

Article

Reappraisal on the Phylogenetic Relationships of the Enigmatic Flightless Bird (*Brontornis burmeisteri*) Moreno and Mercerat, 1891

Federico L. Agnolin ^{1,2}

¹ Laboratorio de Anatomía Comparada y Evolución de los Vertebrados, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”-CONICET, Av. Ángel Gallardo 470, Buenos Aires C1405DJR, Argentina; fedeagnolin@yahoo.com.ar

² Fundación de Historia Natural “Félix de Azara”, Departamento de Ciencias Naturales y Antropología, CEBBAD-Universidad Maimónides, Hidalgo 775 piso 7, Buenos Aires C1405BDB, Argentina

Abstract: The fossil record of birds in South America is still very patchy. One of the most remarkable birds found in Miocene deposits from Patagonia is *Brontornis burmeisteri* Moreno and Mercerat, 1891. This giant flightless bird is known by multiple incomplete specimens that represent a few portions of the skeleton, mainly hindlimb bones. Since the XIX century, *Brontornis* was considered as belonging to or closely related to phorusrhacoid birds. In contrast to previous work, by the end of 2000 decade it was proposed that *Brontornis* belongs to Galloanserae. This proposal was recently contested based on a large dataset including both phorusrhacoids and galloanserine birds, that concluded *Brontornis* was nested among cariamiform birds, and probably belonged to phorusrhacoids. The aim of the present contribution is to re-evaluate the phylogenetic affinities of *Brontornis*. Based on modified previous datasets, it is concluded that *Brontornis* does belong to Galloanserae, and that it represents a member of a largely unknown radiation of giant graviportal birds from South America.



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Keywords: *Brontornis*; Phorusrhacoidea; Galloanserae; South America; Neogene

1. Introduction

The genus *Brontornis* was originally described by Moreno and Mercerat (1891) based on several specimens coming from Lower-Middle Miocene localities at Santa Cruz province, Patagonia, Argentina [1]. This genus contains a single species: *B. burmeisteri* Moreno and Mercerat [2,3]. *Brontornis* was a giant flightless bird of about 2.8 m tall that may have weighed about 350 to 400 kg [2]. Its limb proportions and shape of elements indicate that *Brontornis* was a graviportal bird [4–7], probably a carrion eater [7], or even herbivorous [4,6,8].

On its original description, Moreno and Mercerat [3] include *Brontornis* on its own family Brontornithidae in the Order Stereornithes (this later included several genera now known as phorusrhacoids). In their concept, the Stereornithes were carinate birds with a shared combination of characters between anseriformes, coconiiforms (*Herodiones* therein), and accipitriforms, probably “intermediate” between Anatidae and Cathartidae. Moreno and Mercerat also noted the persistence of “reptilian” (i.e., plesiomorphic) characters in phorusrhacoids. Ameghino [9] made a revision of fossil Patagonian birds and partially resolved the confusion created by Moreno and Mercerat’s [3] work. Ameghino considered the Stereornithes as belonging to Ratitae, and included *Brontornis* among phorusrhacids, a criterion was followed by most authors until Dolgopol de Sáez [10]. She revalidated the Brontornithidae (as Brontorniidae) and based on morphological grounds coined the Order Brontornithes to separate them from remaining phorusrhacoids (encompassed by her in the Order Stereornithes). Despite that, Dolgopol de Sáez was not able to recognize the suprageneric relationships of *Brontornis* and kin and considered that *Gastornis* may be closely related to it. Kraglievich [6,11] followed Dolgopol de Sáez and retained *Brontornis* on its own order Brontornithes (*Brontornitiformes* for Kraglievich, [6]). Subsequent authors

followed Moreno and Mercerat and Ameghino views and considered *Brontornis* and kin as belonging to a different family or subfamily of phorusrhacoid birds [1,12–14], without regard of the distinctive anatomical features cited by Dolgopol de Sáez and Kraglievich.

Posteriorly, Agnolin [8,15,16] proposed that *Brontornis* may not be closely related to phorusrhacoids, but may be included among Galloanseres as a basal member of Anseriformes, a criterion followed by several authors [17–22]. However, Alvarenga et al. [23] returned to previous ideas and sustained that *Brontornis* belongs to Phorusrhacoidea. The arguments exposed by Alvarenga et al. [23] were contested by Agnolin [16], who supported the anseriform affinities for *Brontornis* again.

More recently, Worthy et al. [24] made a comprehensive phylogenetic analysis of Galloanseres, with special emphasis on extinct and flightless fowls. In their impressive analysis, Worthy et al. concluded that *Brontornis* is closely related to phorusrhacoids and considered it as part of Cariamiformes, far from Galloanseres. They argued that the strong differences observed in the postcranial anatomy of *Brontornis* and other cariamiforms are the result of the gigantism and graviportal locomotion of the former.

The aim of the present contribution is to describe and re-describe some materials that has referred to *Brontornis*, as well as to review Worthy et al.'s [24] analysis and re-consider the phylogenetic affinities of *Brontornis*.

