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An *Elaphrocnemus*-like landbird and other avian remains from the late Paleocene of Brazil

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We describe a new avian taxon, *Itaboravis elaphrocnemoides*, gen. et sp. nov., from the late Paleocene fissure fillings of São José de Itaboraí in Brazil. The species is represented by a coracoid and two humeri, which most closely resemble the corresponding elements of the taxon *Elaphrocnemus*, a proposed stem group representative of the Cariamae from the late Eocene and Oligocene of the Quercy fissure fillings in France. *I. elaphrocnemoides* is only the second species of small landbird known from the Paleocene of the Southern Hemisphere. It is tentatively classified in the Cariamae, but we also note morphological similarities of the humerus to that of the palaeognathous Tinamidae. We further describe a carpometacarpus, which exhibits a peculiar morphology not found in any other avian taxon. This bone also shares some features with tinamous and is of a size corresponding to that of *I. elaphrocnemoides*, but cannot be referred to this taxon with confidence. We finally report four morphologically different distal tibiotarsi, one of which may belong to *Eutreptodactylus itaboraiensis*, the only other small bird described from Itaboraí.

Key words: Aves, Cariamae, Tinamidae, *Itaboravis elaphrocnemoides* gen. et sp. nov., Paleocene, Itaboraí, Brazil.

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Introduction

Paleocene avian remains in general are very rare, and this is particularly true for the Southern Hemisphere (Mayr 2007, 2009). The few deposits that have yielded bird remains from this time are widely distributed geographically across Antarctica, South America, northern Africa, and New Zealand. However, the fossils recovered from these localities belong primarily to large cursorial (e.g., ratites and phorusrhacids) or aquatic taxa (e.g., penguins, pelagornithids, and prophaethontids; Mayr 2009). Small terrestrial birds have only been discovered in the late Paleocene fissure fillings of São José de Itaboraí near Rio de Janeiro in southeast Brazil.

The now abandoned and largely inaccessible limestone quarries of this locality have yielded a diverse mammalian fauna from early late Paleocene fissure fillings (about 57–59 million years ago; e.g., Paula-Couto 1952a, b; Ladevèze 2004; Sant'Anna et al. 2004). Bird remains are rare and only three avian species have been described so far, namely the ratite *Diogenornis fragilis* (Alvarenga 1983), the phorusrhacid *Paleopsilopterus itaboraiensis* (Alvarenga 1985), and the tiny (semi-) zygodactyl *Eutreptodactylus itaboraiensis* (Baird and Vickers-Rich 1997), whose phylogenetic affinities are uncertain (Mayr 2009).

The collection of Museu Nacional da Universidade Federal do Rio de Janeiro contains the holotypes of *P. itaboraiensis* and *E. itaboraiensis* (the latter is now lost), as well as other previously undescribed avian specimens from Itaboraí. Although this material mainly consists of fragmentary limb bones, it also includes a well-preserved, nearly complete coracoid and humerus of a small bird, which were collected together. These elements, briefly mentioned by Mourer-Chauviré (1999: 87), are here identified as belonging to a new species, which shares features with *Elaphrocnemus*, a taxon known from abundant late Eocene and Oligocene remains from Europe that is considered related to the extant South American Cariamidae (Mourer-Chauviré 1983), as a stem group representative of Cariamae (sensu Mayr 2009). This new taxon and additional bird material from the site are described, and these new data are brought to bear on our understanding of South American Paleocene diversity.

Osteological terminology follows Baumel and Witmer (1993). Measurements are in millimetres.

Institutional abbreviations.—MN, Museu Nacional da Universidade Federal do Rio de Janeiro, Brasil; NMB, Naturhistorisches Museum Basel, Switzerland; SMF, Forschungsinstitut Senckenberg, Frankfurt am Main, Germany.

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Systematic palaeontology

Aves Linnaeus, 1758

?Cariamae (sensu Mayr 2009)

Itaboravis elaphrocnemoides, gen. et sp. nov.

Fig. 1A, G, H.

Etymology: The genus name is from the type locality and Latin *avis*, bird. The species epithet references similarities with the taxon *Elaphrocnemus* (see description below).

Holotype: MN 4114-V (left coracoid; Fig. 1A).

