh” environment, this sedimentary unit is remarkably noted by the abundant biota that is preserved with a high degree of fidelity. The vertebrate fauna is composed primarily by crocodiles, turtles, frogs, birds, pterosaurs, and numerous fishes (Maisey, 1991; Martill, 1993; 1997; Fielding *et al.*, 2005; Martill *et al.*, 2007a; Martill *et al.*, 2008a; Figueiredo & Kellner, 2009; Pinheiro *et al.*, 2012; Simões *et al.*, 2014; Oliveira & Kellner, 2015). The invertebrate animals was also abundant, with the mainly occurrences of arthropods and mollusks (Maisey, 1991; Martill, 1993; Grimaldi & Engel, 2005; Martill *et al.*, 2007a; Barling *et al.*, 2015). Despite this faunal richness, the flora was also exuberant (Martill *et al.*, 2007; 2012; Mohr *et al.*, 2015), with a diversity characterized by the presence of macro and microfossils of pteridophytes, gymnosperms, angiosperms, palynomorphs, pollens, seeds, etc. (cf. Maisey, 1991; Martill, 1993; Martill *et al.*, 2007a; 2012).

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

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

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

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

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

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

During their life, birds tend to lose feathers by ontogeny, breeding season, and under high stress situations. This latter mechanism is called 'fright molt'. Generally, they tend to release rectrices and semiplumes (Sick, 1984). It is possible that the animals that possessed these structures, released them during similar conditions. The presence of the isolated feathers could occur by animal hunting, *i.e.*, by fish, crocodiles, dinosaurs, or, pterosaurs. Some extant fishes occasionally include birds on their diet by opportunism (Davenport, 1979; French, 1981; O'Brien, 2014; Perry *et al.,* 2013). A good prey-predator example in the Santana Formation, is indicated by the evidence of a conical tooth assigned to a spinosaurid dinosaur, reported inserted in a cervical vertebrae of the ornithocheirid pterosaur (Buffetaut *et al.*, 2004). But, despite the possibility that birds were also prey, the fossil record of the established trophic chain, do not show yet, these animals as a food source of the other organisms, in a way that coprolites did not provide yet, evidence of this diet (Maisey, 1991; Martill, 1993; Lima *et al.,* 2007).

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

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

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

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

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

Until the present day, only a few records of feathers, or filaments considered as 'protofeathers', were found associated with ornithischians dinosaurs (Mayr *et al*., 2002; Xu *et al.,* 2009; Zheng *et al.*, 2009; Sevaliev & Alifanov, 2014; Godefroit *et al.,* 2014). Evidences of sauropod integuments, indicate that they were consisted mainly by scales and osteoderms (Czerkas, 1992). Although, the poor record of feathers in individuals of ornithischia, and the absence in sauropoda, may be also a taphonomic artifact. Despite the occasional events of great sediment deposition, the preservation of the carcass of these animals (often huge), required more time to be completely buried, and so, preserved. This slow process opposes to the rapid burial of feathers as suggested elsewhere (Martill & Davis, 2001), explaining their absence alongside sauropods and great ornithischians bones.

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

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

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

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

Future perspectives

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

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

CONCLUSION

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

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

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

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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 (*Turdus rufiventris*)	Santos (1950)
Two pennaceous feathers	Pirabas Fm	Neogene (Miocene)	Carbonized	Possible semiplumes	Ackerman (1964)
One primary remex	Santana Fm	Cretaceous (Aptian/Albian)	Limonitc/ 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 *Taubacrex granivora*	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 *et al.* (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 *et al.* (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 *et al.* (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)