2. Materials and Methods

2.1. Nomenclature

I follow the taxonomic nomenclature employed by Agnolin [16]. In that contribution I regard as valid the genus *Tolmodus* Ameghino, 1891 instead of *Patagornis* Moreno and Mercerat, 1891, following Patterson and Kraglievich ([14]; contra [2]). Following Agnolin (2006), the genus *Onactornis* is restricted to the species *O. depressus* Cabrera 1939, and probably *O. pozzi* Kraglievich, 1931, and the genus *Devincenzia* is considered as distinct from *Onactornis* and represented by its type species *D. gallinali* Kraglievich, 1932 [2,16,25].

The terms Phorusrhacoidea Ameghino, 1889, and *Phorusrhacos* Ameghino, 1887 are used instead of Phororhacoidea Patterson, 1941 and *Phororhacos* Ameghino, 1889 following Brodkorb [12] and Buffetaut [26].

I follow the anatomical nomenclature employed by Baumel and Witmer [27], with details on muscular attachments and syndesmology taken from Zinoviev [28].

2.2. Phylogenetic Analysis

With the aim to test the phylogenetic relationships of *Brontornis* proposed by Worthy and collaborators [24], I followed the character definition and numbers of Worthy et al. [24] (see Appendix A). The resulting data matrix was composed by 290 characters and 48 taxa.

The matrix was analyzed using TNT 1.5 [29], with all characters weighted equally. 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 in order 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.

Two different phylogenetic analyses were performed (Figure 1). The first one follows strictly that of Worthy et al.'s [24] unconstrained analysis. This resulted in the recovery of 13 Most Parsimonious Trees (MPTs), of 1567 steps, with a consistency index of 0.26, and a retention index of 0.65, which were summarized using a strict consensus tree (see Discussion).

As a branch support measure, Bremer support was calculated, and as a measure of branch stability, a bootstrap resampling analysis was conducted, performing 10,000 pseudoreplicates. Bremer support was calculated after searching for suboptimal trees and not with the script that accompanies the program. Both absolute and GC bootstrap frequencies are also reported (Figure 1).



Figure 1. Phylogenetic analysis depicting the position of *Brontornis burmeisteri*. (A) hypothesis proposed by Worthy et al. [24]; (B) hypothesis proposed in the present study; (C) consensus tree showing branch support measures. From left to right: Bremer support, absolute bootstrap frequency, and GC bootstrap frequency. The arrow indicates the position of *Brontornis*. Abbreviations. Anserif., Anseriformes; Cariam., Cariamiformes; Galli., Galliformes.

The second analysis was carried out with the modifications in the scorings of *Brontornis* and *Gastornis* remarked in the “Discussion” section. This resulted in the recovery of four most parsimonious trees (MPTs) of 1564 steps, with a consistency index of 0.26, and a retention index of 0.65, which were summarized using a strict consensus tree (see Discussion).

2.3. Institutional Abbreviations

FM-P, Field Museum of Natural History, Vertebrate Paleontology Collection; MACN A, Colección Nacional Ameghino, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina; MACN Pv, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina; MLP, Museo de La Plata, Buenos Aires,

Argentina; NHMUK, Natural History Museum of the United Kingdom, London, United Kingdom.

SYSTEMATIC PALEONTOLOGY

Neornithes Gadow, 1893

Galloanseres Sibley and Ahlquist, 1990

Brontornithes Dolgopod de Sáez, 1927

Brontornithidae Moreno and Mercerat, 1891

Brontornis burmeisteri Moreno and Mercerat, 1891

Synonymy. *Rostrornis floweri* Moreno and Mercerat, 1891; *Brontornis platyonyx* Ameghino, 1895; *Liornis floweri* Ameghino, 1895; *Callornis giganteus* Ameghino, 1895 in part; *Eucallornis giganteus* (Ameghino, 1895) Ameghino, 1901 in part [1,2,12,18,19].

Lectotype. MLP-88-91, left femur, tibiotarsus, fibula, and tarsometatarsus belonging to the same individual [12,30].

Diagnosis. Giant bird with graviportal proportions (tibiotarsus/tarsometatarsus ratio: 1.88) and the following unique combination of derived characters: distal end of tibiotarsus strongly anteroposteriorly compressed and with lateral margin forming an acute ridge of bone; distal end of tibiotarsus lacking supratendinal bridge [19], extensor groove shallow, poorly defined and medially tilted, retinacular tubercles feebly developed, prominent pyramidal-shaped prominence (central tubercle for attaching the *lig. meniscotibiale intertarsi*; [19,31]); tarsometatarsus having hypotarsus situated distal to the articular level of proximal cotylae [2], absence of posterior opening of the distal vascular foramen due to the unbifurcated condition of the *canalis interosseus distalis* [10], absence of fossa or scar for the first metatarsal [19], and proximodorsal margin of metatarsal trochlea III strongly projected [32].

Remarks. To date, the only certain member of Brontornithes and Brontornithidae is *Brontornis burmeisteri* [15]. However, recent finding of an incomplete distal tibiotarsus from the Oligocene of Bolivia [33] suggests that *Brontornis*-like taxa were probably more geographically and temporally widespread than thought.

Referred material. MLP 20-110, distal half of a left tibiotarsus with abraded distal condyles (Figure 2); MLP 20-581, distal end of left tibiotarsus without distal condyles (Figure 3).

