PALÆO VERTEBRATA

ARTICLE

A reassessment of the giant birds *Liornis floweri* Ameghino, 1895 and *Callornis giganteus* Ameghino, 1895, from the Santacrucian (late Early Miocene) of Argentina

Eric BUFFETAUT

CNRS (UMR 8538), Laboratoire de Géologie de l'Ecole Normale Supérieure, PSL Research University, 24 rue Lhomond, 75231 Paris Cedex 05, France.
E-mail: eric.buffetaut@sfr.fr

Abstract: The status of the giant bird taxa *Liornis floweri* and *Callornis giganteus* from the Santa Cruz Formation (late Early Miocene) of Patagonia, first described by Ameghino (1895) is reassessed on the basis of a re-examination of the type material at the Natural History Museum, London. *Liornis floweri*, which lacks a Pons supratendineus on the tibiotarsus and has an unbifurcated Canalis interosseus distalis on the tarsometatarsus, is clearly a brontornithid and is considered as a junior synonym of *Brontornis burmeisteri*. Ameghino's replacement of *Callornis* by *Eucallornis* is unjustified. *Callornis giganteus* is a chimera based on a phorusrhacid tarsometatarsus (probably belonging to *Phorusrhacos longissimus*) and a brontornithid tibiotarsus. The latter can be considered as the lectotype of *Callornis giganteus*, which may represent a small morph of *Brontornis burmeisteri* or a distinct taxon. It is referred to here as Brontornithidae indet. The tarsometatarsus described by Dolgopol de Saez (1927a,b) as *Liornis minor* and considered by her as a gracile brontornithid apparently has a bifurcated Canalis interosseus distalis and should therefore be placed among the Phorusrhacidae.

Keywords: Aves, Miocene, Santacrucian, Argentina, *Liornis*, *Callornis*

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INTRODUCTION

In a review of the fossil birds from Argentina, Florentino Ameghino (1895) described several new taxa, many of them based on fragmentary material. The interpretation and synonymy of some of them have since then been a matter of discussion, and divergent opinions have been expressed by the various authors who dealt with the matter. The present paper is an attempt to clarify the status of two of Ameghino's controversial taxa, *Liornis floweri* and *Callornis giganteus*, on the basis of a re-examination of the original material kept at the Natural History Museum, London.

A NOTE ON CLASSIFICATION

One of the main objectives of this reassessment is to determine whether *Liornis* and *Callornis* should be placed among the Phorusrhacidae or among the Brontornithidae. Different answers have been given to this question by various authors (see below), depending in part on the systematic placement of the genus *Brontornis* Moreno & Mercerat, 1891. This genus was initially placed by Moreno & Mercerat (1891) in the family Brontornithidae. It has been claimed (Degrange *et al*., 2012, Tambussi & Degrange, 2013) that Moreno & Mercerat (1891) considered *Brontornis* as related to the Anseriformes, but this is not confirmed by their discussion of this genus. They did compare some morphological features of *Brontornis* bones with those of *Cygnus*, but they also noted that the tarsometatarsus was very different from that of *Cygnus*, and they did not suggest close relationships with Anseriformes. They clearly considered the Brontornithidae as a family of their order Stereornithes, which also included various large ground birds now placed among the Phorusrhacoidea. How Moreno and Mercerat envisioned the position of the Stereornithes among Aves is unclear: they noted that they shared characters with Anseres (ducks and geese), Herodiones (herons and storks), and Accipitres (birds of prey), but also suggested that they were transitional between Anatidae and Vulturidae. Nowhere do they indicate that they consider *Brontornis* as being outside Stereornithes and particularly close to Anseriformes.

Ameghino (1895) accepted Moreno and Mercerat's Stereornithes but proposed different subdivisions at family level within that order. He placed *Brontornis*, as well as *Liornis* and *Callornis*, in the family Phororhacidae (the proper spelling is Phorusrhacidae, see Buffetaut, 2013a), together with *Phorusrhacos* and other taxa considered today as phorusrhacoids. Until the 1920s, Ameghino's classification was followed, with minor variations, by most authors (e.g., Andrews, 1896; Lydekker, 1896; Andreae, 1899; Lambrecht, 1921); although Andrews (1896) noted that there were considerable differences between some of the genera, probably justifying their referral to several families. Gadow (1896a, p. 587) concluded that Stereornithes 'did not any longer convey a taxonomic meaning' – a conclusion that gradually became generally accepted.

The first author who clearly separated *Brontornis* from phorusrhacids was Dolgopol de Saez (1927a), who excluded the family Brontornithidae (which, according to her, also included *Rostrornis* Moreno & Mercerat, 1891 and *Liornis* Ameghino, 1895) from the Stereornithes and placed it in a new bird order, the Brontornithes. Dolgopol de Saez also was the first to clearly establish some of the main morphological characters of the postcranial skeleton that separate brontornithids from phorus-

rhacoids (lack of Pons supratendineus, unbifurcated Canalis interosseus distalis). Kraglievich (1932) to a large extent followed Dolgopol de Saez and distinguished two orders, Brontorniformes (including *Brontornis* and *Liornis*) and Phororhaciformes.

