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A NEW ORNITHUROMORPH BIRD FROM THE LOWER CRETACEOUS OF SOUTH AMERICA

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ABSTRACT—The fossil record of Early Cretaceous birds in South America has been restricted to members of Enantiornithes from the Crato Formation (Aptian) of Brazil. Here we describe a new genus and species of bird discovered at Pedra Branca Mine, Nova Olinda County, Ceará State, Brazil, which adds to the avian fossil record from the Crato Formation. The specimen is represented by an isolated foot that is exposed in plantar view. A plantarly displaced metatarsal III with a well-developed hypotarsus supports its referral to Ornithuromorpha, representing the oldest member of the clade reported for Gondwana. Its unique foot conformation indicates that it may belong to an unknown ornithuromorph clade with some cursory similarities to extant flightless ratites. The presence of Early Cretaceous ornithuromorphs in Brazil indicates that the clade was widespread in Gondwana during the Mesozoic.

<http://zoobank.org/urn:lsid:zoobank.org:pub:08333BA3-F231-4E61-9E89-105C7478AE31>

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP.

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INTRODUCTION

As a result of some impressive finds from Lower Cretaceous deposits in China since the 1990s (Hou et al., 1996; Zhou, 2004; Zhang, 2006; Zhou and Zhang, 2007; Li et al., 2010; Chiappe and Meng, 2016; Wang, Cau et al., 2020), our knowledge of the early evolution and diversification of Mesozoic birds has improved considerably. The Lower Cretaceous Jehol and Changma biotas comprise an extraordinary taxonomic diversity of basal birds. Particularly, Jehol biotas include major Mesozoic clades such as Jeholornithiformes, Sapeornithiformes, Confuciusornithiformes, Enantiornithes and Ornithuromorpha (see summary in Chiappe and Meng, 2016; Mayr 2017). Beyond China, *Ambiortus dementievi* Kurochkin, 1982 is an ornithurine recovered from the Early Cretaceous in Mongolia (e.g., Kurochkin, 1982, 1985a, 1985b, 1988). Outside Asia, well-preserved Early Cretaceous birds are mostly represented by Enantiornithes known from a handful of sites, including Las Hoyas in

Spain and the Crato Formation in Brazil (e.g., Sanz and Lacasa, 1988; Sanz and Bonaparte, 1992; Sanz and Buscalioni, 1992; Sanz et al., 1996; Carvalho et al., 2015a, b). Ornithuromorpha is the clade that includes *Patagopteryx deferrariisi* Alvarenga and Bonaparte, 1992 and *Vorona berivotrensisi* Forster, Chiappe, Krause and Sampson, 1996, Ornithurae, and all birds phylogenetically nested in between (Chiappe, 1996). Stem group ornithuromorphs were reported in Early Cretaceous beds, but they are very rare in number of specimens when compared with Enantiornithes (Zhou and Hou, 2002). Moreover, the Early Cretaceous record of Ornithuromorpha outside Asia is restricted to a few isolated discoveries in Europe, belonging to the specialized clade of diving Hesperornithiformes (Seeley, 1876; Elzanowski and Galton, 1991; Galton and Martin, 2002). In sum, the knowledge of Early Cretaceous ornithuromorphs is almost restricted to Asia and had been, up to now, entirely absent from Gondwanan landmasses. This state of knowledge indicates that we remain largely uninformed about the phylogenetic, temporal, and paleoecological contexts of the early evolutionary history of Ornithuromorpha (You et al., 2006).

Here we describe an isolated bird foot from the Lower Cretaceous (Aptian) Crato Formation in Brazil. We refer the specimen to Ornithuromorpha, and because of its unique morphology, it may be regarded as a new genus and species.

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Geological Setting

The Araripe Basin contains one of the largest outcrop areas of Cretaceous rocks (12,200 km²) among the northeast intracratonic basins of Brazil. This basin formed in the Mesozoic, owing to a Neocomian tectonic event related to the Atlantic opening (Carvalho, 2000; Arai, 2014). The basin is filled with chemical and detrital deposits, and the lithostratigraphic subdivision of these rocks has been extensively reviewed (Beurlen, 1963, 1971; Machado Jr. et al., 1990; Ponte and Appi, 1990; Ponte, 1992; Mabesoone et al., 2000; Neumann and Cabrera, 2002; Neumann et al., 2002; Assine, 2007; Martill, 2007; Martill et al., 2007; Paula Freitas and Borghi, 2011; Rios-Netto et al., 2012; Assine et al., 2014).

The new bird specimen was found in the lower carbonate succession of upper Aptian age (Crato Formation) (Fig. 1), which comprises one of the most important fossil lagerstätten globally. Large numbers of invertebrate, vertebrate, and plant fossils from the Crato lagerstätte show exquisite soft tissue preservation (Martill et al., 2007; Barling et al., 2015; Maldanis et al., 2016; Carvalho et al., 2019; Agnolin et al., 2020; Dias and Carvalho,

2020; Scaramuzza dos Santos et al., 2020). Fossil birds from the Crato Formation are still scarce and represented by remains belonging to Enantiornithes, including *Cratoavis cearensis* Carvalho, Novas, Agnolin, Isasi, Freitas and Andrade 2015 (Carvalho et al., 2015a, b). Collectively, these materials allow important insights into the ecology and evolution of Gondwanan terrestrial ecosystems during the Early Cretaceous.

Some factors underlie the exquisite morphological fidelity of the Crato fossils. These are episodes of anoxia and hypersalinity of lacustrine hypolimnion, short-distance transport of biogenic remains, and short periods of flotation of the carcasses before they reached the substrate and were buried (Dias and Carvalho, 2020; Iniesto et al., 2020).

In the Crato Formation, the succession of micritic limestones with plane-parallel laminations implies protected environments with low benthic activity and gentle bottom currents (Iniesto et al., 2020). The absence of bioturbation associated with the presence of halite pseudomorphs indicates that the lake hypolimnion was possibly hypersaline and hostile for benthic metazoans (Dias and Carvalho, 2020), consistent with the Crato environment being a very shallow lake (Carvalho and Leonardi, 2020; Carvalho et al., 2021) with microbial communities adapted to this stressful environment (Heimhofer and Martill, 2007; Heimhofer et al., 2010; Araújo Jr. and Carvalho, 2015; Catto et al., 2016; Downen et al., 2016; Warren et al., 2017; Varejão et al., 2019). The microbial nature of these laminated limestones is further reinforced by the experiments of Iniesto et al. (2020) concerning the pattern of preservation and the presence of soft tissues in the fossils from the Crato Formation.

MATERIALS AND METHODS

Anatomical nomenclature primarily follows Baumel and Witmer (1993) using the English equivalents of most skeletal terms (see Wilson, 2006). Comparisons with other ornithuromorphs are based on existing literature.