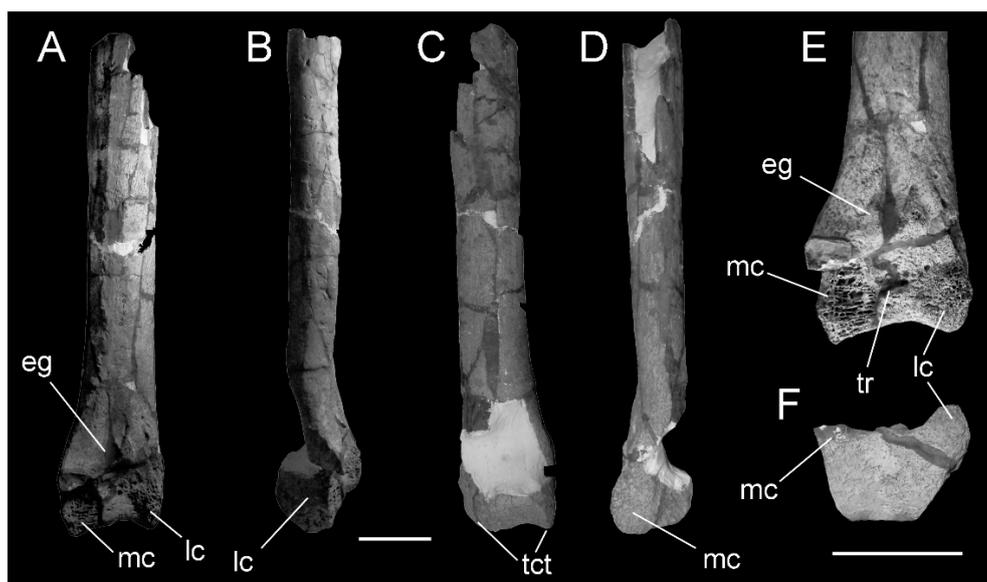


Figure 2. *Brontornis burmeisteri* (MLP 20-110) distal half of left tibiotarsus in (A) anterior; (B) lateral; (C) posterior; (D) medial views; (E) detail of its distal end in anterior view; and (F) distal view. **Abbreviations.** eg, extensor groove; lc, lateral condyle; mc, medial condyle; tct, *trochlea cartilaginosa tibialis*; tr, transverse ridge. Scale bar: 5 cm.

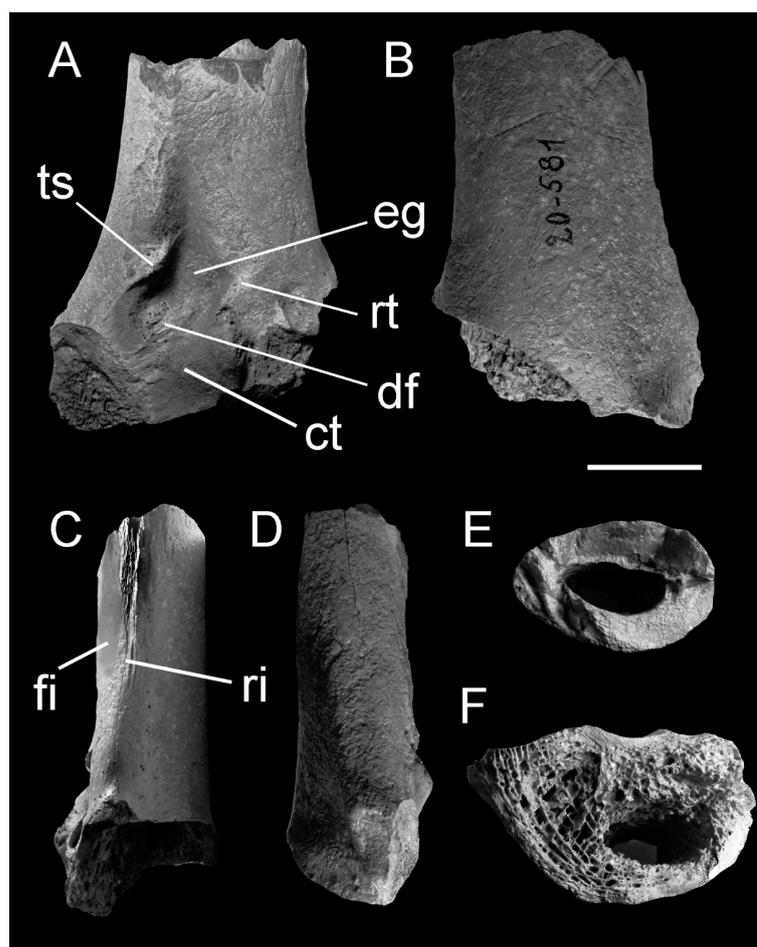


Figure 3. *Brontornis burmeisteri* (MLP 20-581) distal end of left tibiotarsus in (A) anterior; (B) posterior; (C) lateral; (D) medial; and (F) distal views; and (E) cross section of the shaft. **Abbreviations.** ct, central tubercle for the *lig. meniscotibiale intertarsi*; df, distal fossa; eg, extensor groove; fi, surface for fibula; ri, proximodistally extended lateral ridge; rt, possible lateral retinacular tubercle; ts, ridge representing medial retinacular tubercle. Scale bar: 5 cm.

