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FAST TRACK COMMUNICATION

A new genus and species of enantiornithine bird from the Early Cretaceous of Brazil

Um novo gênero e espécie de Ave enantiornithine do Cretáceo Inferior do Brasil

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ABSTRACT: The fossil record of birds in Gondwana is almost restricted to the Late Cretaceous. Herein we describe a new fossil from the Araripe Basin, *Cratoavis cearensis* nov. gen et sp., composed of an articulated skeleton with feathers attached to the wings and surrounding the body. The present discovery considerably extends the temporal record of the Enantiornithes birds at South America to the Early Cretaceous. For the first time, an almost complete and articulated skeleton of an Early Cretaceous bird from South America is documented.

KEYWORDS: *Cratoavis cearensis* nov. gen et sp.; Araripe Basin; Fossil bird.

RESUMO: *No Gondwana, o registro fóssil de aves está praticamente restrito ao Cretáceo Superior. Neste estudo é descrito um novo fóssil da Bacia do Araripe, Cratoavis cearensis nov. gen. et sp., composto por um esqueleto articulado com penas conectadas às asas e circundando o corpo. A presente descoberta amplia consideravelmente o intervalo temporal de registro das aves Enantiornithes na América do Sul ao Cretáceo Inferior. Pela primeira vez, um esqueleto articulado e quase completo de uma ave do Cretáceo Inferior da América do Sul é documentado.*

PALAVRAS-CHAVE: *Cratoavis cearensis nov. gen. et sp.; Bacia do Araripe; Ave fóssil.*

INTRODUCTION

In South America, the Cretaceous avian record is composed of several taxa, including basal ornithothoracine birds, enantiornithes, and derived ornithurines, including Neornithes-like taxa (Walker 1981, Alvarenga & Bonaparte 1992, Chiappe 1993, 1996, Chiappe & Calvo 1994, Clarke & Chiappe 2001, Agnolin & Martinelli 2009, Agnolín 2010). Regarding the regional record, in Brazil, only sparse mentions have been made up to the date. Only three reports of Cretaceous birds are known for the entire country, including unpublished indeterminate enantiornithine birds from Presidente Prudente locality (Alvarenga & Nava 2005), and indeterminate birds from Jales locality (Azevedo *et al.* 2007), both coming from the Adamantina Formation (Turonian-Santonian, Bauru Group). More recently, Candeiro *et al.* (2012) reported from the Late Maastrichtian, fragmentary specimens referable to indeterminated birds and enantiornithes from the Marília Formation, at the Minas Gerais State.

There are also few reports concerning fossil birds from the Araripe Basin. All the available data comes from the Santana Formation, Crato Member. Kellner (2002), Kellner *et al.* (1991, 1994), Martins-Neto and Kellner (1988) and

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Martill and Filgueira (1994) described feathers and plumes with fine details such as colour patterns preserved as dark and light transverse bands. Although they are generally assigned as belonging to Aves, probably are derived from several different taxa, including some non-avian theropod clades, such as Oviraptorosauria, Troodontidae or Dromaeosauridae (Naish *et al*. 2007). On the other hand, osteological remains are restricted to two specimens. The first one, an unlabelled specimen from Senckenberg Museum (Frankfurt, Germany) presents presumed carpal bones associated with three asymmetrical feathers. The second, held in a private collection in Japan, consists of a poorly preserved articulated specimen, with an incomplete skull, vertebrae, ilium, a possible ischium and a probable left hindlimb. Naish *et al*. (2007) considered that this second specimen presents neural spines of the dorsal vertebrae and the morphology of the centre of the dorsal vertebrae that suggest a relationship with the euenantiornithines. More recently, Carvalho *et al*. (2015) described a nearly complete skeleton and associated feathers of a still unnamed enantiornithine bird from the Crato Member (Santana Formation - Aptian, Araripe Basin). The association of feathers and the almost complete skeleton points it as an exceptional fossil bird from the Early Cretaceous deposits. The aim of the present paper is to coin a new name for this specimen, as well as to make some comparisons with other enantiornithine birds.

GEOLOGICAL CONTEXT

The southern hemisphere was deeply changed during the Early Cretaceous times. The intense tectonic activity, related to the initial stages of the Gondwanic crust rupturing, led to the disappear, but also to the flourish of new ecological niches. These events are registered in the interior of Northeastern region of Brazil, in intracratonic basins developed along pre-existing Precambrian structural trends. One of these sedimentary areas is the Araripe Basin, which has 12,200 km^2 and its Early Cretaceous history spans from Berriasian to Albian times (Fig. 1). This basin was mainly filled, during Early Cretaceous, with clastic and chemical rocks (Carvalho 2000). The lithostratigraphy of the basin has been discussed by many authors (Beurlen 1963, 1971; Cavalcanti & Viana 1992, Assine 1992, Ponte 1992, Martill 1993, Martill & Wilby 1993, Viana & Neuman 1999, Assine 2007).