Phylogenetic Analysis

To analyze the phylogenetic relationships of the new specimen among Avialae, we employed the dataset by Wang, O'Connor et al. (2020; see Supplemental Data). The original data matrix is composed by 280 characters and 72 taxa, to which we added the new species. The matrix was analyzed using TNT 1.5 (Goloboff and Catalano, 2016), with all characters equally weighted, and 35 characters treated as ordered. The dataset was analyzed under equally weighted parsimony. A total of 1,800,000 trees was set to be retained in memory. A first search using the algorithms Sectorial Searches, Ratchet (perturbation phase stopped after 20 substitutions) and Tree Fusing (5 rounds) was conducted, performing 1000 replications to find all tree islands (each replication starts from a new Wagner tree). The best tree or trees obtained at the end of the replicates were subjected to a final round of TBR (tree-branch-swapping) algorithm.

SYSTEMATIC PALEONTOLOGY

AVIALAE Gauthier, 1986
 ORNITHOTHORACES Chiappe and Calvo, 1994
 ORNITHUROMORPHA Chiappe, 2002
KARIRIAVIS MATER, gen. et sp. nov.
 (Figs. 2–4)

Holotype—Macrofossils Collection of Universidade Federal do Rio de Janeiro, Department of Geology (UFRJ-DG), code number UFRJ-DG 116 Av. Slab and counterslab including partial right pes, a nearly complete tarsometatarsus and several

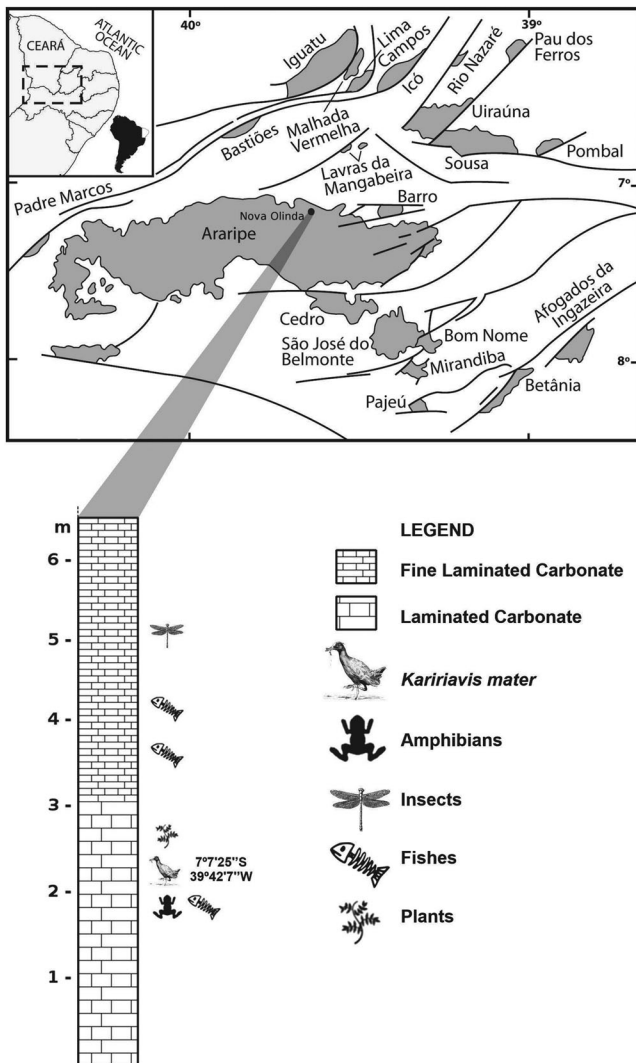


FIGURE 1. The locality (7°7'25"S, 39°42'7"W) and stratigraphic horizon that yielded the holotype specimen of *Kaririavis mater*, gen. et sp. nov. (UFRJ-DG 116 Av) from the Araripe Basin, northeast Brazil.

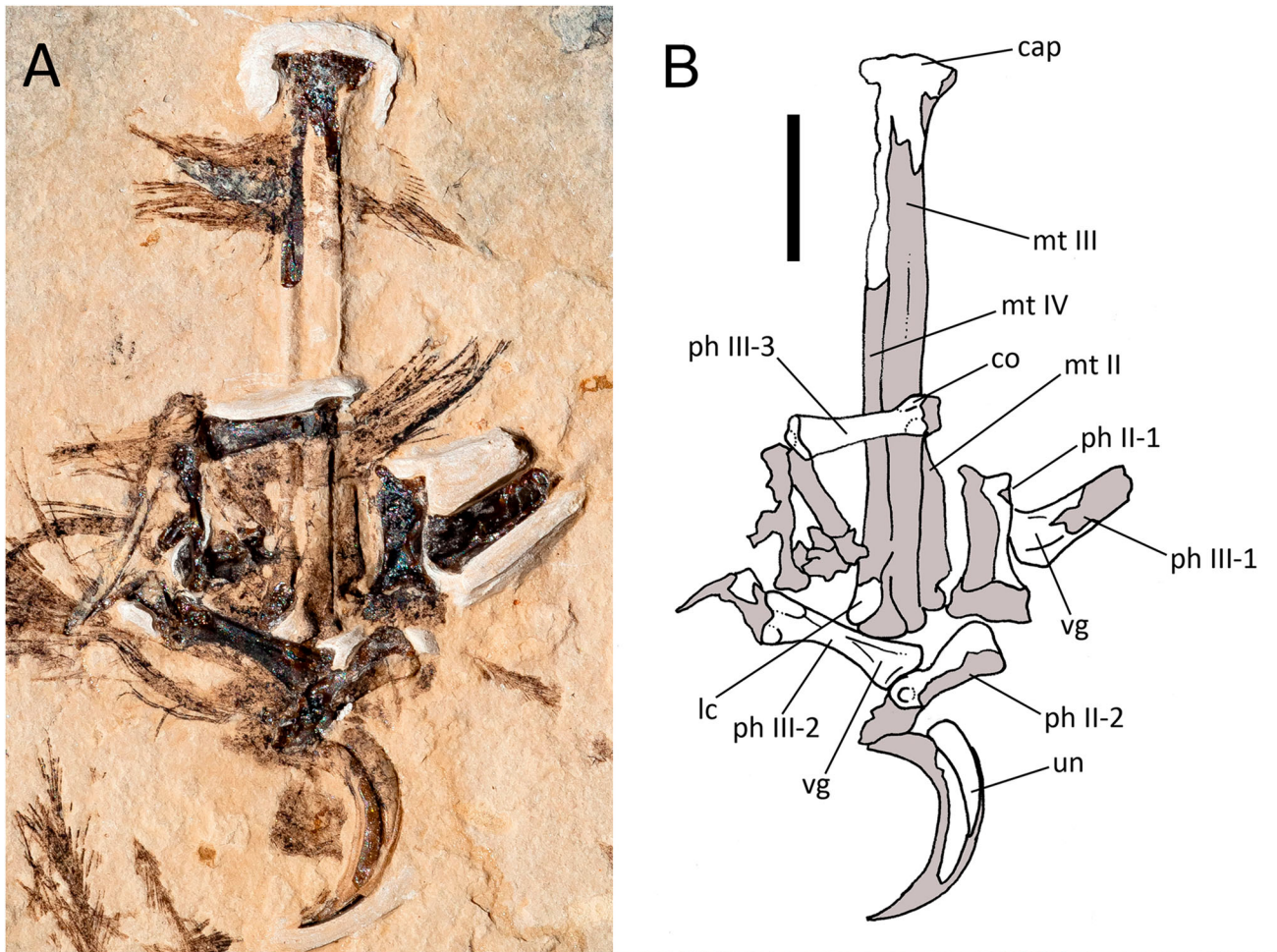


FIGURE 2. **A**, slab of the holotype of *Kaririavis mater*, gen. et sp. nov. (UFRJ-DG 116 Av) from the Lower Cretaceous Crato Formation in Brazil, right side in dorsal view. **B**, interpretative drawing. Broken areas shaded in gray. **Abbreviations:** cap, metatarsal cap; co, distal condyle of phalanx; lc, lateral condyle; mt, metatarsal; ph, phalanx; un, ungual phalanx of digit II; vg, ventral groove. Scale bar equals 5 mm.