Locality and horizon. The specimens come from old collections at the La Plata Museum, and thus, collecting data are scarce. MLP 20-110, originally referred by Moreno and Mercerat [3] to *Rostrornis floweri* (a junior synonym of *B. burmeisteri*; [1,9,12]), comes from the Santa Cruz Formation (Middle Miocene), at Santa Cruz province; more details on provenance are not available [3,30]. MLP 20-581 only figures in the catalogue as “*?Liornis* sp.” without any additional data. However, it is possible to infer that it corresponds to the distal end of tibiotarsus mentioned, and was briefly described by Dolgopol de Sáez [10]. If this is the case, MLP 20-581 was collected by Federico Berry in the Santa Cruz Formation (Middle Miocene) in Santa Cruz province.

3. Description

MLP 20-110 and MLP 20-581 represent the incomplete distal end of tibiotarsi lacking distal condyles. Because both materials are similar in all features, the description is based on the most complete individual (MLP 20-110) and is complemented in some cases by MLP 20-581.

The tibiotarsus shows a nearly straight shaft that is proximally ellipsoidal in cross-section, with convex anterior and posterior surfaces. Distally, the anterior surface of the bone becomes transversely flat. Although poorly preserved, the distal intercondylar fossa is transversely expanded and weakly undercuts the proximal margin of the distal condyles, forming a shallow transverse ridge of bone. Although distal condyles are abraded, they

appear to be not strongly posteriorly extended. The posterior *trochlea cartilaginosa tibialis* is poorly-defined, and is dorsoventrally low, with shallow delimiting crests. The extensor groove (*linea extensoria* in Buffetaut [33]) is aligned with the medial condyle, it is transversely wide and is poorly delimited by very shallow ridges of bone. Although there is no bony bridge on the extensor groove, there is a well-developed ridge of bone on the medial surface of the groove that indicates the insertion of a tendinal sling, which represents a low retinacular tubercle. Limiting the lateral surface of the distal end of the extensor groove there is a pyramidal bump (tubercle central of Ameghino [9]; central tubercle of Buffetaut [19,33]; attachment of the *lig. meniscotibiale intertarsi*; Zinoviev [28]), that is indistinguishable in size and shape from the ascending process of the astragalus [34] fused to the tibia and present in some ratite birds (e.g., *Rhea*, *Aepyornis*; see [33]) and basal ornithurines [35]. The distal crest for the attachment of the transverse ligament appears to be absent. In medial view, the shaft is smoothly convex, whereas in lateral view it shows a prominent proximodistally extended, sharp and acute bony crest.

4. Discussion

4.1. Comments on the Genus *Liornis* Ameghino, 1895

The genus *Liornis* was erected by Ameghino with the aim to include the single species *L. floweri* [2]. The material on which Ameghino based his species was the incomplete distal end of tibiotarsus, tarsometatarsus, and pedal phalanges of a single individual (Figure 4). Ameghino [9,36] assigned it to the Phorusrhacoidea, and distinguished *Liornis* from other terror birds by having the tibiotarsus with anteroposteriorly compressed and transversely expanded shaft, flat anterior surface of the distal shaft without deep muscular ridges and scars, poorly defined extensor groove, and absence of supratendinal bridge. The tarsometatarsus was characterized by its wide and anteroposteriorly compressed shaft and the absence of impression for the hallux. Due to these unique features, Dolgopol de Sáez [10], in his overview of phorusrhacoid birds, considered it as a valid genus, probably related to the genus *Brontornis* within the Brontornithidae (considered by that author as the Order Brontornithes). Kraglievich [6,11] retained *Liornis* as a valid taxon, and considered that due to its hindlimb proportions, it must be distinguished from *Brontornis* at the subfamily level at least, and thus, established the ad hoc subfamily Liorninae within the Brontornithidae [6]. More recently, Brodkorb, in his renowned “*Catalogue of fossil birds*” [12] synonymized *Liornis floweri* to *Brontornis burmeisteri* without discussing this in detail, a point of view followed by Tonni [1] among other authors. Later, Alvarenga [37] and Alvarenga and Hofling [2] considered that *Liornis* was a synonym of *Phorusrhacos longissimus*, but they did not discuss this point of view in detail; a criterion was followed by Bertelli et al. [38] and Alvarenga et al. [23]. More recently, Buffetaut [18,19,33] analyzed the materials of *Liornis floweri* and included it as a junior synonym of *Brontornis burmeisteri*. Ameghino [9] noted that the tarsometatarsus of *Liornis* differs from *Brontornis* in lacking any sign of scar for the hallux and because its tibiotarsus lacks a supratendinal bridge. However, both differences appear to be misinterpretations, probably due to the paucity of available specimens at that time. The presence of a hallux scar proposed by Ameghino (and followed by Agnolin [8]) was most probably a mistake based on artifact bone preservation. As noted by Buffetaut [19], there is no evidence of such scar in any of the available *Brontornis* and “*Liornis*” specimens. Further, the presence of a supratendinal bridge in all available specimens cannot be corroborated; instead, a pyramidal-shaped tubercle delimiting the extensor groove is present [19]. In this way, the differences reported by Ameghino between *Brontornis* and *Liornis* are not valid, and thus, *Liornis* should be considered its junior synonym, following previous authors.