Lambrecht (1933) considered the Stereornithes as a suborder of the order Telmatoformes comprising the families Phororhacidae and Brontornithidae, which could be distinguished on the basis of the osteological characters listed by Dolgopol de Saez.

Subsequently, some authors (Patterson, 1941; Patterson & Kraglievich, 1960; Brodkorb, 1967; Acosta Hospitaleche *et al*., 2001; Alvarenga & Höfling, 2003; Alvarenga *et al*., 2011) did not consider the distinctive characters noted by Dolgopol de Saez as really significant and followed the traditional interpretation of *Brontornis* as an especially large and robust phorusrhacid or phorusrhacoid, usually placed in a distinct family (Brontornithidae) or subfamily (Brontornithinae) depending on the systematic hierarchy chosen by the author.

Agnolin (2007, 2013) proposed a completely different interpretation of *Brontornis*, considering it as a giant basal anseriform, and therefore not closely allied to the Phorusrhacidae. This point of view was accepted by Tambussi (2011), Tambussi & Degrange (2013), and Buffetaut (2014), and is followed in the present paper, in which the distinctive postcranial characters listed by Dolgopol de Saez are considered as valid.

GEOGRAPHICAL AND GEOLOGICAL SETTING

In his original description of *Liornis* and *Callornis* (later unnecessarily emended to *Eucallornis*, see below), Ameghino (1895) did not clearly specify what geological formation the specimens came from, beyond mentioning that they had been found in the Eocene of Patagonia by his brother Carlos. In a review of the geology and palaeontology of Argentina he published a few years later, Ameghino (1898) noted that *Liornis* and *Callornis* were from the Santa Cruz Formation, which he considered as Late Eocene in age. It is well known that Ameghino consistently overestimated the geological antiquity of the Patagonian fossil-bearing formations, and the Santa Cruz Formation is now known to be late Early Miocene in age (Santacrucian South American Land Mammal Age: see Vizcaíno *et al*., 2012). Recent reviews of Santacrucian birds were provided by Tambussi (2011), Degrange *et al*. (2012), and Tambussi & Degrange (2013).

The specimens were collected in Santa Cruz Province, southern Patagonia, by Carlos Ameghino. Some details about their provenance (see below) were provided by Lambrecht (1933) on the basis of a catalogue in the British Museum (Natural History) (as it was then called). When Florentino Ameghino described them in 1895, he had left the La Plata Museum and was working as an independent scientist (Casinos, 2012). The fossils belonged to his private collection. In need of money to fund his brother Carlos's field work in Patagonia, he sold his collection of fossil birds to the British Museum (Natural History) in 1896 (Casinos, 2012; Buffetaut, 2013b). The original material of *Liornis floweri* and *Callornis giganteus* has since then been kept at the Natural History Museum, London.

Institutional abbreviations:

FMNH: Field Museum of Natural Histoty, Chicago, USA. MLP: Museo de La Plata, La Plata, Argentina. NHMUK: Natural History Museum, London, UK.

LIORNIS FLOWERI AMEGHINO, 1895

Liornis floweri was originally placed by Ameghino (1895) among the Stereornithes, in the family Phororhacidae (= Phorusrhacidae: see Buffetaut, 2013a), where he also placed *Brontornis*. Lambrecht's (1933) indication that *Liornis floweri* was erected by Ameghino in 1891 is incorrect. In her revision of Santacrucian ground birds, Dolgopol de Saez (1927a) removed both *Brontornis* and *Liornis* from the Phorusrhacidae and placed them in the family Brontornithidae, which she considered as belonging to a separate order, the Brontornithes. Kraglievich (1932) mostly followed Dolgopol de Saez but placed *Liornis* in its own subfamily, Liorninae, among the 'Brontorniidae'. Brodkorb (1967) went farther and considered *Liornis* as a junior synonym of *Brontornis* (which he placed in a subfamily Brontornithinae within Phorusrhacidae). In more recent reviews, however, *Liornis* has usually not been considered as closely allied to *Brontornis*. Alvarenga & Höfling (2003, p. 65) considered that '*Liornis* Ameghino, 1895, with the species *L. floweri* Ameghino, 1895, and *L. minor* Dolgopol de Saez, 1927, are evident synonyms of *Phorusrhacos* Ameghino, 1887', and listed *Liornis floweri* as a synonym of *Phorusrhacos longissimus*. This opinion was followed by Bertelli *et al*. (2007), Alvarenga *et al*. (2011), and Tambussi & Degrange (2013). Whether *Liornis* should be considered as closely allied to *Brontornis* or as a synonym of *Phorusrhacos* has taken on a new significance since Dolgopol de Saez's idea of a clear separation between brontornithids and phorusrhacids was revived, notably by Agnolin (2007).

Liornis floweri was described by Ameghino (1895) on the basis of the distal part of a right tibiotarsus (Fig.1), the distal end of the left tarsometatarsus (Fig. 2), the first phalanx of digit III, and the first phalanx of digit IV. Ameghino noted that these bones were from a single, not fully grown individual. The

Figure 1. *Liornis floweri* Ameghino, 1895: distal part of right tibiotarsus (NHMUK PV A9058), in cranial (**A**) and caudal (**B**) views. Scale bar: 50 mm. No Pons supratendineus. Referred here to *Brontornis burmeisteri*.

colour and preservation of the specimens are in agreement with this interpretation.