Type locality and horizon: São José de Itaboraí, Rio de Janeiro, southeastern Brazil; early late Paleocene, Itaboraian.

Diagnosis.—The new species is diagnosed by a unique combination of four characters preserved in the holotype specimen: (i) coracoid slender and elongate, with (ii) a markedly concave dorsal surface of extremitas sternalis and (iii) a large dorsal opening to a foramen nervi supracoracoidei that is situated subadjacent to (iv) a slightly convex facies articularis scapularis. That the foramen nervi supracoracoidei both penetrates the coracoid and has an additional, possibly pneumatic, opening into its main body is a proposed autapomorphy of the new taxon. Additional features from the referred humerus with restricted distributions in Aves that characterize the new species include: an indistinct fossa pneumotricipitalis, sulcus scapulotricipitalis, and fossa musculi brachialis of the humerus, a ventrally-facing foramen pneumaticum and sulcus transversus, and a weakly developed crista deltopectoralis.

Referred specimens.—MN 4113-V (right humerus; Fig. 1G); MN 4121-V (distal end of left humerus; Fig. 1H).

Measurements.—Coracoid (holotype), length, 28.8. Humerus (MN 4113-V), length, 46.3; proximal width, 11.6; distal width, 9.4. Humerus (MN 4121-V), distal width, 9.7.

Remarks.—According to private information from the late Fausto Cunha (a former palaeontologist of MN) to one of the authors (HA, personal communication 1985), specimens MN 4113-V and MN 4114-V stem from the same block of calcareous matrix of about 1.4 kg weight, which also yielded a large number of small non-avian bones. Both bones have the same colouration, match in size, and resemble the corresponding elements of *Elaphrocnemus*. We thus consider it likely that they belong to the same individual (see Alvarenga 1983, 1985 for other associated avian bones from Itaboraí).

Description and comparisons.—The coracoid, from a small bird about the size of *Crypturellus tataupa* (Tinamidae), most closely resembles that of *Elaphrocnemus* (Fig. 1B), from which it is mainly distinguished by a proportionally smaller extremitas omalis and the presence of a large foramen nervi supracoracoidei; this foramen is absent in *E. phasianus* and small in *E. crex* (Mourer-Chauviré 1983). It is an elongate bone with a slender shaft. The dorsoventrally flat processus acrocoracoideus lacks pneumatic openings. The facies articularis clavicularis does not overhang the sulcus supracoracoideus, which exhibits a shallow, ovate fossa in its dorsal section. By contrast, in *Elaphrocnemus* the facies articularis clavicularis forms a small lip that overhangs the sulcus supracoracoideus. The facies articularis scapularis is slightly convex and merges into the facies articularis humeralis. A processus procoracoideus is absent. The foramen nervi supracoracoidei penetrates the main body of the coracoid, and the portion between the two openings forms a narrow strut. Its ventral opening is large, ovate and situated close to the facies articularis scapularis. Most notably, this foramen also opens into the interior of the bone. It thus seems to have also served as an opening for a pneumatic diverticulum of the air-sac system as in Tinamidae (see discussion). As in *Elaphrocnemus*, the dorsal surface of the extremitas sternalis is markedly concave. The crista articularis sternalis is dorsoventrally narrow, and the medial margin of the extremitas sternalis bears a small flange. The processus lateralis is broken.

The humerus is similar to the corresponding bone of *Elaphrocnemus* (Fig. 1I), but differs in the very low crista deltopectoralis (large and triangular in *Elaphrocnemus*) and the very shallow and faint fossa musculi brachialis (distinct in *Elaphrocnemus*). In these two features the element more closely resembles Tinamidae (e.g., Fig. 1J). Instead of running along the cranial surface of the bone, the sulcus transversus is situated on its ventral side, as in *Elaphrocnemus* and extant Cariamidae as well as few other taxa such as Tinamidae (Fig. 1J). There is no fossa pneumotricipitalis, and the ventral surface of the proximal end, which bears the small foramen pneumaticum, is flat. The crista bicipitalis is weakly developed with little ventral projection; at its distal tip there is a distinct fovea for insertion of musculus scapulohumeralis caudalis. The intumescentia humeri is not raised but flat throughout. The caput humeri is very weakly projected proximally and only slightly caudally deflected. The tuberculum ventrale bears a distinct depression for insertion of musculus coracobrachialis caudalis. The shaft of the bone is only slightly curved craniocaudally. As in *Elaphrocnemus*, as well as Tinamidae and the non-neornithine Mesozoic *Ichthyornis*, a sulcus scapulotricipitalis is virtually absent. The processus flexorius is well developed and reaches distally beyond the condylus ventralis. Unlike the condition in *Elaphrocnemus*, there is no well-developed tuberculum supracondylare dorsale. The condylus dorsalis is slightly narrower and the condylus ventralis more weakly developed and elongate than in *Elaphrocnemus*. On the ventral surface of the distal end the two depressions for insertion of musculus pronator profundus and ligamentum humerocarpale (Ballmann 1969; Meyers 1996) are rather indistinct.