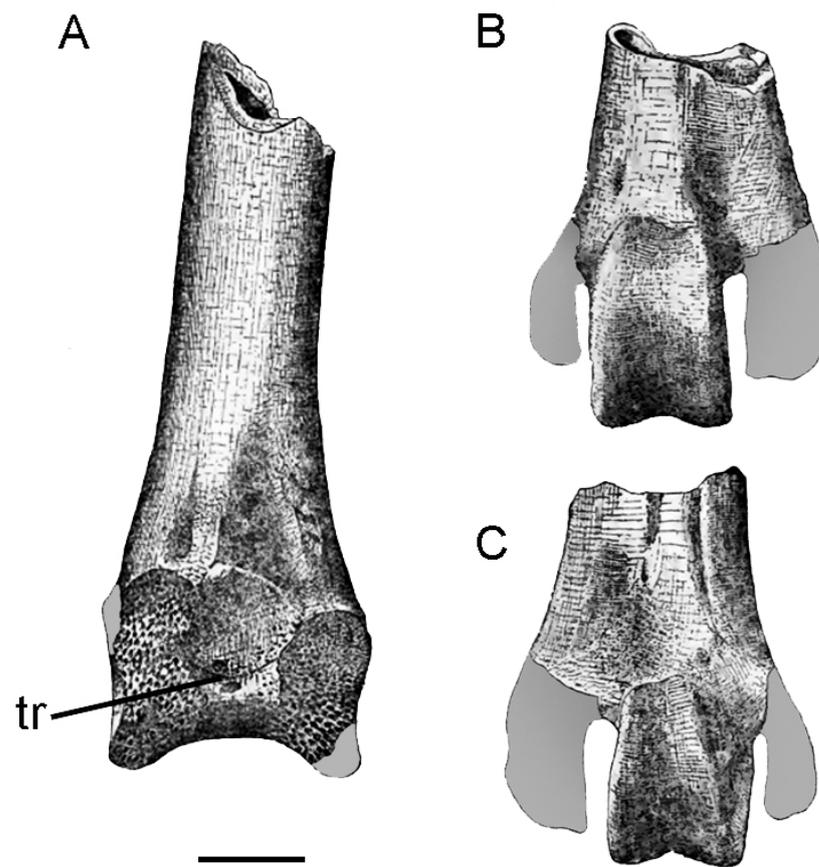


Figure 4. *Brontornis burmeisteri*; specimens on which Ameghino [9] based the species *Liornis floweri* Ameghino, 1895 (NHMUK PV A9058 and NHMUK PV A580). (A) right distal half of tibia-tarsus in anterior view; (B,C) distal end of left tarsometatarsus in (A) anterior; and (B) posterior views. (A–C) modified from Ameghino (1895). **Abbreviations.** tr, transverse ridge. Scale bar: 5 cm.

In sum, the tibia-tarsus of *Brontornis* (including *Liornis*) clearly departs from that of phorusrhacids (and most birds; Figure 5) in a unique combination of characters, including distal end strongly anteroposteriorly compressed with its lateral margin forming an acute ridge, strongly medially oriented medial condyle, small and rounded distal condyles that are joined by a transversely oriented ridge, low and poorly defined *trochlea cartilaginis tibialis*, absence of a supratendinal bridge, poorly excavated extensor groove that is medially tilted, feebly developed retinacular tubercles, and the presence of a prominent pyramidal-shaped prominence for attaching the *lig. meniscotibiale intertarsi* [3,10,19,33]. With this new evidence at hand, I re-scored the tibia-tarsus of *Brontornis* in the Worthy et al. [24] data matrix (see below).