According to Lambrecht (1933), the specimens were found at the Monte Observación locality (see map in Vizcaíno *et al*., 2012, fig. 1.2). As the massive phalanges are not especially diagnostic, the discussion below is based on the tibiotarsus and tarsometatarsus.

Tibiotarsus (NHMUK PV A9058): only part of the shaft and the distal end of the tibiotarsus are preserved (Fig. 1). The condyles are both missing. The whole bone is flattened craniocaudally. The most salient feature of the specimen is the absence of a Pons supratendineus on the well-preserved cranial face of the bone. Instead, there is a strong median tubercle shaped like a three-sided pyramid, located slightly proximal to the proximal ends of the condyles (Ameghino's 'tubercule intercondylien'). More proximally, the medial margin of the shaft, corresponding to the distal part of the Linea extensoria, is thickened medially, forming a convex ridge. Between this ridge and the tubercle, the surface of the bone forms a groove-like depression that must have accomodated the tendon of the Musculus extensor digitorum longus, which in birds with an ossified Pons supratendineus passes below the bony bridge (Baumel & Witmer, 1993). In *Liornis floweri*, the bridge must have been ligamentous, as in various groups of birds (Baumel & Witmer, 1993). It should be noted that that area of the tibiotarsus is very well preserved, without any indication of breakage, so that there is no reason whatsoever to assume that a bony Pons supratendineus was originally present but was subsequently destroyed. Alvarenga & Höfling (2003) criticised Dolgopol de Saez for not taking into account a possible destruction of the Pons supratendineus in her discussion of brontornithids, but in the present case such a destruction can clearly be excluded. The lack of an ossified Pons supratendineus separates *Liornis floweri* from the Phorusrhacidae, in which this bony bridge is always present. The condition in *Liornis floweri* is similar to that seen in *Brontornis burmeisteri.* There has been a certain amount of confusion in this regard because of erroneous interpretations. In their original description of *B. burmeisteri*, Moreno & Mercerat (1891) noted that on the type specimen that region was damaged, but stated that they believed a supratendinal bridge had been present. Ameghino (1895), who did not have a *Brontornis* tibiotarsus in his collection, claimed that a supratendinal bridge was present. However, Dolgopol de Saez (1927a) remarked that on the type material there is no evidence of a bridge, a fact also mentioned by Agnolin (2007). An examination of the lectotype specimen (MLP 88-91) in the La Plata Museum has confirmed that the Pons supratendineus is absent. Although the area where the median tubercle should be is very poorly preserved, there is a medial ridge as on the tibiotarsus of *Liornis floweri*. In the morphology of the distal end of the tibiotarsus, *Liornis floweri* is thus very similar to *Brontornis* and quite different from phorusrhacids. As noted by Dolgopol de Saez (1927a), Moreno & Mercerat (1891) referred to *Rostrornis floweri* (a taxon recognised as a junior synonym of *Brontornis burmeisteri* by Ameghino as early as 1891) a large incomplete tibiotarsus completely similar in size and morphology to the corresponding bone of Ameghino's *Liornis floweri*. This specimen (Moreno & Mercerat, 1891, plate 4, fig. 1) is also extremely similar to the type tibiotarsus of *Brontornis burmeisteri*.

Tarsometatarsus (NHMUK PV A580): the tarsometatarsus fragment described by Ameghino (1895), and also figured by Lambrecht (1933, fig. 152) comprises only the distal end of the bone, and only the median trochlea is preserved (Fig. 2). Although Alvarenga & Höfling (2003) considered *Liornis floweri* as a junior synonym of *Phorusrhacos longissimus*, they listed specimen NHMUK PV A580 under *Brontornis burmeisteri*. The most systematically important character of the specimen is the condition of the Canalis interosseus distalis, which has its distal opening in the Incisura intertrochlearis lateralis and its proximal opening as the Foramen vasculare distale on the dorsal face of the bone. The canal is not bifurcated and there is no opening on the plantar face of the bone. As noted by Ameghino (1895), this distinguishes *Liornis floweri* from *Phorusrhacos*. Dologopol de Saez (1927a) emphasized the significance of this character (Fig. 3), pointing out that in phorusrhacids the canal is bifurcated, with an opening on the plantar face of the tarsometatarsus and one in the Incisura intertrochlearis lateralis, while in *Brontornis* (as already noted by Ameghino, 1895) and other brontornithids, it has a single distal exit, in the Incisura intertrochlearis lateralis. The tarsometatarsus of *Liornis floweri* clearly shows the brontornithid condition.