Stratigraphic and geographic range.—Type locality and horizon only.

Aves indet. A

Fig. 1D.

Material.—MN 4115-V (right carpometacarpus; Fig. 1D)

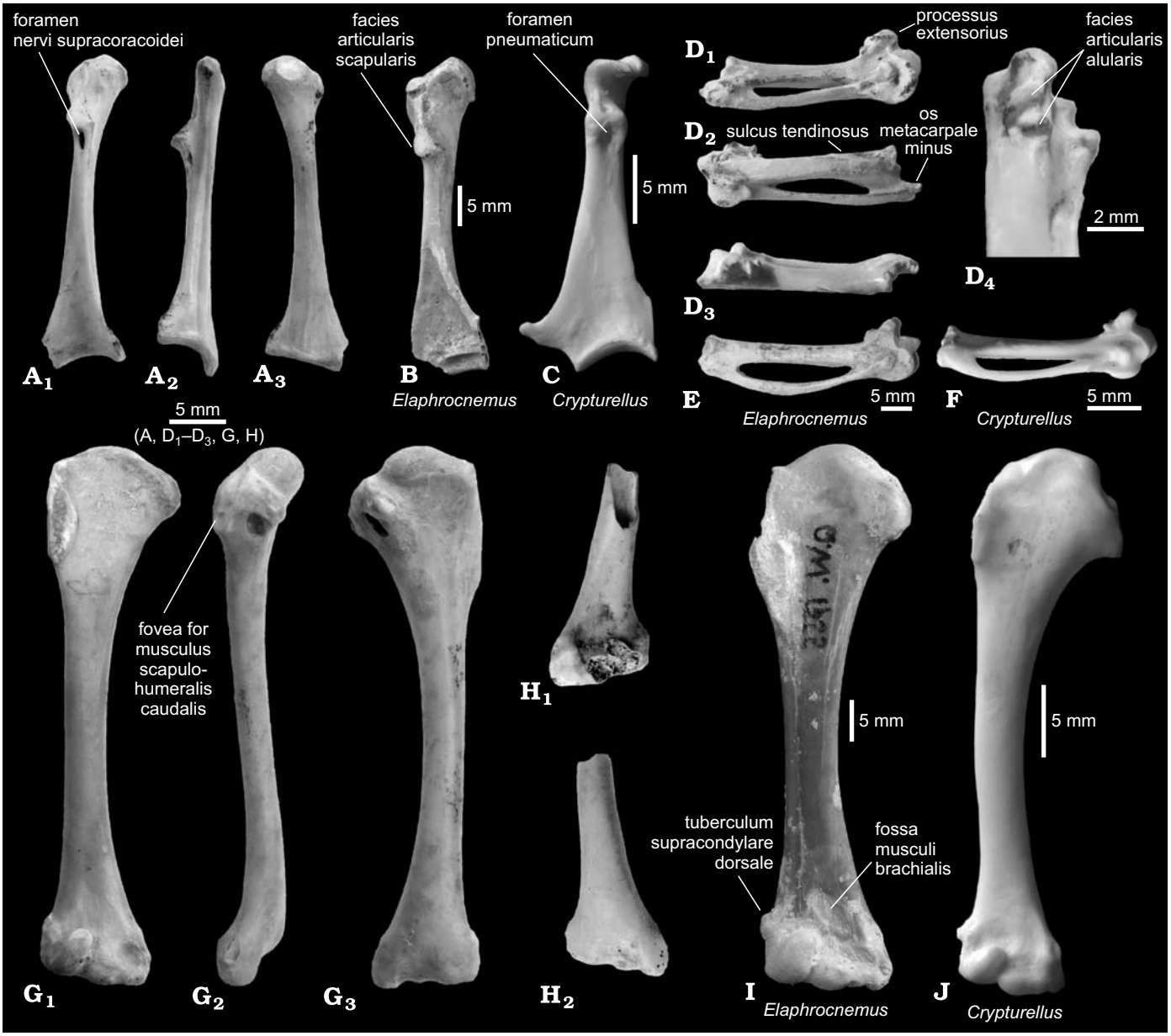

Fig. 1. Humerus, coracoid, and carpometacarpus from the late Paleocene of Brazil in comparison to Idiornithidae and extant Tinamidae. **A**. *Itaboravis elaphrocnemoides* gen. et sp. nov. from the Itaboraian of São José de Itaboraí, left coracoid (holotype, MN 4114-V), in dorsal (A_1), medial (A_2), and ventral (A_3) views. **B**. Left coracoid of *Elaphrocnemus phasianus* Milne-Edwards, 1892 (NMB Q.D.242) from the late Eocene of France, in dorsal view. **C**. Left coracoid of extant *Crypturellus parvirostris* (Wagler, 1827) (Tinamidae) (SMF 2164), in dorsal view. **D**. Right carpometacarpus of an undertermined bird (Aves indet. A) (MN 4115-V) from the Itaboraian of São José de Itaboraí, in ventral (D_1), dorsal (D_2), and cranial (D_3) views, with detail of processus extensorius (D_4). **E**. Right carpometacarpus of *E. phasianus* (NMB Q.D. 434) from the late Eocene of France, in ventral view. **F**. Right carpometacarpus of extant *C. parvirostris* (SMF 2164), in ventral view. **G**. Right humerus of *I. elaphrocnemoides* (MN 4113-V) from the late Eocene of France, in cranial (G_1), ventral (G_2), and caudal (G_3) views. **H**. Distal end of left humerus of *I. elaphrocnemoides* (MN 4121-V) from the late Eocene of France, in cranial (H_1) and caudal (H_2) views. **I**. Left humerus of *E. phasianus* (NMB Q.W.1755) from the late Eocene of France, in cranial view; reversed to facilitate comparisons. **J**. Left humerus of extant *C. parvirostris* (SMF 2164), in cranial view.

from *S*ão José de Itaboraí, Rio de Janeiro, southeastern Brazil; early late Paleocene, Itaboraian.

Measurement.—Length, 19.8.