The new fossil was collected in the Crato Member (Aptian) of Santana Formation (Fig. 2). The outcrops are distributed around Chapada do Araripe plateau, in the southern Ceará, western Pernambuco and south-eastern Piauí States (Martill 1993, Viana & Neuman 1999). This lithostratigraphic unit is considered a fossil Lagerstätte, due the large amount and quality of its fossil preservation. The Crato Member fossils probably represent one of the most well-known terrestrial flora and fauna from the Aptian time. In fact, a large amount of faunistic remains has been described, including worms, insects, spiders, fishes, basal lizards, turtles, crocodiles, non-avian dinosaurs and possible birds (see Martill *et al*. 2007).

The Crato Member comprises essentially laminated carbonate strata with some inter-bedded levels of fine sandstones, marls and clays. This succession is interpreted as a lacustrine environment, in a rift basin context, that constituted an important area for an abundant endemic biota. The climate was at that time hot and arid. The connection between South America and Africa as a single, large continental block did not allow a higher humidity, in what was the continental interior. During the time interval of the carbonate succession, where the new bird species was found, occurred many important environmental changes. The climate gradually became more humid, as the tectonic events that drove the separation of South America and Africa led to the origin of the equatorial Atlantic Ocean (Carvalho 2004, Carvalho & Pedrão 1998, Medeiros *et al*. 2014).

The distribution of the laminated limestones of Crato Member throughout the Araripe Basin, allowed Martill *et al*. (2007) to estimate the depositional area as a water body with a minimum extent of some 18,000 km^2. The brackish water was an alkaline environment, in which occurred some hypersaline stages represented by carbonates with pseudomorphs of halite crystals. Menon and Martill (2007) observed that the lack of reworked horizons within as much as 13 meters of laminite suggests considerable water depth and deposition probably under anoxic botton water. The integration of lithological and petrographic evidences by Heimhofer *et al*. (2010) indicates that the bulk of Crato Member limestone was formed via authigenic precipitation of calcite from within the upper water column, most probably induced and/or mediated by phytoplankton and picoplankton activity. The isotopic evidence indicates a shift from closed to semi-closed conditions towards a more open lake system during the onset of laminate deposition of the Crato Member.

The dating of this interval was presented by Rios-Netto *et al*. (2012). The biostratigraphical framework to the Alagoas Stage, based on palynological analyses proceeded on 167 samples from 14 wells drilled at the Eastern portion of the Araripe Basin, showed only the P-270.2 and P-280.1 subzones of Regali and Santos (1999). These subzones are assigned to the late Aptian (119 – 113 Ma).