apparently unconnected pedal phalanges, which are tentatively identified as follows: digit II phalanges 1 and 2; digit III phalanges 1 to 3; two indeterminate phalanges of digit IV; ungual phalanx of digit II (Figs. 2–4). At least 10 contour feathers are preserved in close association with the foot bones.

Etymology—The genus name is coined from Kariri, in reference to the Kariri people of northeastern Brazil, and avis, from the Latin ‘bird’; gender is feminine. The species epithet is derived from the Latin mater: ‘mother’, for being the oldest ornithuromorph from South America.

Locality and Horizon—The specimen reported herein comes from Pedra Branca Mine, Nova Olinda County, Ceará State, Brazil (7°7′25″S, 39°42′7″W; Fig. 1). The specimen was found in strata belonging to the Crato Formation, Lower Cretaceous (Aptian; Carvalho et al., 2019).

Diagnosis—*Kaririavis mater*, gen. et sp. nov. is a sparrow-sized bird displaying the following features that are characteristic for Ornithuromorpha: a plantarily displaced metatarsal III, and a well-developed hypotarsus. *Kaririavis mater* differs from Ornithurae in having metatarsal fusion restricted to proximal end, very shallow proximal intercotylar eminence, and distally open vascular foramen between metatarsals III and IV. *Kaririavis mater* is diagnosable on the basis of the following combination of characters (autapomorphies marked with an asterisk*) that

distinguishes it from other Cretaceous members of Ornithuromorpha: proximal end of metatarsal II not expanded and overlapped plantarily by metatarsal III, shaft of metatarsal II thinner than metatarsal IV, hypotarsus distally extended and forming a medio-laterally thick crest that extends distally beyond the mid-length of metatarsal III*, distal metatarsal III with a small lateral flange defining a vascular opening with metatarsal IV, trochlea of metatarsal III with prominent lateral condyle, and proportionally large ungual phalanx of digit II, representing 1/3 of the total length of the tarsometatarsus.

Measurements—Maximum proximodistal length of metatarsal II: 17.5 mm; maximum proximodistal length of metatarsal III: 19.6 mm; maximum proximodistal length of metatarsal IV: 18.3 mm; maximum proximodistal length of ungual phalanx: 6.6 mm.

Description

The tarsometatarsus is exposed in plantar view (Figs. 2 and 3). Metatarsals I and V are not preserved. The distal tarsals are fused to the metatarsals, forming a proximal tarsometatarsal cap. Proximally, the metatarsals are co-ossified, but they are distally free. The proximal cotylae are subequal-sized and separated from each other by a low intercotylar eminence.

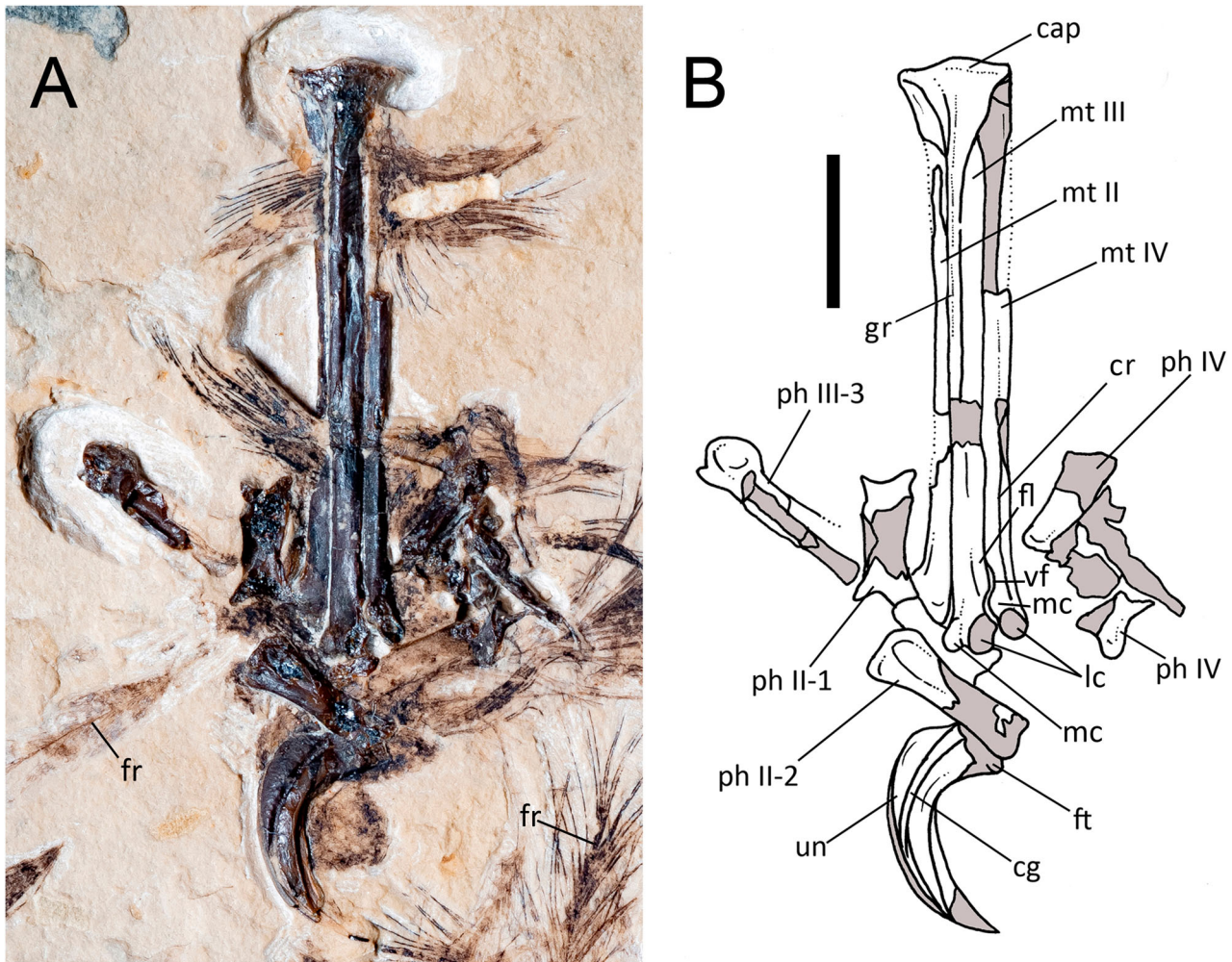


FIGURE 3. **A**, counterslab of the holotype of *Karirivavis mater*, gen. et sp. nov. (UFRJ-DG 116 Av) from the Lower Cretaceous Crato Formation in Brazil, right side in plantar view. **B**, interpretative drawing. Broken areas shaded in gray. **Abbreviations:** **cap**, metatarsal cap; **cg**, collateral groove; **cr**, plantar crest; **fl**, flange; **fr**, feather rachis; **ft**, flexor tubercle; **gr**, longitudinal groove of hypotarsus; **lc**, lateral condyle; **mc**, medial condyle; **mt**, metatarsal; **ph**, phalanx; **un**, ungual phalanx of digit II; **vf**, vascular foramen. Scale bar equals 5 mm.