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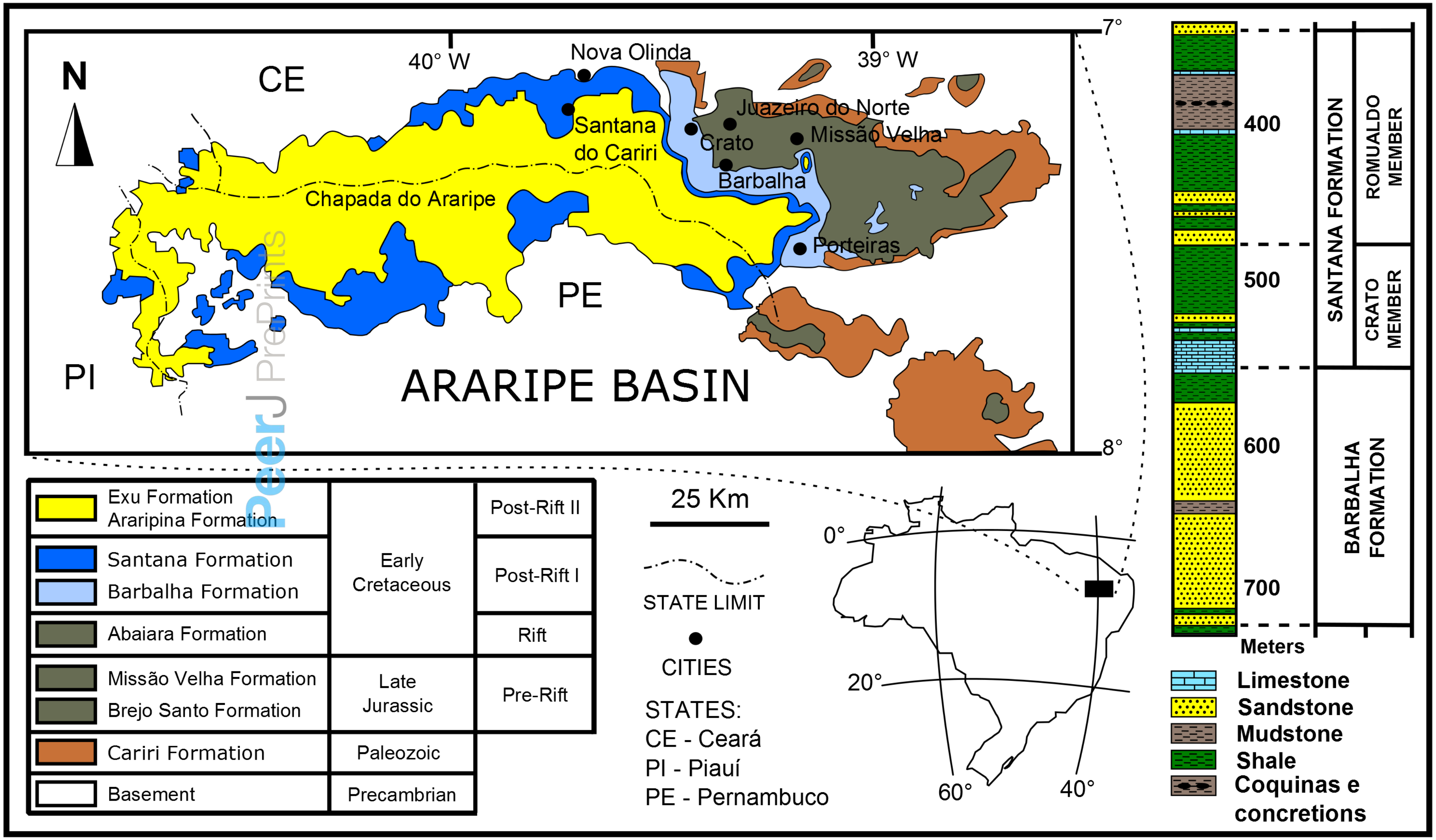

Figure 1. The Araripe Basin locality, the stratigraphic columns, units and chronology. (Adapted and modified from Coimbra *et al.*, 2002; Vianna & Neumann, 2002; Assine, 2007)

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

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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