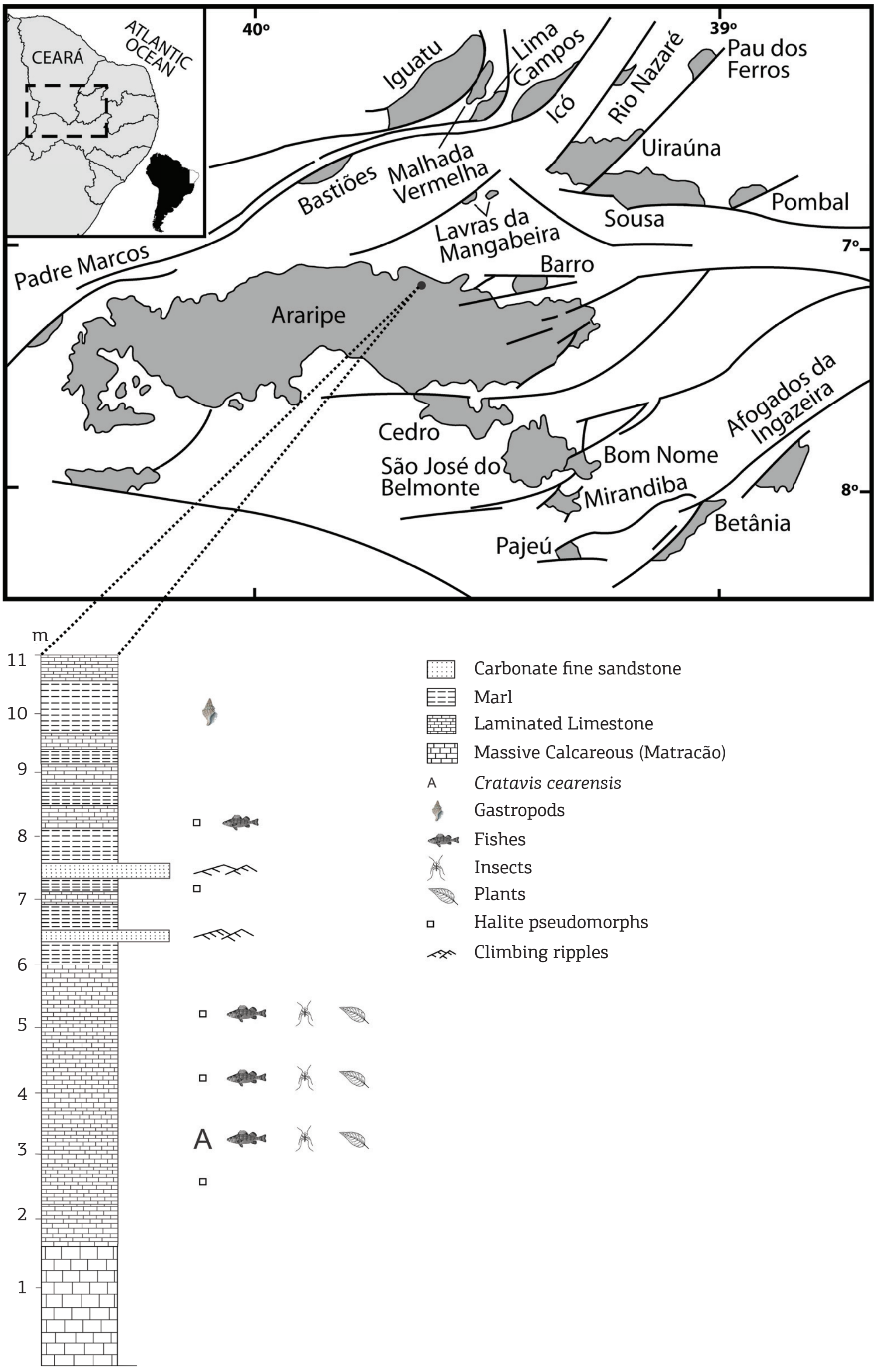


Figure 1. Location map of the Araripe Basin in the context of the Cretaceous Brazilian Northeastern intracratonic basins and stratigraphical profile from the location where the fossil was collected. Pedra Branca Mine, Nova Olinda County, Brazil (7° 6' 51.9" S and 39° 41' 46.9" W).

Figure 2. Outcrop where the fossil was collected. Pedra Branca Mine, Nova Olinda County, Brazil (7º 6’ 51.9” S and 39º 41’ 46.9” W).

THE FOSSIL PRESERVATION

The Crato Member fossils are known by their exceptionally preservation. Specimens may be preserved three-dimensionally or at least with only minor compaction. Soft tissues, colour patterns and fine details, are exquisite, with preserved delicate structures of the anatomy of plants, invertebrates and vertebrates (Grimaldi 1990, Brito & Martill 1999, Martill *et al*. 2007). In plants, many fossils are preserved more or less entire, often with roots, stems, leaves, sporangia and flowering structures attached. The original organic material is generally covered or replaced by goethite (Mohr *et al.* 2007). The preservation of invertebrates, such as arthropods, can be highly variable. Therefore, there are essentially, two types: replacement by goethite, or as black, carbonaceous replicas with finely disseminated pyrite (Menon & Martill 2007). In vertebrates, like fishes, it is common fully articulated skeletons, and occasionally with *in situ* stomach contents. An important feature of the high-quality soft-tissue preservation are found in pterosaurs, including cranial crest, wing membranes and wing fibers, claw sheaths, foot webs and a heel pad (Maisey 1991, Campos & Kellner 1997, Frey *et al*. 2003, Pinheiro *et al*. 2012).