Description and comparisons.—The bone has a distinctive morphology that is not matched by any other known avian taxon. It most closely resembles the carpometacarpus of the Tinamidae (Fig. 1F), from which it, however, differs in several other osteological characteristics (see below). It is very short, stocky, and the proximal end is distinctly twisted relative to the distal, as in Tinamidae. As also seen in some Tinamidae, a deep sulcus tendinosus crosses the distal half of the bone, from its cranial to the dorsal surface. In most neognathous birds, this groove is essentially dorsally devel-

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oped with no significant cranial extent. The processus extensorius is low and has a broadly rounded tip. The facies articularis alularis is bipartite and exhibits two articulation facets (Fig. 1D$_4$). The fossa infratrochlearis is deep, and the large and knobby processus pisiformis is centrally positioned. On the ventral surface of the proximal end of the bone, there is a very small pneumatic opening between the processus pisiformis and the processus extensorius.

The proximoventral rim of the trochlea carpalis is smooth rather than with a notch as in Tinamidae. The fovea carpalis caudalis is very shallow. The os metacarpale minus is connected by a ridge to the processus pisiformis, and caudal to this ridge there is a distinct depression (facies ligamentalis interna of Ballmann [1969]). A ventrally facing tubercle on the proximal os metacarpale minus that is present in most Cariamae is absent; this tubercle is also absent in *Elaphrocnemus*. Distally, the os metacarpale minus conspicuously exceeds the os metacarpale majus in length. Its distal end is pointed with a small caudoventral incision. As in extant Tinamidae, the ventral surface of the broad symphysis metacarpalis distalis is convex.