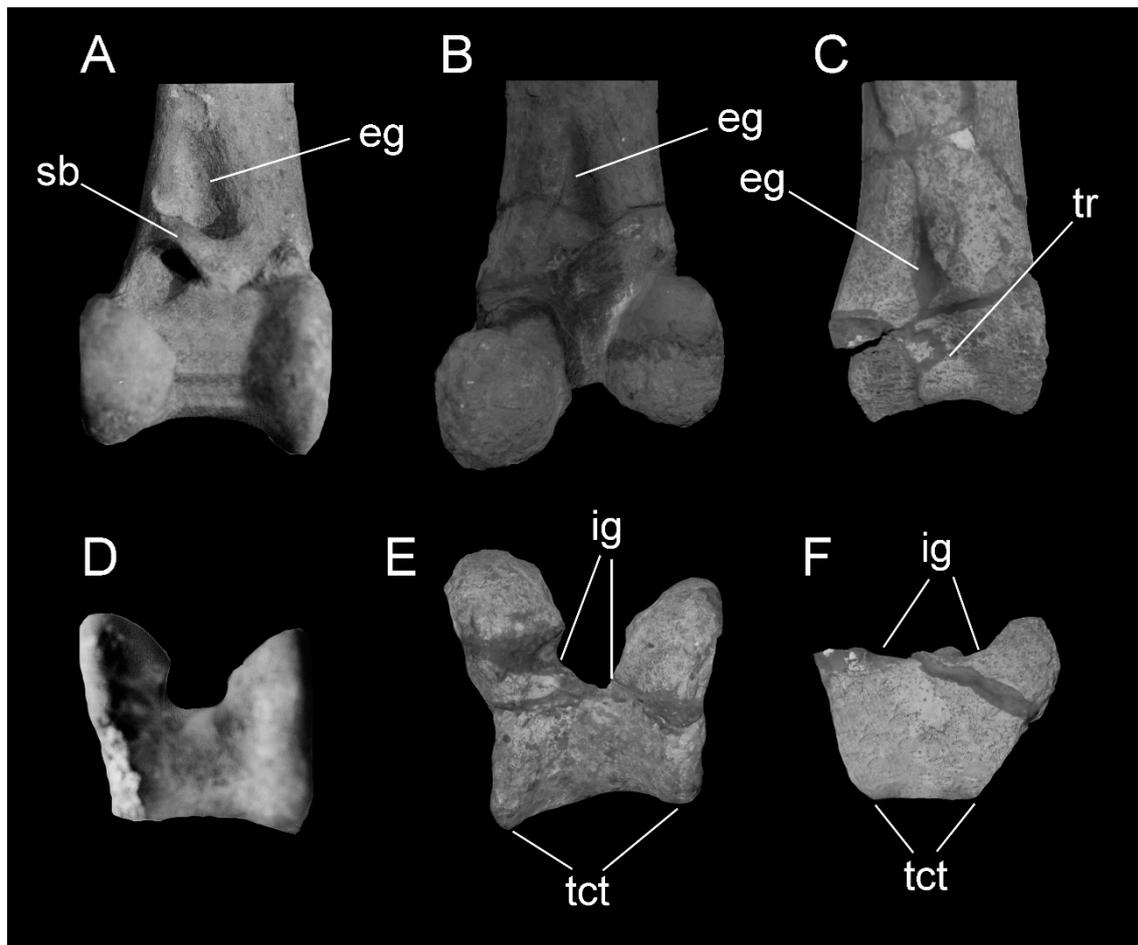


Figure 5. Distal end of left tibiotarsus of (A,D) *Onactornis pozzii* (MACN Pv-6554); (B,E) *Brontornis burmeisteri* (MLP 20-92/93); (C,F) *Brontornis burmeisteri* (MLP 20-110) in (A–C) anterior; and (D–F) distal views. **Abbreviations.** eg, extensor groove; ig, anterior intercondylar groove; sb, supratendinal bridge; tct, *trochlea cartilaginis tibialis*; tr, transverse ridge. Not to scale.

4.2. The Quadrate Bone Referred to *Brontornis burmeisteri* Moreno and Mercerat, 1891

Skull material referred to as *Brontornis* is very scarce and consists of isolated and incomplete jaws, as well as a single and incompletely preserved right quadrate bone [2]. The latter was ambiguously associated with *Brontornis* remains [3], and as such, it was not included in their data matrix by Worthy et al. [24], a criterion with which I concur.

In any way, this quadrate shows several features that are worth analyzing. This element was interpreted by Agnolin [8] as having only two condyles, constituting an important piece of evidence for galloanserine affinities of *Brontornis*. However, Agnolin misinterpreted the quadrate bone anatomy of *Brontornis* as demonstrated by Worthy et al. [24]. The later authors compared the quadrate with that of the phorusrhacid *Tolmodus* and found some similarities, including the presence of three quadrate condyles. In the view of these authors, the quadrate indicates that *Brontornis* belongs to Neoaves and not to Galloanseres.

However, the *Brontornis* quadrate (MLP 20-111; Figure 6) is different from the homologue of any known bird, especially with those of phorusrhacoids such as *Tolmodus* and *Patagorhacos* [39,40].