The studied bird specimen show articulated skeleton with feathers and plumes. There are probably soft tissues around the skull, sometimes presented as a dotted surface, resembling skin fragments. Also around the skull there is a distinct brownish pigmentation, due the presence of small plumes. The skull shows an orbit round and large, with a partially preserved sclerotic ring. There is a short beak. There are the bones and impression of both forelimbs and wings. The wings and body present small brownish contour feathers with pennaceous and plumaceous vanes. The forelimbs are only partially present, with the humerus, radius, ulna and some finger bones. It is possible to recognize one short claw. In the hindlimbs it is observed white-yellowish elongated muscular fibers bordering the femur. The foots present four long digits with curved claws. In the abdominal area there are some long and thin bones that were probably part of a gastralia. After a short pygostyle there are two long parallel rectrices feathers preserved as fine impressions with calamus, rachis and pennaceous vanes. It is possible to observe on them colour patterns as dark lunar transversal bands on the first third of the feather. The bones are preserved three-dimensionally, although sometimes show partial crushing. They are of a dark brown colour and generally occur as articulated bones.

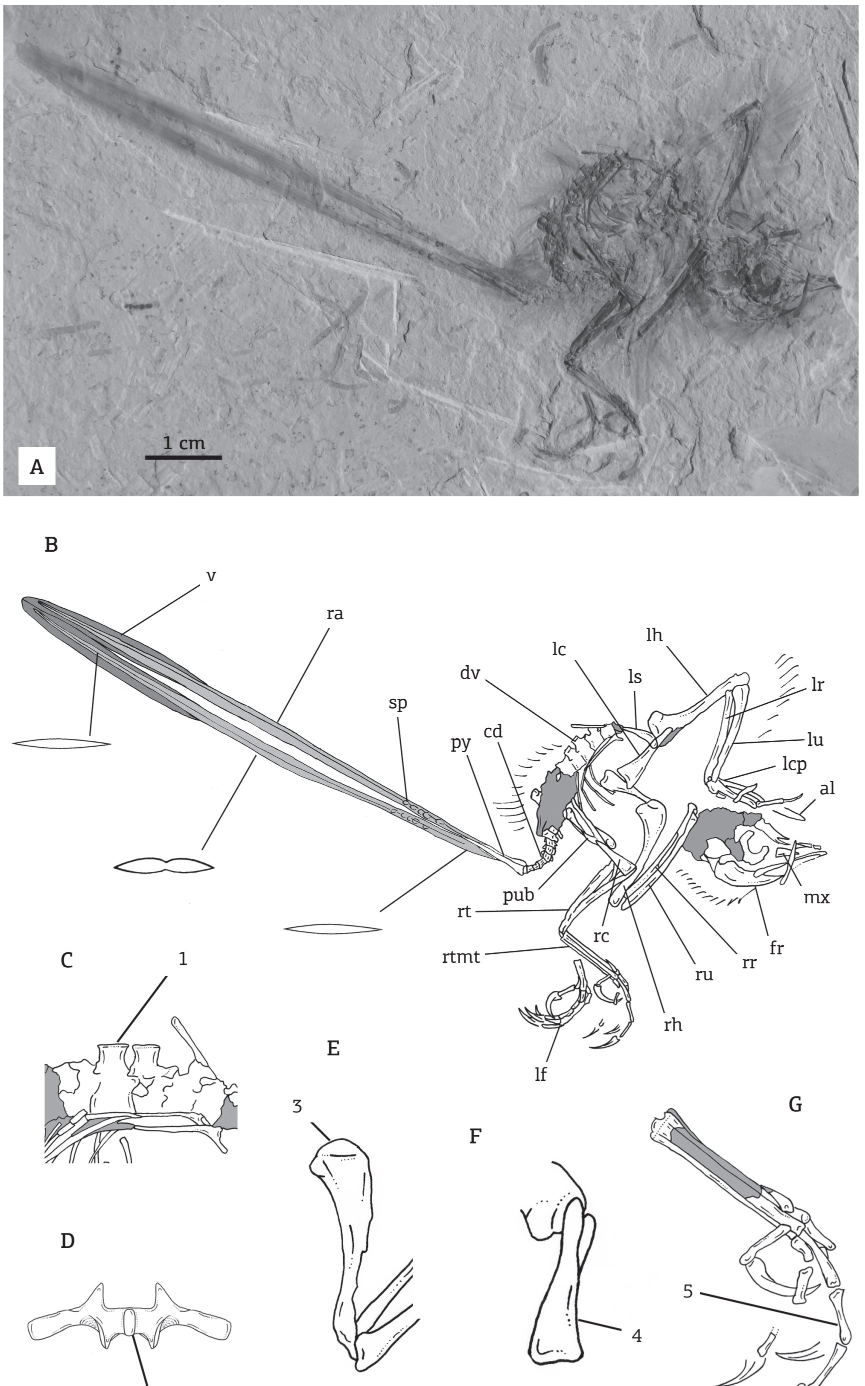
This exquisite preservation occurred in a context of alkaline, hypersaline water. Menon and Martill (2007) considered that high salinities, and also anoxic bottom waters, may inhibit macro-scavengers and bioturbation, allowing in this way that the carcasses could remain intact for a considerable time. There are also an important role of the microbial communities, in which microbial mats are partly responsible for limiting attacks from scavengers and preventing disarticulation. Other aspect concerns to the environment of the depositional area. As demonstrated by Brocklehurst *et al.* (2012), Mesozoic birds living nearby fluviolacustrine environments, due the taphonomic processes, tend to be more complete than those living in marine or other terrestrial environments.