The proximal end of metatarsal II is mediolaterally narrow and largely overlapped (plantarly) by metatarsal III. The shaft of metatarsal II is the narrowest of all metatarsals. The trochlea of the bone is mediolaterally expanded, being subequal in size to the trochlea of metatarsal III. The trochlea of metatarsal II is markedly medially angled and lacks a well-defined ginglymoid articulation. There is no sign of a scar for anchoring the metatarsal I (Fig. 2).

Metatarsal III is the largest element of the tarsometatarsus, being approximately two times wider than metatarsals II and IV. The trochlea is more distally placed than that of the other metatarsals. Despite being exposed only in plantar view, the metatarsal III appears to be plantarly displaced throughout its entire length with respect to metatarsals II and IV. It is plantarly exposed along all its length and shows sub-parallel lateral and medial margins of the shaft (Figs. 2 and 3).

The proximal end of metatarsal III is robust and mediolaterally expanded. It shows a well-developed and prominent hypotarsus, represented by a single crest (Fig. 3). The hypotarsus is sub-triangular in plantar view, with a distally oriented apex. Along its medial margin, metatarsal III shows a long plantar crest that extends from the hypotarsus down/distally

to the mid-length of the bone. This crest shows a well-defined hypotarsal groove on its proximal third. The shape of the hypotarsus in *Karirivavis mater* corresponds to the non-sulcate type of Mayr (2016). The longitudinal groove extending along the plantar crest probably corresponds to the passage of flexor digitorum longus. Near its distal end, the lateral margin of the bone forms a shallow concavity that is proximally delimited by a small flange of bone. This forms a gap with metatarsal IV, indicating the presence of a precursor of the vascular foramen, which is present in more derived birds (e.g., *Ichthyornis dispar*, *Patagopteryx deferrariisi*, *Struthio camelus*).

In spite of its poor preservation, the distal end of metatarsal III presents a well-defined and prominent trochlea with well-developed condyles, which are separated by a deep intercondylar groove. The condyles are relatively low and ovoid in contour, the lateral one being notably larger and more prominent than the medial one (Fig. 3).

Metatarsal IV is poorly preserved, and most of its proximal half is eroded. The preserved portion of the bone indicates that it was mediolaterally narrow proximally and that its proximal end was plantarly overlapped by the metatarsal III

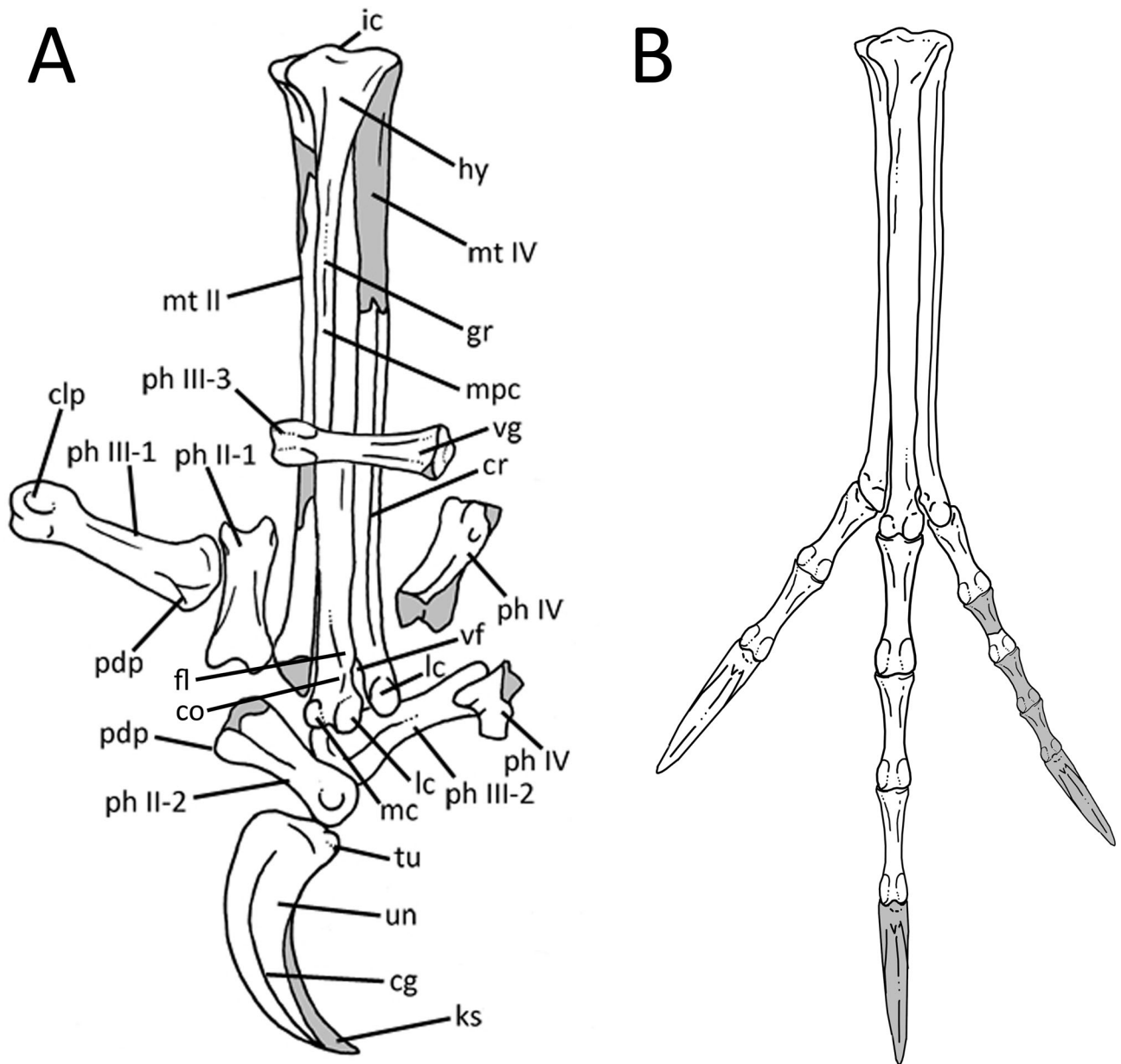


FIGURE 4. **A**, reconstruction of preserved remains of *Kaririavis mater*, gen. et sp. nov. from the Lower Cretaceous Crato Formation in Brazil, based on slab and counterslab of the holotype specimen (UFRJ-DG 116 Av). **B**, reconstruction of the foot of *Kaririavis mater* (not in scale); restored bones shaded in gray. **Abbreviations:** **cg**, collateral groove; **clp**, collateral ligamental pit; **co**, concavity; **cr**, plantar crest; **fl**, flange; **gr**, longitudinal groove of hypotarsus; **hy**, hypotarsus; **ic**, intercotylar eminence; **ks**, keratinous sheath; **lc**, lateral condyle; **mc**, medial condyle; **mpc**, medianoplantar crest; **mt**, metatarsal; **pdp**, posterodorsal process; **ph**, phalanx; **tu**, flexor tubercle; **un**, ungual phalanx of digit II; **vf**, distal vascular foramen; **vg**, ventral groove. Scale bar equals 5 mm.