To sum up, in the absence of a Pons supratendineus on the tibiotarsus and in the unbifurcated Canalis interosseus distalis on the tarsometatarsus, *Liornis floweri* differs markedly from

Figure 2. *Liornis floweri* Ameghino, 1895: distal part of left tarsometatarsus (NHMUK PV A580), in dorsal (**A**) and plantar (**B**) views. Scale bar: 50 mm. No exit of the Canalis interosseus distalis on the plantar face. Referred here to *Brontornis burmeisteri.*

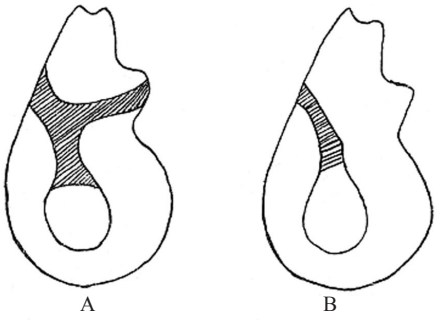

Figure 3. Longitudinal sections through the distal end of the tarsometatarsus showing the condition of the Canalis interossesu distalis in phorusrhacids and brontornithids, after Dolgopol de Saez (1927a). In phorusrhacids (**A**), the canal is bifurcated, with a distal exit in the Incisura intertrochlearis lateralis and a caudal exit on the plantar face of the bone. In brontornithids (**B**), the canal is not bifurcated, with a single distal exit in the Incisura intertrochlearis lateralis.

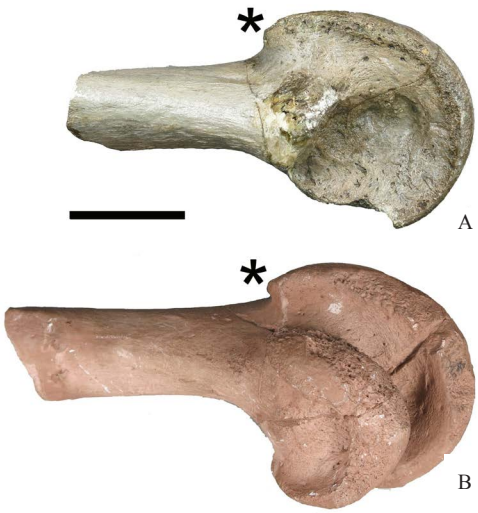

Figure 4. The distal end of the tarsometatarsus, in medial view, in *Liornis floweri* (NHMUK PV A580) (**A**) and *Brontornis burmeisteri* (FMNH-P13259; cast in Natural History Museum, London) (**B**), showing the projecting proximodorsal margin of the median trochlea (asterisk).

the Phorusrhacidae and typically shows the brontornithid condition. There is thus every reason to follow Dolgopol de Saez (1927a) and to place it among the Brontornithidae. The type material of *Liornis floweri* is in fact extremely similar to *Brontornis burmeisteri*. As noted by Ameghino (1895), the bones of *Liornis floweri* are nearly as large as those of *Brontornis burmeisteri*, even though they belong to an individual that, according to him, was not fully grown (in any case, as pointed out by Alvarenga & Höfling, 2003, there was considerable size variation in *Brontornis*, perhaps indicative of sexual dimorphism). Beyond size, *Brontornis burmeisteri* and *Liornis floweri* appear to be morphologically very close. Similarities in the tarsometatarsus include a notable dorsoplantar compression and a very large middle trochlea with a proximally projecting proximodorsal margin (Fig. 4); this feature is considered as characteristic of the 'Brontornithinae' by Alvarenga & Höfling (2003, fig. 8). As noted above, Brodkorb (1967) considered *Liornis* as a junior synonym of *Brontornis*. However, a potentially significant difference between these two giant birds was pointed out by Ameghino (1895), who claimed that the tarsometatarsus of *Brontornis burmeisteri* bears a well-marked facet for the hallux (Fossa metatarsi I) on its plantar face, whereas there is no sign of that facet in *Liornis floweri*. There is indeed no trace of such a facet on the tarsometatarus of *Liornis floweri*. The question is whether there is really a distinct facet for the hallux in *Brontornis burmeisteri,* as claimed by Ameghino (1895), followed more recently by Agnolin (2007). Moreno & Mercerat (1891) claimed that the plantar surface of the type tarsometatarsus (MLP 88-91) was too poorly preserved to provide definite information, but thought it likely that a hallux was present. An examination of that specimen at the Museo de La Plata has revealed no evidence of a well-defined facet for the hallux. Ameghino's drawing of a right tarsometatarsus in his collection (Ameghino, 1895, fig. 24) does show a well-defined oval depression in the medial half of the plantar face. The nearly complete right tarsometatarsus figured by Ameghino (1895, fig. 23) does not appear to be in the Ameghino collection at the Natural History Museum, London (see also list of specimens in Alvarenga & Höfling, 2003). However, the distal extremity of a right tarsometatarsus

Figure 5. Distal end of a right tarsometatarsus (NHMUK PV A578) referrable to *Brontornis burmeisteri*, in dorsal (**A**) and plantar (**B**) views. Scale bar: 50 mm. There is no evidence of an articular facet for the hallux on the plantar face.