SYSTEMATIC PALEONTOLOGY

Aves Linnaeus 1758
Ornithothoraces Chiappe 1996
Enantiornithes Walker 1981
Euenantiornithes Chiappe & Walker 2001
Cratoavis cearensis nov. gen. et sp. (Figs. 3 and 4)

Holotype

UFRJ-DG 031 Av (Universidade Federal do Rio de Janeiro, Departmento de Geologia collection), nearly complete skeleton, preserved in two slabs, including skull, nearly complete fore and hindlimbs, vertebral column and pectoral and pelvic girdles. However, as is usual in fossils preserved in two slabs, the bones are cracked. Some crushing and displacement of bones has occurred. Several bones, however, remain in articulation. The skull and neck are rotated ventrally with respect to the rest of the skeleton, and are exposed on the left side, whereas most of remaining skeleton is exposed on the right side. The skull and mandible suffered strong crushing and



al: alula; cd: free caudal vertebrae; dv: dorsal vertebrae; fr: frontals; lc: left coracoid; lcp: left carpometacarpus; lf: left foot; lh: left humerus; lr: left radius; ls: left scapula; lu: left ulna; mx: maxilla; pub: pubes; py: pygostyle; ra: rachis; rc: right coracoid; rh: right humerus; rr: right radius; rt: right tibiotarsus; rtmt: right tarsometatarsus; ru: right ulna; sp: colour spots; v: vanes.

Diagnostic features of Cratoavis nov. gen.: 1: fan-shaped and dorsally thick neural spines; 2: transverselly thick caudal neural spine; 3: proximaly convex humeral head; 4: medially concave coracoid shaft; 5: very long and slender digit III.

Figure 3. Holotype specimen of *Cratoavis cearensis* nov. gen. et sp. (UFRJ-DG 031Av), with selected skeletal elements showing diagnostic features. (A) main slab; (B) interpretative drawing of the skeleton and feathers; (C) dorsal vertebrae in right lateral view; (D) caudal vertebra in dorsal view; (E) left humerus in caudal view; (F) left coracoid in sternal view; (G) right foot.

Figure 4. Reconstruction of *Cratoavis cearensis* nov. gen. et sp. (art by Deverson Pepi).

deformation, and most bones cannot be individualized. The pelvic girdle and hindlimb remain in anatomical position, whereas the pectoral girdle has been displaced ventrally with respect of the dorsal column. The minor slab shows better preserved bones than the main slab. It contains the impression of the skull, and both forelimbs and fragments of pectoral girdle. The ischia and sternum are not preserved.

The small size of the individual, the lack of fusion of tarsometatarsus, tibiotarsus, and carpometacarpus, supports the interpretation that the individual corresponds to an early ontogenetic stage (Chiappe *et al*. 2007; Carvalho *et al*. 2015). However, fused vertebral centra, as well as well-defined epiphyses of long bones, extensive pubic apron, and absence of surface pitting, indicate that the individual was probably adult specimen (Sanz *et al*. 1997). In this way, we are not certain about the ontogenetic stage of the specimen.

Diagnosis

Minute Enantiornithes, diagnosed on the basis of the following combination of characters (autapomorphies marked by an asterisk): dentate maxilla, strongly concave medial margin of coracoid, dorsal vertebrae with fan-shaped and very well-developed neural spines, caudal neural spines transversely thick, proximally rounded humeral head, tibiotarsus shorter than femur and subequal in length to metatarsals, very elongate pedal phalanges of digit III*, and very long rectrices, much longer than total body size*.

Etymology

Cratoavis nov. gen., the generic name derives from the combination of the Crato Member lithostratigraphic unit, where the specimen was found, and the zoological group Aves. The specific epithet *cearensis* refers to the Ceará State, where the fossil was collected.