(Fig. 3). Distally, metatarsal IV becomes thicker. Along its plantar surface, it shows a prominent and rounded plantar crest that reaches the proximal end of the distal metatarsal trochlea. The trochlea is not well-preserved. However, it shows strongly asymmetrical condyles, with the lateral one being larger and more distally extended than the medial one. An intercondylar groove seems absent, suggesting that the metatarsal IV lacks a distal ginglymoid articulation (Fig. 3).

The phalanges are mixed up and not well preserved, and most anatomical features are difficult to interpret. All elements show

well-developed distal ginglymoidal articulations with prominent distal condyles separated by well-defined intercondylar grooves. Collateral ligament pits are deep, ellipsoidal in contour, and dorsally displaced. Extensor fossae located proximal to the trochleae are well-defined and relatively deep. The proximodorsal and proximoventral processes are thick, but not prominent.

Because of the lack of a clear articular sequence and poor preservation of each pedal element, we offer only a tentative identification of the phalanges (Figs. 2–4). Foot phalanges of digit II are the largest. Phalanx II-1 is notably shorter than

RESULTS

Phylogenetic Position and Comparisons of *Kaririavis mater*

II-2. Ungual phalanx II-3 is robust and relatively large, representing 1/3 of the total tarsometatarsus length. Its ventral margin is strongly curved, showing a prominent and well-defined flexor tubercle. A keratinous sheet covers the unguial phalanx, increasing the ventral curvature and extending the claw by about 25%.

Non-ungual phalanges of digit III are notably narrow and elongate, with well-defined distal articular surfaces. Phalanx III-1 is notably stouter and longer than phalanx III-3, which is the smallest of the preserved elements of the foot. The phalanges display a ventral longitudinal groove, but this may be the result of a preservation artifact. Two very incompletely preserved phalanges of digit IV are present. They are shorter than phalanges from other digits and show relatively large distal articular trochleae (Figs. 2–4).

Some feathers were found close to the foot of *Kaririavis mater* (Figs. 2 and 3). Despite them being dissociated from the specimen, they were close enough to the remains, so we believe they probably belonged to this individual. The specimens present the typical aspect of plumulaceous feathers, classified as downy feathers (see Sayão et al., 2011; Prado et al., 2016). The feathers present a dark brownish color but are not very well preserved. The proximal portion of the feathers is eroded, but the rachis is visible in some specimens. Barbs and barbules are present. The barbs are elongate, and although the feathers are not complete, some of them appear to be longer than the corresponding rachis.

The phylogenetic analysis performed including *Kaririavis* resulted in the recovery of 15 most parsimonious trees (MPTs) of 1,247 steps, with a consistency index of 0.310, and a retention index of 0.654, which were summarized using a strict consensus tree (Fig. 5). *Kaririavis mater* is referred to the Ornithuromorpha on the basis of the presence of a plantarly displaced metatarsal III, and of a well-developed hypotarsus (Kurochkin, 2000; Clarke and Norell, 2002; Clarke et al., 2006; O'Connor et al., 2010; Zelenkov, 2017; Fig. 5). Further, metatarsal IV is more distally projected than the proximal margin of the trochlea of metatarsal III, which is a derived feature shared by species of *Gansus* and Ornithurae (Liu et al., 2014). These characters suggest that *K. mater* belongs to Ornithuromorpha. However, the phylogenetic position of *K. mater* among ornithuromorphs remains uncertain because of its unique combination of derived and plesiomorphic features and the incomplete nature of its holotype.

Kaririavis mater shows several plesiomorphic features that are not present in other members of Ornithuromorpha: in *K. mater*, the fusion of metatarsals is restricted to its proximal end, a condition shared with confuciusornithids, Enantiornithes and basal ornithuromorphs (e.g., *Archaeorhynchus spathula* Zhou and Zhang, 2006, *Schizooura lii* Zhou, Zhou, and O'Connor, 2012, *Mengciusornis dentatus* Wang, Cau, Kundrát, Chiappe, Ji, Wang, Li and Wu, 2020, *Zhongjianornis yangi* Zhou, Zhang and Li, 2010; Chiappe, 1996; Chiappe et al., 1999; Zhou and