Stegmann (1965) reported that this distal elongation of the os metacarpale minus serves to prevent hyperextension of the major wing digit. An equally extensively elongated os metacarpale minus is absent in Tinamidae and Cariamae, in which the os metacarpale minus may be slightly more distally projected or subequal in extent to the os metacarpale majus. However, the condition seen in the fossil is more closely approached in, for example, Cuculidae, Musophagidae, Trochilidae, Passeriformes, Piciformes, and Meropidae. The spatium intermetacarpale widens distally. The distal section of the os metacarpale majus has a rugose caudal surface; the facies articularis digitalis major is weakly developed.

Apart from being proportionally shorter and more twisted, the carpometacarpus distinctly differs from that of *Elaphrocnemus* (Fig. 1E) in a number of features, including the weakly projected processus extensorius, the bipartite facies articularis alularis, the less bowed os metacarpale minus, and conspicuous projection of the latter distally beyond the os metacarpale majus.

Aves indet. B

Fig. 2A.

Material.—MN 4119-V (distal left tibiotarsus; Fig. 2A) from São José de Itaboraí, Rio de Janeiro, southeastern Brazil; early late Paleocene, Itaboraian.

Measurement.—Distal width, 2.2.

Remarks.—This bone is from a tiny bird much smaller than *Itaboravis elaphrocnemoides* and could possibly belong to *Eutreptodactylus itaboraiensis*, which is the only bird of comparable size known from Itaboraí. The mediolateral width of the proximal end of the tarsometatarsus of *E. itaboraiensis* is unknown, but its shaft has a width of 1.6 mm (Baird and Vickers-Rich 1997), and the bone is thus close to the distal tibiotarsus MN 4119-V in size. The holotype of *E. itaboraiensis* came from the same set of bones, from the collection of MN, as the specimens in this study. Unfortunately it is impossible to make further comparisons to confidently refer MN 4119-V, because the holotype specimen of *E. itaboraiensis* was a tarsometatarsus and is now lost (Baird and Vickers-Rich 1997). The pons supratendineus is narrow. The medial tuberositas retinaculi extensoris is situated far proximally. The condyli have about equal depth, but the (damaged) condylus medialis is mediolaterally much narrower than the condylus lateralis. The trochlea cartilaginis tibialis is proximodistally wide and shallow.

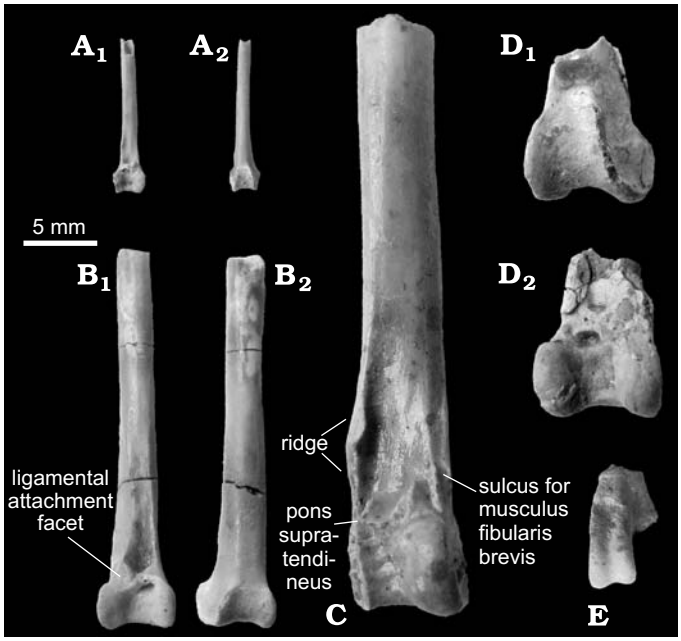

Fig. 2. Undetermined avian remains from the late Paleocene of Brazil. **A**. Distal left tibiotarsus of Aves indet. B (cf. *Eutreptodactylus itaboraiensis* gen. et sp. nov.) (MN 4119-V), in cranial (A_1) and caudal (A_2) views. **B**. Distal right tibiotarsus of Aves indet. C (MN 4116-V), in cranial (B_1) and caudal (B_2) views. **C**. Distal left tibiotarsus of Aves indet. D (MN 4117-V) lacking condylus medialis, in cranial view. **D**. Distal left tibiotarsus of Aves indet. E (MN 4118-V), in cranial (D_1) and caudal (D_2) views. **E**. Distal left tarsometatarsus of an undetermined bird (?Aves indet. D or E) (MN 4120-V), in dorsal view.