Locality and horizon

Pedra Branca Mine, Nova Olinda County, Ceará State, Brazil (7° 6´51.9´´ S and 39° 41´46.9´´ W). Araripe Basin, Santana Formation, Crato Member (Early Cretaceous, Aptian).

COMPARISONS

The holotype of *Cratoavais cearensis* was described in detail by Carvalho *et al.* (2015), and thus, description is not repeated here. Thus, only main comparisons with other Enantiornithes, with the aim to sustain its recognition as a new taxon are here afforded.

Enantiornithes are the most diverse lineage of Mesozoic birds with over 60 species named (Chiappe & Walker 2002, O´Connor 2009). However, in spite of its good fossil record and high diversity, at least a third of named species are based upon extremely fragmentary specimens (O´Connor 2009). Diagnosing a new species of Enantiornithes or justifying higher-level relationships may represent a difficult taxonomic task, mainly due to their small size and homogeneous morphology, and because of it, their taxonomy remains largely unreviewed (O´Connor & Dyke 2010). After, we made comparisons between *Cratoavis* nov. gen. and different enantiornithine genera and clades.

Cratoavis nov. gen. is referred as Enantiornithes on the basis of the following synapomorphies (Carvalho *et al.* 2015): proximally forked and distally constricted pygostyle with a ventrolateral process, convex lateral margin of coracoid, scapulocoracoid articulation with scapular pit and coracoid tuber, distal end of metacarpal III more distally extended than the metacarpal II, distal tarsals fused to proximal metatarsus, but remaining portion of metatarsals free. Sereno (2000) also added a suite of purported synapomorphies that may allow to reinforce the inclusion of *Cratoavis* nov. gen. to Enantiornithes: metatarsal I with posteriorly reflected distal condyles ("J" shaped) and the distal condyles joined along its dorsal margin.

Referral of *Cratoavis* nov. gen. to Euenantiornithes is based on the following derived features (Chiappe & Walker 2002; see Carvalho *et al.* 2015): parapophyses placed on the central part of the thoracic vertebra, prominent bicipital crest of humerus, shaft of radius with a longitudinal groove on its posterior surface, very large posterior femoral trochanter, and metatarsal IV significantly thinner than metatarsals II and III.

Chiappe and Walker (2002) indicate that Euenantiornithes may exclude some basal enantiornithes. Among them, they cited *Iberomesornis* and *Noguerornis*. As member of Euenantiornithes, *Cratoavis* nov. gen. may be clearly distinguished from both genera. At first sight, *Cratoavis* nov. gen. resembles *Iberomesornis* in having plesiomorphically anteroposteriorly short cervical and dorsal vertebral centra, and a simple proximal humeral morphology (Sanz & Bonaparte 1992; Sereno 2000). However, *Cratoavis* nov. gen. differs in having fan-shaped distal margin of dorsal neural spines, in contrast to *Iberomesornis* in which they are low and with a subcuadrangular contour (Sereno 2000), well-developed neural spines on caudal vertebrae, ulna as long as humerus (longer than humerus in *Iberomesornis*; Sereno, 2000), and gracile pedal phalanges. Furthermore, *Cratoavis* nov. gen. is distinguished by the poorly known *Noguerornis* by having a wider intermetacarpal space, and by a nearly straight humeral shaft (Chiappe & Lacasa-Ruiz 2002).

The inclusion of *Cratoavis* nov. gen. within Euenantiornithes seems well sustained. However, as pointed out by Walker & Dyke (2009), in spite of the anatomical distinctiveness and ecological variability, the phylogenetic relationships among euenantiornithine genera still remains in state of flux, and little phylogenetic resolution has been achieved, lacking consensus about their interrelationships (Chiappe & Walker 2002; Chiappe *et al.* 2007; O´Connor *et al.* 2011a, 2011b, 2013). In this way, the position of *Cratoavis* nov. gen. within Euenantiornithes is unresolved, as indicated by Carvalho *et al.* (2015). However, the combination of anatomical traits present in specimen UFRJ-DG 031 Av serves as basis to coin the new genus and species Cratoavis cearensis within enantiornithines.