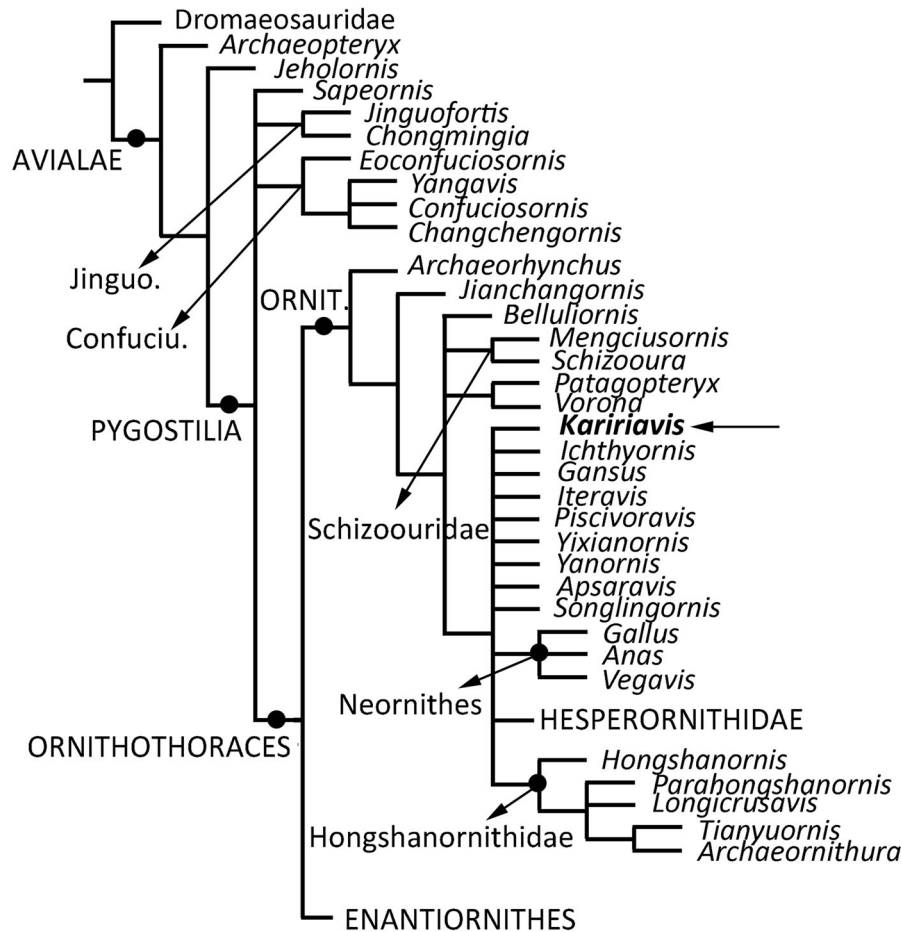


FIGURE 5. Strict consensus tree showing the phylogenetic position of *Kaririavis mater*, gen. et sp. nov. (UFRJ-DG 116 Av) among avialans. Data matrix taken from Wang, O'Connor et al. (2020; see Supplemental Data). **Abbreviations:** **Confuciu.**, Confuciosornithidae; **Jinguo.**, Jinguoformitidae; **ORNIT.**, Ornithuromorpha.

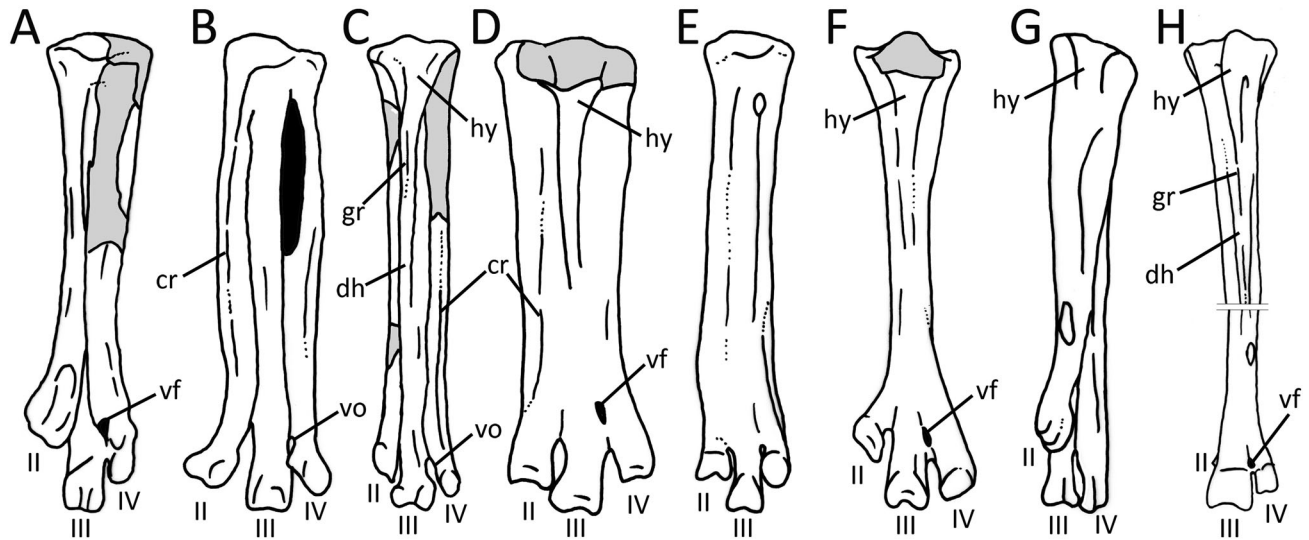


FIGURE 6. Comparisons of right tarsometatarsi of selected birds in plantar view. **A**, *Evgenavis nobilis* (Confuciusornithidae), redrawn from O'Connor et al. (2014); **B**, *Soroavisaurus australis* (Enantiornithes), redrawn from Chiappe (1993); **C**, *Kaririavis mater*, gen. et sp. nov.; **D**, *Patagopteryx deferrariisi*, redrawn from Chiappe (2002); **E**, *Vorona berivotrensis*, redrawn from Forster et al. (2002); **F**, *Ichthyornis dispar*, redrawn from Clarke (2004); **G**, *Fumicollis hoffmani* (Hesperornithidae), redrawn from Bell and Chiappe (2015); **H**, *Struthio camelus* (Paleognathae). **Abbreviations:** **cr**, plantar crest; **dh**, distal extension of the hypotarsus; **gr**, longitudinal groove on the hypotarsus; **hy**, hypotarsus; **vf**, vascular foramen; **vo**, vascular opening. Not to scale.

Zhang, 2006; Zhou and Li, 2010; Zhou et al., 2012; Wang, O'Connor et al., 2020).

Kaririavis mater displays other plesiomorphic traits, such as a proximal intercotylar eminence represented by a small swelling, a condition shared with Enantiornithes and basal ornithuromorphs such as *Yixianornis grabaui* Zhou and Zhang, 2001, *Apsaravis ukhaana* Norell and Clarke, 2001, and *Patagopteryx deferrariisi* Alvarenga and Bonaparte, 1992 (Clarke et al., 2006) (Fig. 6). Further, *K. mater* shows a distally open vascular foramen between metatarsals III and IV, similar to the condition exhibited by some Enantiornithes, such as *Yungavolucris brevipedalis* Chiappe, 1993, *Avisaurus archibaldi* Brett-Surman and Paul, 1985, and *Soroavisaurus australis* Chiappe, 1993 (O'Connor and Forster, 2010), whereas in most ornithuromorphs the foramen is totally enclosed by bone (Chiappe, 1996; Bell et al., 2010; Fig. 6).

In addition to the aforementioned plesiomorphic features, *K. mater* also shares with Enantiornithes a proportionally narrow shaft and small trochlea of metatarsal IV (also shared with confuciusornithids and the basal ornithuromorph *Khinganornis hulunbuirensis* Wang, Cau, Kunderát, Chiappe, Ji, Wang, Li and Wu, 2020; O'Connor et al., 2014), distally expanded metatarsal II trochlea with respect to metatarsal shaft (in *K. mater* this trochlea is smaller than that of metatarsal III, whereas in most Enantiornithes and confuciusornithids the trochlea of metatarsal II is wider than that of metatarsal III; Sereno, 2000; O'Connor et al., 2014), and proportionally large unequal phalanges (Chiappe and Calvo, 1994; Sereno, 2000; Zhang et al., 2001; Wang et al., 2014; Fig. 6).

In *K. mater* as in Enantiornithes, *Mystriornis cyrili* Kurochkin et al., 2011 and confuciusornithids, the metatarsal II trochlea is mediolaterally expanded and dorsoplantarily compressed and is notably medially angled (also present in confuciusornithids and the ornithuromorph *Schizooura lii*; Sereno, 2000; O'Connor et al., 2014; Wang, O'Connor et al., 2020).