(NHMUK PV A578), with a similarly broken inner trochlea and corresponding dimensions may be a fragment of the originally more complete bone illustrated by Ameghino. This specimen (Fig. 5) shows no trace of the very distinct facet shown on Ameghino's figure; in the area in question, there is only a poorly defined flat area that does not resemble an articular facet. In addition, a cast of the distal half of a well preserved *Brontornis* tarsometatarsus from the collections of the Field Museum of Natural History (FMNH-P13259, listed and figured by Alvarenga & Höfling, 2003, fig. 8), kept at the Natural History Museum, London, also shows no evidence of a distinct scar for the hallux. The presence of a hallux, or at least of a scar for the articulation of the hallux on the tarsometatarsus, in *Brontornis* should therefore be considered as highly doubtful. Another possibility is that the presence of a hallux was not constant in *Brontornis*, as sometimes happens in birds: as noted by Gadow (1896b, p. 405), in the Kittiwake (*Rissa*), 'its condition varies almost individually from being nearly functional to absence'. However that may be, none of the specimens that have been examined shows the very distinct scar figured by Ameghino (1895) and it seems likely that *Brontornis* in fact had no hallux (the lack of a Fossa metatarsi I in brontornithids may be an additional character separating them from phorusrhacoids, in which a facet for the hallux is present). Therefore, the lack of such a feature on the tarsometatarsus of *Liornis floweri* does not appear to justify its separation from *Brontornis*. In view of the considerable similarities between the type material of *Liornis floweri* and the corresponding elements in *Brontornis burmeisteri*, it seems advisable to follow Brodkorb (1967) and to consider *Liornis floweri* as a junior synonym of *Brontornis burmeisteri.*

CALLORNIS GIGANTEUS AMEGHINO, 1895

Ameghino (1895) described a fragmentary right tibiotarsus (NHMUK PV A9057; Fig. 6) and an incomplete right tarsometatarsus (NHMUK PV A581; Fig. 7) as *Callornis giganteus*. According to Lambrecht (1933), the material came from La Cueva locality, a few km SW of the Monte Observación site where the material of *Liornis floweri* was found (see Vizcaíno *et al*., 2012, fig. 1.2). In 1901, following a mention of *Callornis latus* (a taxon from the Early Miocene *Colpodon* beds that apparently was never really described), Ameghino emended the generic name to *Eucallornis*, *Callornis* being supposedly preoccupied (Ameghino, 1901). Ameghino did not mention

what the senior homonym was. A search through the zoological literature did not reveal any previous use of *Callornis* as a valid name. In fact, previous uses of the genus name *Callornis* for a bird were incorrect subsequent spellings of *Calornis*, a name erected by Gray (1841) for sturnids (starlings) from Southeast Asia and Australasia. In addition, Gray's *Calornis* was preoccupied by *Calornis* Billberg, 1820, a butterfly (Billberg 1820) (in both cases *Calornis* has turned out to be preoccupied and is no longer in use). As stated by the International Code of Zoological Nomenclature (article 56.2), 'even if the difference between two genus-group names is only one letter, they are not homonyms'. Therefore *Callornis* Ameghino, 1895 cannot be considered as a junior homonym of *Calornis*, and Ameghino's *Eucallornis* should be considered as an unjustified replacement name. Therefore, the genus name *Callornis* is used here, rather than *Eucallornis*.

Callornis was placed by Ameghino in the Phorusrhacidae. Brodkorb (1967) considered *Callornis giganteus* as a junior synonym of *Phorusrhacos longissimus*, a conclusion shared by Cuello (1988), Alvarenga & Höfling (2003), Bertelli *et al*. (2007), Agnolin (2009), Alvarenga *et al*. (2011), and Tambussi & Degrange (2013).

Although he referred the two above-mentioned specimens to *Callornis giganteus*, Ameghino (1895) did not explain why he associated them and did not suggest that they belonged to a single individual. The two bones have different colours (brown for the tibiotarsus, light grey for the tarsometatarsus), which does not suggest that they are from the same individual.

Tibiotarsus (NHMUK PV A9057): as noted by Ameghino, it is the distal third of the bone and the distal end, including the condyles, is missing (Fig. 6). The most significant feature is the absence of a Pons supratendineus. This cannot be explained by poor preservation, as the surface of the bone in that area is very well preserved. The reliefs on the cranial face of the bone are generally similar to those on the tibiotarsus of '*Liornis floweri'*, but more accentuated. There is a strong, more or less central tubercle and a well-marked ridge along the medial margin (corresponding to the distal end of the Linea extensoria). As noted by Ameghino (1895), the longitudinal groove (Sulcus extensorius) for the extensor muscles of the toes is very deep, more so than in '*Liornis floweri'*. By the absence of a Pons supratendineus the specimen differs clearly from the tibiotarsi of the Phorusrhacidae, and the reliefs on its craniodistal part are similar to the condition in Brontornithidae.

Tarsometatarsus (NHMUK PV A581): only the distal end of the bone is preserved; the medial trochlea is missing (Fig. 7). The most salient character of the bone is that the Canalis interosseus distalis is bifurcated, with a distal exit in the Incisura intertrochlearis lateralis and a caudal exit on the plantar face of the bone. As noted by Ameghino (1895), this condition is the same as that in *Phorusrhacos*. In brontornithids, as noted above, the Canalis interosseus distalis is not bifurcated and opens distally in the Incisura intertrochlearis lateralis, without a plantar exit.