Cratoavis nov. gen. clearly differs from basal clade Longipterygidae (composed by *Boluochia, Longirostravis, Longipteryx, Shanweiniao, Rapaxavis, Shnegjingornis*; O´Connor *et al.* 2009, 2010; Li *et al.* 2012) by lacking an elongate and acute rostrum, coracoid transversely narrower, poorly curved pedal unguals, and relatively longer tarsometatarsus and manus, among other anatomical details. On the other side it may be distinguished from the avisaurids *Soroavisaurus, Lectavis, Yungavolucris, Intiornis* and *Neuquenornis* in having nearly flat cranial surface of metatarsal III (Chiappe 1993; Chiappe & Calvo 1994; Novas *et al.* 2011). Furthermore, *Cratoavis* nov. gen. differs from *Neuquenornis* in having a more stouter metatarsus and transversely wider coracoid (Chiappe & Calvo 1994). Dorsal vertebrae are shorter than those of *Neuquenornis* (Chiappe & Calvo 1994). Moreover, *Cratoavis* nov. gen. differs from *Intiornis, Soroavisaurus,* and *Avisaurus* in lacking a medially oriented II trochlea of metatarsus (Varricchio & Chiappe 1995; Novas *et al.* 2011). In addition, *Intiornis* and *Soroavisaurus* exhibit a proximal fenestra between metatarsals III and IV (Novas *et al.* 2011). *Lectavis* and *Yungavolucris* clearly differ from *Cratoavis* nov. gen. in having highly specilized metatarsals, the former exhibits a very stout and wide metatarsus, whereas the second shows extremely elongate and gracile metatarsals (Chiappe 1993).

Cratoavis nov. gen. differs from the basal euenantiornithine *Protopteryx* in lacking a procoracoid process and lateral process on coracoid, in having reduced manual phalanx 1-I, and proximally fused carpometacarpus (Zhang & Zhou 2000). From the flightless enantiornithine *Elsornis*, *Cratoavis* nov. gen. differs in several anatomical details, including a much more expanded and well-developed proximal end of the humerus, and a more gracile and straighter ulnar shaft (Chiappe *et al.* 2007).

The humerus of *Cratoavis* nov. gen. is relativelly elongate and gracile, whereas in the Boahiornithidae *Boahiornis, Sulcavis, Alethoalaornis, Xiangornis* is much more robust and stouter (Li *et al.* 2009; Hu *et al.* 2011; O´Connor *et al.* 2013). Rounded humeral head differs from the saddle-shaped condition present in most Enantiornithes (e.g., *Elsornis, Cathayornis, Concornis, Gobipteryx, Halimornis, Eoalulavis, Gurilynia, Otogornis, Hebeiornis, Gracilornis, Sulcavis, Sinornis, Martinavis, Elbretornis* and *Enantiornis*; Sanz *et al.* 1995, 2002; Sereno *et al.* 2002, Zhou & Hou 2002; Chiappe *et al.* 2002, 2007; Zhang *et al.* 2004, Walker & Dyke 2009; Li & Hou 2011; O´Connor *et al.* 2013), a character that was considered as synapomorphy of enantiornithes by previous authors (O´Connor *et al.* 2013). In *Cratoavis* nov. gen. the transverse ligamental groove and the capital groove of the humerus are poorly defined, which differs from the deep and well-defined groove present in *Eoenantiornis* (Zhou *et al.* 2005) and *Otogornis* (Zhou & Hou 2002), and other derived forms (e.g., *Concornis, Halimornis, Martinavis, Elbretornis* and *Enantiornis*; Sanz *et al.* 1995, Chiappe *et al.* 2002; Walker & Dyke 2009). In this aspect, *Cratoavis* nov. gen. is reminiscent to that of more basal taxa, such as *Iberomesornis* and *Eocathayornis* (Sanz & Bonaparte 1992; Zhou 2002) in lacking deep capital groove and the transverse ligamental groove.

The ulna is nearly as long as the humerus, a condition that contrast with that of some highly derived Euenantiornithes, such as *Elbretornis* and *Enantiornis*, in which the ulna is much shorter than humerus (Walker & Dyke 2009). The radius shaft appears to the wider proximally than at its distal end, a condition shared with *Iberomesornis* and *Enantiornis* (Sereno 2000; Walker & Dyke 2009).

Cratoavis nov. gen. manus is subequal to total ulnar length, whereas in *Hebeiornis* and *Eoalulavis* the manus is much shorter (see Sanz *et al.* 2002; Zhang *et al.* 2004).

Cratoavis nov. gen. shows a gracile and elongate carpometacarpus, whereas *Sinornis, Cathayornis, Houshanornis, Pengornis, Xiangornis,* and *Bohaiornis* show a very robust and wide metacarpal II (Sanz *et al*. 1995; Sereno *et al*. 2002; Zhou *et al*. 2008; Wang *et al*. 2010). Furthermore, *Gracilornis* differs in having strongly bowed metacarpal III (Li & Hou 2011).