In spite of a number of enantiornithine features, *K. mater* differs from Enantiornithes (including *Cratoavis cearensis*, which was found in roughly coeval beds; Carvalho et al.,

2015a, b) in having a plantarily displaced metatarsal III. In Enantiornithes such as *Yungavolucris brevipedalis*, *Avisaurus archibaldi*, *Soroavisaurus australis*, and *Gobipteryx minuta* Elzanowski, 1974, as well as some basal ornithuromorphs such as *Patagopteryx deferrariisi*, *Archaeorhynchus spathula*, *Bellulornis rectusunguis* Wang, Zhou, and Zhou, 2016 and *Vorona berivotrensis*, the metatarsals are coplanar (Brett-Surman and Paul, 1985; Elzanowski, 1995; Chiappe, 1996, 2002; Forster et al., 1996, 2002; Wang, Zhou et al., 2016). In *K. mater* there is a slender shaft of metatarsal II, being subequal to slightly narrower to metatarsal IV, features that are widespread among non-enantiornithine basal birds. On the contrary, in Enantiornithes (including *Cratoavis cearensis*), metatarsal II is relatively stout, especially at its proximal end, where it overlaps with metatarsal III (Chiappe, 1993). The enantiornithine *Lectavis bretincola* Chiappe, 1993 has a well-developed plantar projection that may be similar to a hypotarsus, though unlikely homologous, because it is present on metatarsal II. In *Lectavis bretincola*, as occurs in all Enantiornithes, the proximal end of metatarsal II is wider than metatarsal III and proximally overlaps it. This condition is very different from ornithuromorphs, including *K. mater* (Fig. 6).

Notably, the absence of entire fusion of metatarsals present in *K. mater* is considered typical of the basal ornithuromorph clade Schizoouridae (the clade including *Schizooura lii* and *Mengciusornis dentatus*; Wang, O'Connor et al., 2020). Further, *K. mater* resembles *Mengciusornis dentatus* and *Schizooura lii* in that metatarsal III is the longest and most robust of the foot, followed by metatarsal IV, and the distal vascular foramen is not enclosed by bone (Wang, O'Connor et al., 2020). However, *K. mater* differs from Schizoouridae in having a plantarily displaced metatarsal III, instead of the coplanar condition of metatarsus in Schizoouridae (Wang, O'Connor et al., 2020), in having a low and mound-like hypotarsus (forming a well-defined calcaneal crest in *Mengciusornis dentatus*), a more distally extended metatarsal II trochlea (Wang, O'Connor et al., 2020), and in the absence of proximal vascular foramina (present in

Mengciusornis dentatus; Wang, O'Connor et al., 2020), among other anatomical details.

In plantar view, the tarsometatarsus of *K. mater* is not excavated, as in other taxa such as confuciusornithids, Enantiornithes and basal ornithuromorphs (e.g., *Mystiornis cyrili*, *Vorona berivotrensis*, *Patagopteryx deferrariisi*, *Belluliornis rectusunguis*, *Jianchangornis microdonta*, *Schizooura lii*, *Yixianornis grabaui*, *Hongshanornis longicresta* Zhou and Zhang, 2005; Forster et al., 2002; Zhou et al., 2009, 2012; O'Connor et al., 2014; Wang, Zhou et al., 2016) where the plantar surface of metatarsal III is flat or gently concave and limited by the medial and lateral plantar crests of metatarsal II and IV, respectively (Fig. 6). This depression must have been the area of insertion of several digital muscles, as well as of tendons of flexor digital musculature (Chiappe, 2002). This contrasts with that observed in *K. mater* and most of the remaining ornithuromorphs, in which the proximal end of metatarsal III is plantarly displaced with respect to that of metatarsals II and IV (Chiappe, 2002; Clarke and Norell, 2002; Clarke et al., 2006; Zhou et al., 2014).

Having a plantarly displaced metatarsal III that is notably wide and stout and showing a nearly uniform shaft that is exposed along the metatarsal length are characters that appear unique to *K. mater*. In fact, almost all birds including Enantiornithes and ornithuromorphs (except for some spheniscids) have a metatarsal III that is proximally pinched and hidden behind metatarsals II and/or IV (Brett-Surman and Paul, 1985). However, this condition is somewhat reminiscent to that present in extant ratites and *Palaeotis weigelti* Lambrecht, 1928, which have a relatively robust hypotarsus on metatarsal III, ending on a notably wide trochlea (Mayr, 2019). However, in ratites, in contrast to *K. mater*, the metatarsal III displaces dorsally near the distal end of the tarsometatarsus (Gilbert et al., 2016).

A similar condition of metatarsal III is present in the basal ornithuromorph *Hollanda luceria* Bell, Chiappe, Erikson, Suzuki, Watabe, Barsbold, and Tsogbaatar 2010, and probably *Khinganornis hulunbuiensis* (see Wang, Cau et al., 2020). However, *K. mater* differs from both genera in lacking entire fusion of distal metatarsals, and particularly from *Hollanda luceria*, in retaining an open distal vascular foramen, a low proximal intercotylar eminence, a mediolaterally wider distal metatarsal II trochlea, and a much stouter tarsometatarsus (Bell et al., 2010). *Kaririavis mater* also differs from *Khinganornis hulunbuiensis* in lacking the laterally sloped tarsometatarsus (Wang, Cau et al., 2020). In spite of the common presence of an entirely exposed plantar surface of metatarsal III, the condition of *K. mater* is very different: it shows a mediolaterally thicker metatarsal III that is widely exposed in plantar view and that becomes mediolaterally wide proximally. This condition is unique to *K. mater*.

In *K. mater* the hypotarsus is morphologically simple. It lacks proximal vascular foramina, unlike crownward ornithuromorphs, such as hongshanornithids, *Patagopteryx deferrariisi*, *Gansus yumenensis*, *Iteravis huchzermeyeri*, *Hollanda luceria*, and ornithurines (Bell et al., 2010; O'Connor et al., 2010; Zhou et al., 2014; M. Wang et al., 2015), in which the vascular foramina are well defined.

In *K. mater* the hypotarsus is mediolaterally stout and rounded, and does not form tendinal canals, or calcaneal crests as in modern birds, resembling in this aspect other basal ornithuromorphs such as *Patagopteryx deferrariisi*, *Apsaravis ukhaana* Clarke and Norell, 2002 and hesperornithids (Chiappe, 1996, 2002; Clarke and Norell, 2002; Bell and Everhart, 2009; Bell et al., 2015), whereas more basal ornithuromorphs lack signs of a hypotarsus (e.g., *Archaeorhynchus spathula*, *Schizooura lii*, *Vorona berivotrensis*, and *Hollanda luceria*; Forster et al., 1996; 2002; Zhou and Zhang, 2006; Bell et al., 2010; Kurochkin et al., 2011).