Lambrecht (1933) was aware of the conflicting characters observable on the bones referred by Ameghino to *Callornis giganteus*, noting that the tibiotarsus showed brontonithid characters while the tarsometatarsus exhibited phorusrhacid features. This led him to the conclusion that *Callornis* seemed to be intermediate between the Brontornithidae and the Phorusrhacidae. In fact, as mentioned above, there is no convincing evidence that the two bones on which Ameghino (1895) based his description of *Callornis giganteus* belong to the same form, and it is much more likely that that taxon is a chimera: the tibiotarsus belongs to a brontornitthid and the tarsometatarsus to a phorusrhacid. As noted above, various authors have already suggested that *Callornis giganteus* is a junior synonym of *Phorusrhacos longissimus*. This can only apply to the tarsometatarsus, which is indeed similar in size and morphology to tarsometatarsi referred to *Phorusrhacos longissimus*. Once that bone has been removed from *Callornis giganteus*, the only specimen referrable to that taxon is the tibiotarsus, which belongs to a brontornithid, and can be proposed as the lectotype

Figure 6. Distal part of a right tibiotarsus (NHMUK PV A9057) referred to *Callornis giganteus* by Ameghino (1895), in cranial (**A**) and caudal (**B**) views. Scale bar: 50 mm. The lack of a Pons supratendineus is a bronthornithid character.

Figure 7. Distal part of a right tarsometatarsus (NHMUK PV A581) referred to *Callornis giganteus* by Ameghino (1895), in dorsal (A) and plantar (B) views. Scale bar: 50 mm. The presence of an exit of the Canalis interosseus distalis on the plantar face indicates a phorusrhacid rather than a brontornithid. Referred here to *Phorusrhacos longissimus*.

of *Callornis giganteus*. The question then arises of the status of that taxon among Brontornithidae. Despite general similarities with *Brontornis burmeisteri* (including the specimen originally designated as *Liornis floweri*), differences can be observed. NHMUK PV A9057 is about one-third smaller than NHMUK PV A9058 (first described as *Liornis floweri*) and MLP 88-91 (part of the type specimen of *Brontornis burmeisteri*). Considering its degree of ossification and strong development of bony tubercles and ridges, NHMUK PV A9057 is unlikely to be from a juvenile individual. The size difference may be related to sexual dimorphism, which has already been postulated in *Brontornis* by Alvarenga & Höfling (2003); in that case, *Callornis giganteus* could possibly be considered as a junior synonym of *Brontornis burmeisteri*, NHMUK PV A9057 belonging to a small morph of that taxon. Alternatively, NHMUK PV A9057 could be considered as a distinct taxon. Support for that interpretation may be based on relatively slight morphological differences already noted by Ameghino (1895), notably the great depth of the Sulcus extensorius and the corresponding prominence of the reliefs on both sides of it. Dolgopol de Saez (1927a,b) described as *Liornis minor* a tarsometatarsus from the Santa Cruz Formation that she placed among the Brontornithidae because of its supposedly unbifurcated Canalis interosseus distalis. That bone is 40 cm long and thus about the size of the tarsometatarsus of *Phorusrhacos longissimus* (Dolgopol de Saez, 1927a), and is significantly more slender than the tarsometatarsus of *Brontornis burmeisteri*, even when compared with relatively small representatives of that species, such as FMNH-P13259 (see Alvarenga & Höfling, 2003, fig. 2). Dolgopol de Saez (1927a,b) did not provide a detailed diagnosis for the new species, beyond the fact that it was somewhat smaller than *Liornis floweri*. She clearly considered it as a gracile brontornithid. Brodkorb (1967) considered *Liornis minor* as a junior synonym of *Brontornis burmeisteri*. However, examination of the specimen in the Museo de La Plata revealed what appears to be an opening for the Canalis interosseus distalis on the plantar face of the bone, and Alvarenga & Höfling (2003) are in all likelihood correct in their conclusion that *Liornis minor* is in fact a junior synonym of *Phorusrhacos longissimus*. The specimen described by Dolgopol de Saez therefore cannot be used as supporting evidence for the presence of a relatively small and slender brontornithid in the Santa Cruz Formation in addition to the huge *Brontornis burmeisteri*. It should also be noted that several tibiotarsi from the Santa Cruz Formation lacking a Pons supratendineus are kept in the La Plata Museum (including the specimen collected by Berry, MLP 20-110, referred to *Liornis* by Dolgopol de Saez, 1927a, and MLP 20-581). They are referrable to brontornithids. Variations in size and morphology among brontornithid specimens from the Santa Cruz Formation will have to be assessed before conclusions can be reached concerning the number of taxa present in it. For the time being, it thus seems advisable to refer to the tibiotarsus (NHMUK PV A9057) included in Ameghino's description of *Callornis giganteus* as Brontornithidae indet.