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. PeerJ reviewing

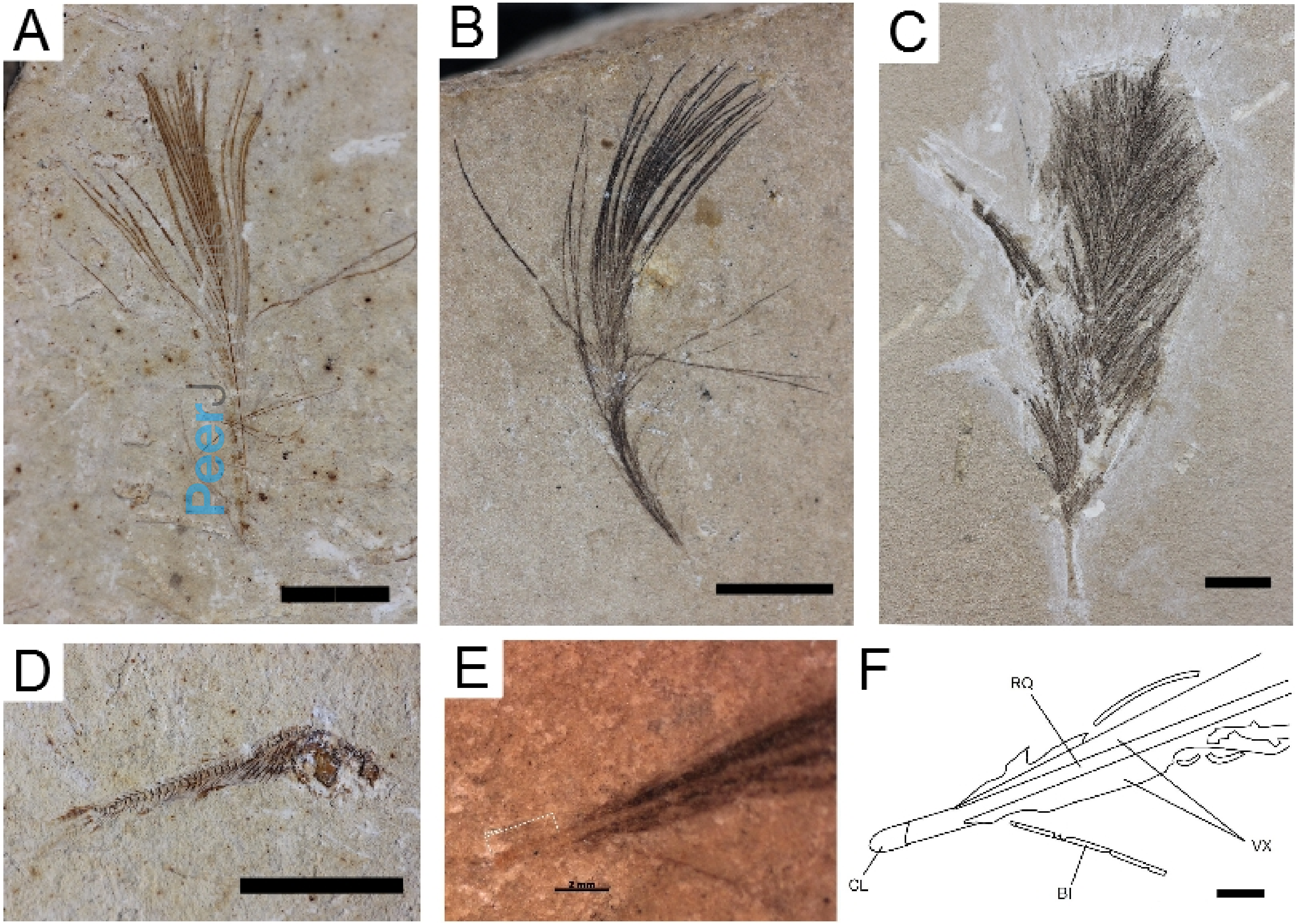
A
B
C
D
E
2 mm
F
RQ
VX
CL
BI

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.

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

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

Table 4(on next page)

Taxonomic assignment

Table 4. Classification of the described feathers. PeerJ reviewing

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Table 4. Classification of the described feathers.