K. mater exhibits a simple-shaped hypotarsus that grades distally into a long plantar crest that shows a longitudinal groove, a condition shared with extant ratites as *Struthio*, *Rhea* and *Casuaris* (Cracraft, 1974; Gilbert et al., 2016; Mayr, 2019). This contrasts with the more complex condition of basal neornithines, which show well-developed hypotarsal crests, grooves and canals (e.g., *Vegavis*, Clarke et al., 2006; Mayr, 2019) and the proximodistally short hypotarsus present in most basal ornithuromorphs (e.g., *Mengciusornis dentatus*, *Gansus yumenensis*, *Iteravis huchzermeyeri* Zhou, ÓConnor, and Wang, 2014, *Ichthyornis dispar* Marsh, 1872, *Hesperornis regalis* Marsh, 1972; Chiappe, 2002; Galton and Martin, 2002; Clarke, 2004; Zhou et al., 2014; Wang, ÓConnor et al., 2016). The shape of the hypotarsus in *K. mater* corresponds to the non-sulcate type of Mayr (2016). Its long plantar crest shows a longitudinal groove along its plantar margin that in all probability corresponds to the passage of flexor digitorum longus, as occurs in paleognathous birds such as ratites and lithornithiforms (Houde, 1988).

DISCUSSION

Foot Morphology of *Kaririavis mater* and its Paleocological Implications

Although *K. mater* is represented by an isolated foot, some anatomical features may be indicative of its habits and ecological adaptations. *Kaririavis mater* lacks most features often present in many modern aquatic and semiaquatic birds, including elongate and gracile toes, a laterally compressed distal tarsometatarsus and a highly recessed trochlea II (You et al., 2006).

The unique foot morphology of *K. mater* does not match the pattern observed in other basal birds. As indicated above, it lacks a well-developed medial plantar longitudinal crest and plantar projection of the medial trochlea of metatarsal II. These act as medial barriers for muscle tendons, preventing them from slipping away from the digit when the toes are strongly flexed, or allow for the splaying of the digits in the case of raptorial birds (Zelenkov and Dyke, 2008). Further, there are no deep grooves or fossae proximal to the trochleae of the phalanges of digits II and IV for the anchoring of flexor and extensor tendons and musculature, which is the usual condition among perching birds (O'Connor et al., 2014).

In birds, the hypotarsus guides the tendons of the pedal flexor muscles and its morphology therefore shows some correlation with the use and arrangement of the toes. As indicated by Mayr (2016), predominantly terrestrial birds, such as lithornithids and most ratites, have a simple hypotarsus, similar to that of *K. mater*. In these taxa, the hypotarsus is represented by an embossment and a shallow groove for the deep plantar tendon of the flexor digitorum longus, suggesting similar foot function. On the other hand, complex hypotarsal morphology is restricted to neognathous birds with remarkable swimming or grasping capabilities (Mayr, 2016).

In addition, the ankle extensors of living birds are proportionately larger than in other reptiles, pass over a tibial cartilage, and are united as an 'Achilles' tendon' (the tendon of musculus gastrocnemius), inserting onto the hypotarsus (Hutchinson, 2002). Thus, the presence of a hypotarsus in *K. mater* may imply the correlated presence of a tibial cartilage and a neornithine-like 'Achilles' tendon'.

In *K. mater* the only available unguis phalanx (presumably corresponding to digit II) is proportionately stout and distally hooked, with relatively large flexor tubercles (in Enantiornithes, well-developed flexor tubercles are not present; e.g., Chiappe, 1993; Chiappe and Calvo, 1994; Kurochkin, 1995; Sanz et al., 2002; Carvalho et al., 2015a, b). The unguis morphology of

K. mater strongly differs from that of other Early Cretaceous ornithuromorphs (e.g., *Archaeorhynchus spathula*, *Gansus yumenensis*, Songlingornithidae, Hongshanornithidae, Schizouridae; Hou and Liu, 1984; Hou, 1997; You et al., 2006; Zhou and Zhang, 2006; O'Connor et al., 2010), which show small and dorsoplantarly short ungual phalanges. These features could imply a distinct ecological niche for *K. mater* contrasting with most Early Cretaceous ornithuromorph birds, which are interpreted as semiaquatic in habit.

In extant birds, the height of the flexor tubercle is hypothesized to be correlated to the tension needed to grip with more prominent tubercles. In cursorial birds, a flat tubercle could be advantageous, as it limits friction with the ground (Livezey and Zusi, 2006). Significantly, the presence of large flexor tubercles on *K. mater*'s foot is incongruent with the terrestrial habits that may be inferred from its metatarsal shape.

In sum, *K. mater* shows a combination of foot features that precludes a clear knowledge about its habits and the paleoecological niche that it occupied. However, the morphology of its tarsometatarsus is strongly suggestive of terrestrial habits for *K. mater*.

Paleobiogeographic Implications

The oldest record of Ornithuromorpha occurs in the middle Lower Cretaceous (Hauterivian-Barremian) in China (Wang et al., 2015) and roughly coeval beds in Mongolia (O'Connor and Zelenkov, 2013). In contrast, several ornithuromorphs, representing different lineages are recorded in early Aptian Jehol deposits (see Zhou et al., 2003; O'Connor et al., 2011; Wang et al., 2015, 2020). Recent findings of basal ornithuromorph from coeval beds in Inner Mongolia imply an extended paleogeographic range for the early diversification of Mesozoic birds in eastern Asia (Wang, O'Connor et al., 2020).

The discovery of diverse basal ornithuromorphs in the Jehol Biota, together with records of members of this clade mostly from the early Late Cretaceous of Europe, prompted the hypothesis that the center of origin and diversification of the clade was Eurasia, most probably East Asia (Zhou and Zhang, 2007; Zelenkov et al., 2017).

The present report of the basal ornithuromorph *Kaririavis mater* in Aptian beds in Brazil considerably expands the paleobiogeographic distribution of this clade. In fact, *K. mater* constitutes one of the oldest worldwide occurrences for Ornithuromorpha, as well as the first from Gondwana, with an age close to those species from China. As we have already noted (Carvalho et al., 2015b), "Jehol birds" were probably not unique to China and Mongolia, but more geographically widespread. In this sense, *K. mater* reinforces the idea that "Jehol Birds" are probably not unique to eastern Asia, but represent an example of a biota coming from a series of lagerstätte, serendipitously first found in Asia, which displays multiple sites of extraordinary fossil preservation (Zhou et al., 2003, Zhou, 2006). Despite our limited knowledge of Early Cretaceous birds, it is notable that *K. mater* exhibits a morphology that is very different from the Early Cretaceous Asian avifaunas, with a large hypotarsus and other distinctive anatomical features. This may be the result of biogeographic differences between these bird assemblages. Therefore, *K. mater* represents another indication that the phylogenetic diversity of the Mesozoic Gondwanan avifauna is likely far greater than has been sampled thus far (Fig. 6).

CONCLUSION

We describe *Kaririavis mater*, gen. et sp. nov., the first occurrence of an ornithuromorph bird from the Early Cretaceous in South America. This taxon bears a unique combination of plesiomorphic (e.g., tarsometatarsus distally unfused; proportionally

small trochlea IV; and proportionally strong proximal and ungual phalanges) and derived features (e.g., plantarly located metatarsal III; well-developed hypotarsus). *Kaririavis mater* shows several unique features including a notably robust and well-exposed metatarsal III, large and strongly hooked claws and small body size. These traits contrast with most Early Cretaceous ornithuromorph birds, which are interpreted as semiaquatic in habits. The finding of *K. mater* in South America demonstrates that basal ornithuromorph birds were present and probably diversified by Aptian times in the southern hemisphere.

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