CONCLUSIONS

The revision of the original material presented above clarifies the status of the species *Liornis floweri* and *Callornis giganteus*, with implications for our knowledge of the anatomy and diversity of giant terrestrial birds from the Santa Cruz Formation of Patagonia. The basis for a reassessment of both taxa is a clear distinction between brontornithids and phorusrhacoids, as first advocated by Dolgopol de Saez (1927a). Two characters have proved to be of special significance in this respect:

- the lack of a Pons supratendineus on the tibiotarsus of brontornithids, whereas it is present in phorusrhacoids.

- an unbifurcated Canalis interosseus distalis in brontornithids, whereas it is bifurcated in phorusrhacoids.

Both the tibiotarsus and the tarsometatarsus referred to *Liornis floweri* by Ameghino (1895) display the brontornithid condition. Because of general similarity in size and morphology, *Liornis floweri* is considered here as a junior synonym of *Brontornis burmeisteri*, despite the fact that Ameghino (1895) reported the presence in *Brontornis* of a facet for the hallux on the tarsometatarsus that is not present on the specimen referred to *Liornis floweri* by Ameghino. A review of the available evidence suggests that there was no such facet in *Brontornis*.

The case of *Callornis giganteus* is more complex, since among the bones referred to it by Ameghino (1895), the tibiotarsus shows clear brontornithid characters, whereas the tarsometatarsus is not distinguishable from that of *Phorusrhacos*. *Callornis giganteus* is therefore considered as a chimera. Once the phorusrhacid tarsometatarsus is removed from it, however, the name can be applied to a brontornithid taxon. Whether it should be considered as a junior synonym of *Brontornis burmeisteri*, or as a distinct, smaller and more slender form is uncertain. A re-examination of *Liornis minor*, described by Dolgopol de Saez (1927a,b) on the basis of a tarsometatarsus as a slender brontornithid, has shown that the specimen in question in all likelihood belongs to a phorusrhacid, as already noted by Alvarenga & Höfling (2003), so that there is no strong evidence for a slender brontornithid different from *Brontornis burmeisteri* in the Santa Cruz Formation. Brontornithid tibiotarsi from the Santa Cuz Formation exhibit a certain amount of variation in size and morphology (with more or less accentuated reliefs on the cranial face). For the time being, specimen NHMUK PV A9057 is better considered as Brontornithidae indet.

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BIBLIOGRAPHY

Acosta Hospitaleche, C., Tambussi, C.P., Reguero, M., 2001. Catálogo de los tipos de aves fósiles del Museo de La Plata. Serie Técnica y Didáctica del Museo de La Plata 41, 1-28.

Agnolin, F.L., 2007. *Brontornis burmeisteri* Moreno and Mercerat, un Anseriformes (Aves) gigante del Mioceno medio de Patagonia, Argentina. Revista del Museo Argentino de Ciencias Naturales 9, 15-25. doi: 10.22179/REVMACN.9.361

Agnolin, F.L., 2009. Sistemática y filogenia de las aves fororracoideas (Gruiformes, Cariamae). Buenos Aires, Fundación de Historia Natural "Félix de Azara".