Aves indet. C

Fig. 2B.

Material.—MN 4116-V (distal right tibiotarsus; Fig. 2B) from São José de Itaboraí, Rio de Janeiro, southeastern Brazil; early late Paleocene, Itaboraian.

Measurement.—Distal width, 5.2.

Remarks.—This bone comes from a species the size of *Itaboravis elaphrocnemoides* and has a distinctive morphology, which is not matched by any extant avian taxon. Most notably, the cranial surface of the shaft lateral of the sulcus extensorius is unusually sloped cranio-caudally, and there is a distinct, subtriangular ligamental attachment facet above the condylus lateralis (Fig. 2B$_1$). The wide sulcus extensorius

is medially situated; the pons supratendineus is narrow. Both condyli have equal height, but the medial one is very narrow and somewhat medially splayed. The trochlea cartilaginis tibialis is low, much more so than in the tibiotarsus of the preceding taxon ("Aves indet. B").

With regard to the widely separated and low condyli and the low trochlea cartilaginis tibialis, the bone resembles the distal tibiotarsus of the putative podargid *Quercypodargus olsoni* from the late Eocene Quercy fissure fillings in France (Mourer-Chauviré 1989), from which it, however, differs in the presence of the subtriangular ligamental attachment facet.

Aves indet. D

Fig. 2C.

Material.—MN 4117-V (distal left tibiotarsus lacking condylus medialis; Fig. 2C) from São José de Itaboraí, Rio de Janeiro, southeastern Brazil; early late Paleocene, Itaboraian.

Measurement.—Distal width as preserved, 8.0.

Remarks.—The sulcus extensorius is far medially situated and medially bordered by a distinct ridge; a pons supratendineus seems to have been present, but is broken. The trochlea cartilaginis tibialis is low and shallow. Along the lateral margin of the distal shaft there is a distinct sulcus for the tendon of musculus fibularis brevis.

Concerning the medially situated sulcus extensorius, the bone resembles the distal tibiotarsus of the palaeognathous Tinamidae, but the fragmentary specimen does not allow a reliable identification.

Aves indet. E

Fig. 2D.

Material.—MN 4118-V (distal left tibiotarsus; Fig. 2D) from São José de Itaboraí, Rio de Janeiro, southeastern Brazil; early late Paleocene, Itaboraian.

Measurement.—Distal width, 8.1.

Remarks.—This bone is poorly preserved and does not exhibit distinctive characteristics. A pons supratendineus is present and the condylus medialis is slightly smaller than the condylus lateralis. The trochlea cartilaginis tibialis is higher and deeper than in the tibiotarsus of the previous taxon ("Aves indet. D").

Aves indet. (?D or E)

Fig. 2E.

Material.—MN 4120-V (fragmentary distal end of left tarsometatarsus; Fig. 2E) from São José de Itaboraí, Rio de Janeiro, southeastern Brazil; early late Paleocene, Itaboraian.

Measurement.—Width of trochlea metatarsi III, 5.0.

Remarks.—This bone fragment consists of the trochlea metatarsi III only. In size, it would be roughly correspondent with the tibiotarsi of the two aforementioned taxa (Aves indet. D and E).

Discussion

Given the continuing lack of consensus on the interrelationships among extant birds, the limited fossil material available, and the fact that few Paleocene birds have been described, it is not surprising that phylogenetic assessment of *Itaboravis elaphrocnemoides* gen. et sp. nov. is not straightforward. The morphologically distinctive coracoid of the new species resembles that of *Elaphrocnemus* to a high degree in, e.g., its elongate, slender shape, other characters such as the absence of a processus procoracoideus and proposed derived details, such as the convex facies articularis scapularis and the deeply concave dorsal surface of the extremitas sternalis. Three species of *Elaphrocnemus* were reported from the late Eocene and Oligocene of the Quercy fissure fillings in France, where the late Eocene *E. phasianus* is among the most abundant taxa in the old (19th century) collections (Mourer-Chauviré 1983; Mayr and Mourer-Chauviré 2006, 2008; Mayr 2009). *Elaphrocnemus* is known from skull remains and numerous specimens representing all major postcranial bones, and is currently classified in the Idiornithidae, a taxon proposed as part of Cariamae (Mayr 2009).