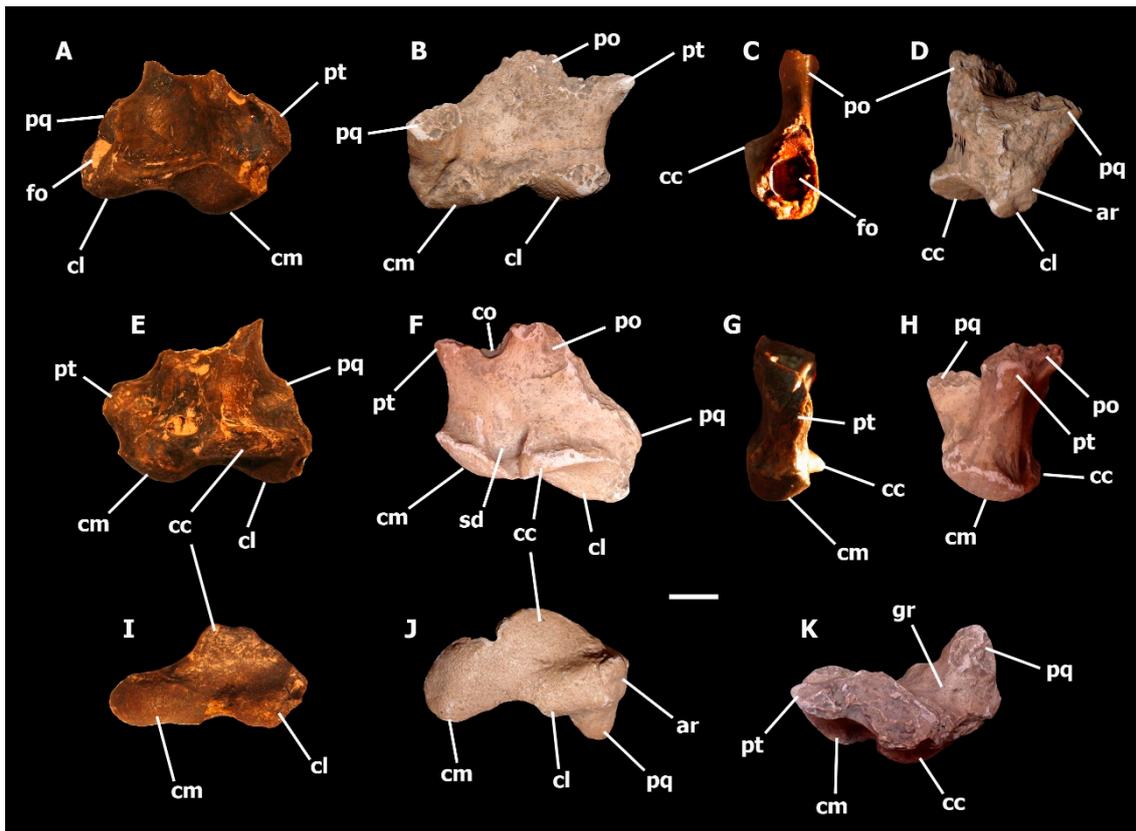


Figure 6. Comparisons between the quadrate referred to *Brontornis burmeisteri* (B,D,F,H,J,K; plaster copy of MLP 20-111) and the phorusrhacid *Patagorhacos terrificus* (A,C,E,G,I) in (A,B) anterior; (C,D) lateral; (E,F) posterior; (G,H) medial; (I,J) distal; and (K) proximal views. **Abbreviations.** ar, extended articular surface; cc, caudal condyle; cl, lateral condyle; cm, medial condyle; co, concave surface separating the pterygoid and orbital processes; fo, quadratojugal fossa or fovea; gr, wide groove separating the quadratojugal process and the orbital process; po, orbital process; pq, quadratojugal process; pt, pterygoid process; sd, supracondylar depression or fossa. Scale bar: 2 cm for B,D,F,H,J,K; 1 cm for A,C,E,G,I.

The distal end of the quadrate shows two well-defined condyles that are relatively elongate and differently oriented from that of phorusrhacids (Figure 6I,J). Worthy et al. [24] recognized the existence of a caudal condyle. However, I am not certain about the homology of this structure. At first, in contrast with phorusrhacids and other birds, this “caudal condyle” is represented by a shelf-like prominence that is dorsally positioned with respect to the distal condyles and shows a flattened to slightly concave distal “articular” surface. This condition is very different from that known in most other birds, such as in *Patagorhacos*, in which this condyle is at level with the medial and lateral condyles and is notably convex (Figure 6I). A bony flange somewhat similar to that present in *Brontornis* is exhibited by dromornithid anseriforms [41]. In *Brontornis* the “caudal condyle” is medially separated from the medial condyle by an oval-shaped and well-defined supracondylar depression that is unique to this taxon.

The pterygoid condyle is represented by an acute and prominent process that differs from that of most birds, including phorusrhacids, in which it is represented by a rounded articular surface. In pseudodontornithids and some anseriforms such as *Anseranas* and *Dendrocygna*, this condyle is also represented by a prominent and relatively acute process [31,42]. It is separated from the orbital process by a well-defined concave surface that is only represented by its base.

A particular trait of *Brontornis* is its unique and massive pyramidal-shaped quadratojugal process that is very different from the condition reported for most birds. Further, there is no evidence of a quadratojugal fossa or fovea, contrasting with the condition of most birds. Remarkably, the presence of a robust quadratojugal process and the ab-

sence of a quadratojugal fovea are features only known in conjunction in dromornithid anseriforms [41,43] and some ratites [43]. Further, *Brontornis* quadrate lacks any sign of pneumaticity, resembling also in this aspect dromornithids and ratite birds [43].

In sum, the quadrate of *Brontornis* is very apomorphic and is not matched by any known bird. The existence of a third condyle, the “caudal condyle” is somewhat dubious. The morphology of this condyle clearly departs from that of other birds, and because of its position it is possible that it does not contact the mandible; it is very similar to a bony flange present in dromornithid anseriforms. Further, as remarked by Worthy et al. [24] the association of this bone with those unambiguously belonging to *Brontornis* is not clear.

Characters modified from Worthy et al. (2017)

As indicated above, and based on the detailed review of new specimens, several postcranial features of *Brontornis* should be reinterpreted, and this has impact on the codifications carried out by Worthy et al. [24]. As follows, we discuss the changes made on *Brontornis* scorings.

Femur

ch#213. *Brontornis burmeisteri* re-scored from 1 to 0. As observed in the femur of *Brontornis* the patellar groove of the distal end of femur is notably transversely wide (see pl. III Figure 1 in Moreno and Mercerat [3]), being much wider than the lateral condyle. In this way, I re-score *Brontornis* as 0.

Tibiotarsus

ch#240. *Brontornis burmeisteri* re-scored from 1 to 0. As indicated in the description above, there exists a pyramidal-shaped prominence at the lateral surface of the extensor groove that represents the attachment for the lig. meniscotibiale intertarsi of Zinoviev [28]. The presence of such prominence is uncommon among birds (it is present in some flightless ratites as *Emeus*, among others) and may be considered an autapomorphic feature of *Brontornis* (see [19]; Figure 3).

ch#246. *Brontornis burmeisteri* re-scored from ? to 0. In the distal end of tibiotarsus MLP 20-581 the groove for the *m. fibularis* is anteriorly extended, as shown by the concave impression located at the lateral surface of the extensor groove (Figures 2 and 3).

ch#247. *Brontornis burmeisteri* re-scored from ? to 0. In the distal end of tibiotarsus MLP 20-581 a ridge located adjacent to the extensor groove, represents in all probability the lateral retinacular tubercle (Figure 3).

ch#248. *Brontornis burmeisteri* re-scored from 1 to 0. This character is somewhat difficult to score, especially because of the absence of a supratendinal bridge in *Brontornis*. However, as can be extrapolated from the distal end of tibiotarsus MLP 20-581, the distal aperture of the extensor groove shows a subvertically oriented main axis, and thus, it is here scored as such (Figure 3).