Agnolin, F.L. 2013. La posición sistemática de *Hermosiornis* (Aves,

Phororhacoidea) y sus implicancias filogenéticas. Revista del Museo Argentino de Ciencias Naturales 15, 39-60.
Alvarenga, H. & Höfling, E., 2003. Systematic revision of the Phorusrhacidae (Aves: Ralliformes). Papéis Avulsos de Zoologia 43, 55-91. doi: 10.1590/S0031-10492003000400001
Alvarenga, H., Chiappe, L., Bertelli, S., 2011. Phorusrhacids: the terror birds. In Dyke, G, Kaiser, G, (Eds), Living dinosaurs. The evolutionary history of modern birds.Wiley, Chichester, pp. 187-208. doi: 10.1002/9781119990475.ch7
Ameghino, F., 1891. Enumeración de las aves fósiles de la República Argentina. Revista Argentina de Historia Natural 1, 441-453.
Ameghino, F., 1895. Sur les oiseaux fossiles de Patagonie. Boletín del Instituto Geográfico Argentino 15, 501-602.
Ameghino, F., 1898. Sinopsis geológicopaleontológica de la Argentina. Segundo Censo de la República Argentina 1, 112-255.
Ameghino, F., 1901. L'âge des formations sédimentaires de Patagonie (suite). Anales de la Sociedad Científica Argentina 51-52, 65-91.
Andreae, A., 1899. Zusammenfassendes Referat über die fossilen Riesenvögel aus Patagonien, speziell *Phororhacos*. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie 2, 322-330.
Andrews, C.W., 1896. Remarks on the Stereornithes, a group of extinct birds from Patagonia. The Ibis 2, 1-12. doi: 10.1111/j.1474-919x.1896.tb06971.x
Baumel, J.J., Witmer, L.M., 1993. Osteologia. In Baumel, J.J., King, A.S., Breazile, J.E., Evans, H.E., Vanden Berge, J.C. (Eds), Handbook of avian anatomy: Nomina anatomica avium. 2nd edition. Publications of the Nuttall Ornithological Club 23, 45-132.
Bertelli, S., Chiappe, L.M., Tambussi, C., 2007. A new phorusrhacid (Aves: Cariamae) from the Middle Miocene of Patagonia, Argentina. Journal of Vertebrate Paleontology 27, 409-419. doi: 10.1671/0272-4634(2007)27[409:ANPACF]2.0.CO;2
Billberg, G. J., 1820. Enumeratio insectorum in Musaeo Gust. Joh. Billberg. Stockholm, Typis Godelianis. doi: 10.5962/bhl.title.49763
Brodkorb, P., 1967. Catalogue of fossil birds. Part 3 (Ralliformes, Ichthyornithiformes, Charadriiformes). Bulletin of the Florida State Museum 11, 99-220.
Buffetaut, E., 2013a. Phororhacoidea or Phorusrhacoidea? A note on the nomenclature of the "terror birds". Annales de Paléontologie 99, 157-161. doi: 10.1016/j.annpal.2013.02.004
Buffetaut, E., 2013b. Who discovered the Phorusrhacidae? An episode in the history of avian palaeontology. In Göhlich, U.B., Kroh, A. (Eds), Palaeornithological Research 2013. Proceedings of the 8th International Meeting of the Society of Avian Paleontology and Evolution. Wien, Naturhistorisches Museum, pp. 123-133.
Buffetaut, E., 2014. Tertiary ground birds from Patagonia (Argentina) in the Tournouër collection of the Muséum National d'Histoire Naturelle, Paris. Bulletin de la Société géologique de France 185, 207-214. doi: 10.2113/gssgfbull.185.3.207
Casinos, A., 2012. Un evolutionista en el Plata. Florentino Ameghino. Buenos Aires, Fundación de Historia Natural «Félix de Azara».
Cuello, J.P., 1988. Lista de las aves fósiles de la région neotropical y de las islas antillanas. Paula-Coutiana 2, 3-79.
Degrange, F.J., Noriega, J.I., Areta, J.I., 2012. Diversity and paleobiology of the Santacrucian birds. In Vizcaíno, S.F., Kay, R.F., Bargo, M.S. (Eds), Early Eocene Paleobiology in Patagonia: High Latitude Paleocommunities of the Santa Cruz Formation. Cambridge University Press, Cambridge, pp. 138-155. doi: 10.1017/CBO9780511667381.010
Dolgopol de Saez M., 1927a. Las aves corredoras fósiles del Santacrucense. Anales de la Sociedad Científica Argentina 103, 145-160.
Dolgopol de Saez M., 1927b. *Liornis minor*, una especie nova de ave fósil. Physis 8, 584-585.
Gadow, H., 1896a. Letter on the relationships of the Stereornithes. The Ibis 2, 586-587.
Gadow, H., 1896b. Hallux. In Newton, A., Gadow, H. (Eds), A dictionary of birds. Adam and Charles Black, London, pp. 404-405.
Gray, G.R., 1841. A list of the genera of birds, with their synonyms, and an indication of the typical species of each genus. London, Taylor.
Kraglievich, L., 1932. Una gigantesca ave fósil del Uruguay, *Devincenzia gallinali* n. gen. n. sp., tipo de una nueva familia, Devincenziidae, del Orden Stereornithes. Anales del Museo de Historia Natural de Montevideo 3, 323-355.
Lambrecht, K., 1921. Aves. In Diener, C. (Ed.), Fossilium Catalogues. I: Animalia, Pars 12. W. Junk, Berlin, pp. 1-104.
Lambrecht, K. 1933. Handbuch der Palaeornithologie. Berlin, Gebrüder Borntraeger.
Lydekker, R., 1896. Stereornithes. In Newton, A., Gadow, H. (Eds), A dictionary of birds. Adam and Charles Black, London, pp. 904-908.
Moreno, F. P., Mercerat, A., 1891. Catálogo de los pájaros fósiles de la República Argentina conservados en el Museo de La Plata. Anales del Museo de La Plata 1, 7-71.
Patterson, B., 1941. A new phororhacoid bird from the Deseado Formation of Patagonia. Geological Series of the Field Museum of Natural History 8, 49-54.
Patterson, B., Kraglievich, J.L. 1960. Systemática y nomenclatura de las aves fororracoideas del Plioceno argentino. Publicaciones del Museo Municipal de Historia Natural y Tradicional de Mar del Plata 1, 1-52.
Tambussi, C.P., 2011. Palaeoenvironmental and faunal inferences based on the avian fossil record of Patagonia and Pampa: what works and what does not. Biological Journal of the Linnean Society of London 103, 458-474. doi: 10.1111/j.1095-8312.2011.01658.x
Tambussi, C.P., Degrange, F.C., 2013. South American and Antarctic continental Cenozoic birds. Paleobiogeographic affinities and disparities. Dordrecht, Springer. doi: 10.1007/978-94-007-5467-6
Vizcaíno, S.F., Kay, R.F., Bargo, M.S., 2012. Background for a aleoecological study of the Santa Cruz Formation (late Early Miocene) on the Atlantic coast of Patagonia. In Vizcaíno, S.F., Kay, R.F., Bargo, M.S. (Eds), Early Eocene Paleobiology in Patagonia: High Latitude Paleocommunities of the Santa Cruz Formation. Cambridge University Press, Cambridge, 1-22. doi: 10.1017/CBO9780511667381.002