Because two humeri and a coracoid can be assigned to *Itaboravis elaphrocnemoides*, the species appears to have been among the more abundant small birds in Itaboraí, which may support assignment of the only carpometacarpus of comparable size to *I. elaphrocnemoides*. On the other hand, the Itaboraí material includes distal tibiotarsi of four different small to medium-sized taxa, and the avifauna appears to have been diverse. Contrary to the humerus and coracoid, which were found in the same block of matrix, we have no evidence other than size that the carpometacarpus indeed belongs to *Itaboravis*. This bone clearly differs from that of *Elaphrocnemus* (see description and Fig. 1) and, except for the extreme distal projection of os metacarpale minus, resembles the carpometacarpus of the Tinamidae in a number of features (see description). The Itaboraí carpometacarpus is further distinctly shorter than the coracoid of *Itaboravis*, whereas the carpometacarpus is only slightly shorter than the coracoid in *Elaphrocnemus*.

As detailed in the description, however, *Itaboravis* is also distinguished from *Elaphrocnemus* in several features of the holotype coracoid and referred material. Some characteristics of the humerus, which are shared by *Itaboravis* and *Elaphrocnemus*, also occur in the palaeognathous Tinamidae, such as the ventral position of the foramen pneumaticum and sulcus transversus, the absence of a fossa pneumotricipitalis, and the indistinct sulcus scapulotricipitalis. The humerus further agrees with that of Tinamidae and differs from the humerus of *Elaphrocnemus* in the low crista deltopectoralis, the flat intumescentia humeri, and the shallow fossa musculi brachialis. At least the latter two features are, however, also found in the non-neornithine taxon *Ichthyornis* (Clarke 2004) and are presumably plesiomorphic for neornithine birds (which is also true for the indistinct sulcus scapulotricipitalis). Despite its

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very different overall morphology, the coracoid of the new taxon agrees with that of tinamous in the presence of a pneumatic opening below the facies articularis scapularis, which in tinamous however does not also serve as foramen for the supracoracoideus nerve.

Although the indistinct fossa musculi brachialis and sulcus scapulotricipitalis of the humerus may indeed indicate a position of *Itaboravis* outside Neognathae (Mayr and Clarke 2003), at least the latter feature also occurs in *Elaphrocnemus*, whose position within Neoaves is uncontested and supported by, e.g., the absence of basipterygoid processes. We consider affinities to *Elaphrocnemus* to be best supported by current evidence and thus tentatively assign *Itaboravis* to the Cariamae. We note, however, that this classification is mainly based on overall similarity, and especially if the carpometacarpus indeed belongs to the taxon, there remains a possibility that *Itaboravis* is a stem group representative of the Tinamidae with a very different coracoid morphology.

Independent of its exact phylogenetic affinities, *Itaboravis* is of significance because it documents a previously unrecognized, distinctive Paleocene avian taxon, and thus adds to the mounting evidence that earliest Cenozoic avifaunas were already diverse. None of the avian taxa described from Itaboraí has been reported from other Paleocene avifaunas, but our knowledge of birds in the earliest Cenozoic certainly still is too poor for far-reaching general conclusions. The low crista deltopectoralis of the humerus of *I. elaphrocnemoides* indicates rather weak flight capabilities, perhaps comparable to those of extant Tinamidae. As is also the case for Paleocene avifaunas in Europe (Mayr 2007, 2009), the Itaboraí avifauna thus apparently includes a significant number taxa with weak or no (*Diogenornis* and presumably also *Paleopsilopterus*) flight capabilities. Whether this is indicative of particular features of earliest Cenozoic ecosystems, such as the absence of large mammalian predators, should be addressed in future studies.

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