SPECIMEN	MORPHOTYPE	EVOLUTIONARY-DEVELOPMENTAL MODEL	MORPHOTYPE MODEL PRESENT OF THE FOSSIL RECORD
GP/2E-7853	Downy feathers	IIIb	Morphotype 4
GP/2E-7854			
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 moderntype 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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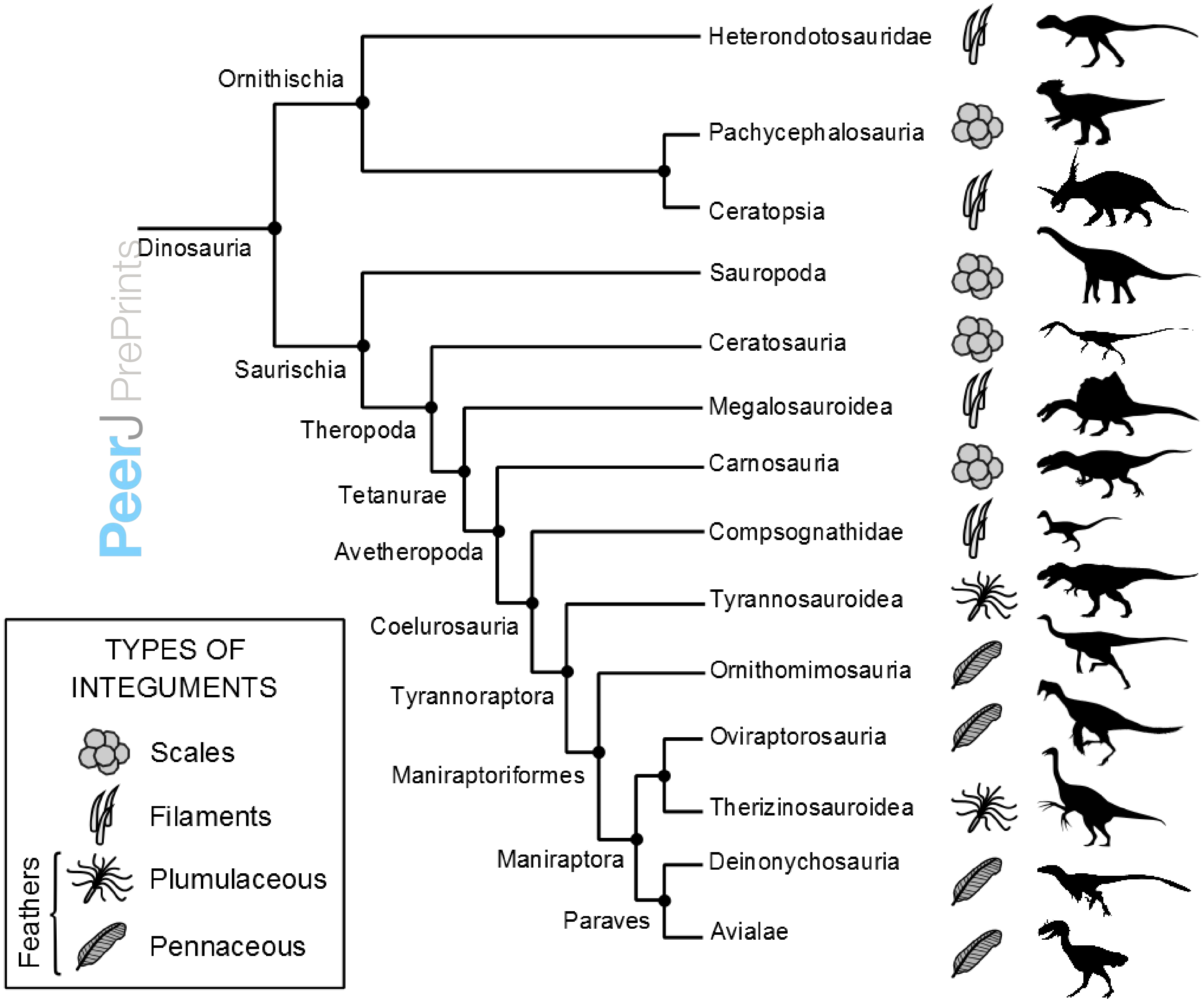
Heterondotosauridae
Ornithischia
Pachycephalosauria
Ceratopsia
Dinosauria
Sauropoda
Ceratosauria
Saurischia
Megalosauroidea
Theropoda
Carnosauria
Tetanurae
Compsognathidae
Avetheropoda
Tyrannosauroidea
Coelurosauria
Ornithomimosauria
Tyrannoraptora
Oviraptorosauria
Maniraptoriformes
Therizinosauroidea
Maniraptora
Deinonychosauria
Paraves
Avialae
TYPES OF INTEGUMENTS
Scales
Filaments
Feathers
Plumulaceous
Pennaceous

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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