The gracile coracoid of *Cratoavis* nov. gen. differs from the more robust and distally expanded coracoid present in *Bohaiornis, Shenqiornis, Sulcavis, Xiangornis, Eoalulavis, Enantiophoenyx* (Dalla Vecchia & Chiappe 2002; Wang *et al*. 2010; Hu *et al*. 2011; O´Connor *et al*. 2013), and from the splint-like coracoids of *Neuquenornis* (Chiappe & Calvo 1994) and *Gobipteryx* (Kurochkin 1996).

The femoral head is anterodorsally oriented, and a fovea capitis appears to be absent, in contrast to other enantiornithines (e.g., *Martinavis*; Walker & Dyke 2009).

The tarsometatarsus of *Cratoavis* nov. gen. is very gracile and metatarsals are strongly adpressed to each other. This morphology differs from the stouter tarsometatarsus of *Bahiornis, Liaoningornis, Alethoalaornis, Sulcavis, Houshanornis,* and *Gobipteryx* (Li *et al*. 2009; Wang *et al*. 2010; Hu *et al*. 2011; O´Connor 2012; O´Connor *et al*. 2013). *Qilania* exhibits an extremelly elongate tibiotarsus and tarsometatarsus, which differs from the morphology seen in *Cratoavis* nov. gen. (Ji *et al*. 2011).

Non-ungual phalanges 1-IV and 2-IV are relatively elongate and its combined length clearly surpasses the distal end of phalanx 1-III, whereas in *Iberomesornis* they do not surpasses such level (Sereno 2000). Non-ungual phalanges of pedal digit III are very narrow and extremelly elongate, being much longer than metatarsal III. In other Enantiornithes (e.g., *Iberomesornis*; Sereno 2000), with the exception of some Bohaiornithidae (Wang *et al.* 2014) the combined length of these phalanges is subequal or shorter than metatarsal III length.

Cratoavis nov. gen. shows short and robust cervical and dorsal vertebral centra, a condition similar to that of *Eoalulavis* (Sanz *et al*. 2002), which differs from the elongate centra present in *Sulcavis, Huoshanornis, Hebeiornis, Cathayornis,* and *Concornis* (Sanz *et al*. 1995; Zhang *et al*. 2004; O´Connor & Dyke 2010; Wang *et al*. 2010; O´Connor *et al*. 2013). *Cratoavis* nov. gen. shares with *Cathayornis*, *Eoalulavis* and *Sinornis* (Zhou & Hou 2002; Sanz *et al*. 2002; Sereno *et al.* 2002) presence of fan-shaped neural spines of dorsal vertebrae, being different from the rectangular contour seen in remianing enantiornithes.

Distal tail feathers are rather elongate, being 30% longer than total body length. Presence of a pair of elongate distal feathers have been reported for several birds, such as *Confusiusornis* (Chiappe *et al*. 1999) and in some Enantiornithes (e.g., *Protopteryx, Dapingfangornis, Bohaiornis*; Zhang & Zhou 2000; Li *et al*. 2006; Hu *et al*. 2011), but in known genera, the rectrices are proportionally much shorter than in *Cratoavis* nov. gen. No remains of hindlimb feathers are recognized in *Cratoavis* nov. gen., in contrast with other Enantiornithes, such as *Cathayornis* and other basal birds, in which they conform a wing-like structure (Zheng *et al*. 2012).

Carvalho *et al*. (2015) phylogenetic analysis resulted in an unresolved phylogenetic position for *Cratoavis* nov. gen., and thus, those authors were unable to find a close relative to *Cratoavis* nov. gen. However, it exhibits some similarities with a handfull of Enantiornithes that are worthy to mention. *Cratoavis* nov. gen. shares with *Pengornis* and *Eoenantiornis* the combination of a globose humeral head that projects further proximally than the deltopectoral crest, a poorly defined capital groove on proximal humerus, and short dorsal vertebral centra (Zhou *et al*. 2008; Wang *et al*. 2010). Presence of globose humeral head was also probably present in the poorly known genus *Xiangornis*. On the basis of the comparisons made above, we conclude that *Cratoavis* nov. gen. represents a valid genus of Enantiornithes, and can be diagnosed on the basis of a unique combination of characters.

CONCLUSIONS

Cratoavis cearensis nov. gen. et sp. constitutes the first named bird from the Mesozoic of Brazil and the Early Cretaceous of South America. It constitutes an important addition to the meager record of South American Cretaceous birds, and constitutes one of the more complete Mesozoic bird specimen from Gondwana. It also expands the list in which skeletal elements have been found in association with feathers, including long tail rectrices.

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