Tarsometatarsus

ch#253. *Brontornis burmeisteri* re-scored from 1 to 0. In a completely preserved *Brontornis* tarsometatarsus (FM-P13259) the lateroplantar margin of the cotyle is notably dorsally projected, and consequently, it is re-scored as 0 (Figure 7). This character was previously considered by Bourdon [44] as a synapomorphy of the clade Anseriformes + Pelagornithidae.

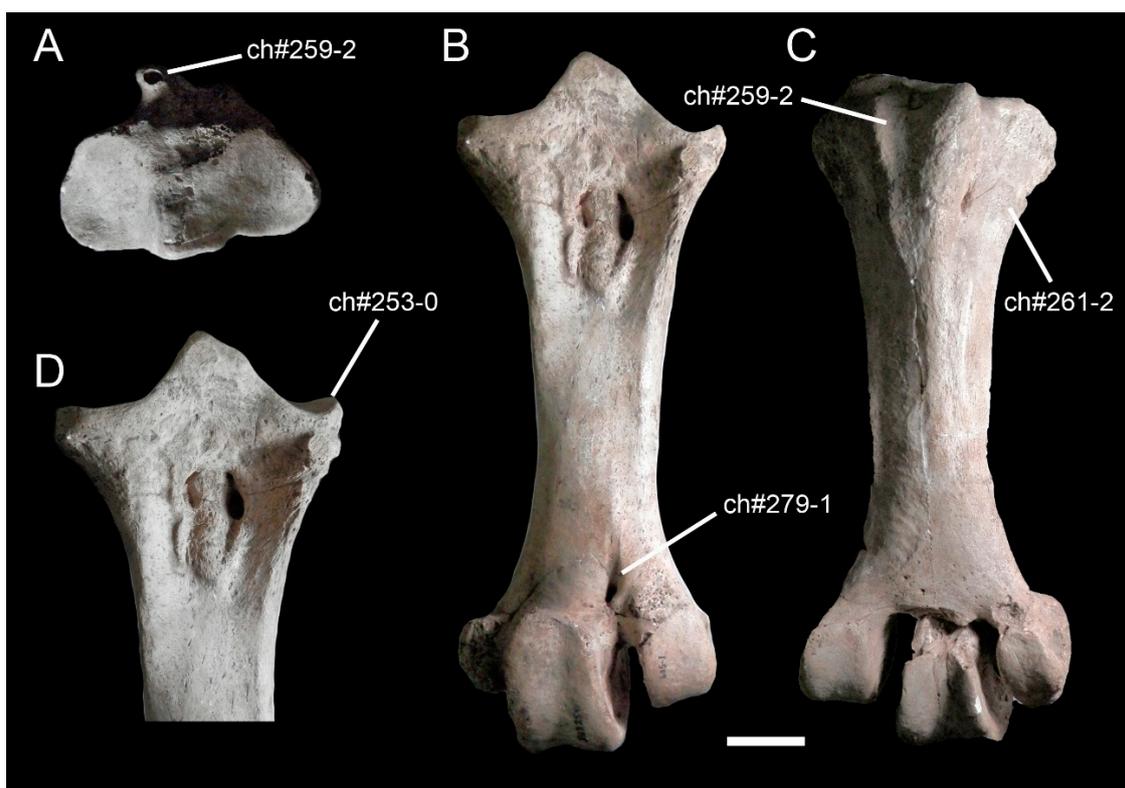


Figure 7. Left tarsometatarsus of *Brontornis burmeisteri* (plaster copy of FM-P13259) in (A) proximal, (B) anterior, and (C) posterior views. (D) detail of the proximal region of the tarsometatarsus in anterior view. The notation includes the characters that were modified from Worthy et al. [24]. ch#253-0, plantar-lateral side of *cotyla medialis* elevated proximally; ch#259-2, hypotarsus with two ridges; ch#261-2, surface from medial calcaneal ridge to anterior margin of medial shaft concave (shallow fossa parahypotarsalis medialis); and ch#279-1, *foramen vasculare distale* small and distinct. Scale bar for A to C: 4 cm; D, 3.5 cm.

ch#254. *Gastornis parisiensis* re-scored from 1 to 0. A complete tarsometatarsus of *G. parisiensis* described and illustrated by Martin [45], Buffetaut and Angst [46], and Mourer Chauviré and Bourdon [47] clearly showed that the intercotylar eminence of the tarsometatarsus in this taxon was prominent and proximally extended. In addition, *G. geiselensis* (a species closely related or even a synonym of *G. parisiensis*) shows prominent intercotylar eminence [48].

Gastornis giganteus was re-scored from 1 to ?. The tarsometatarsus of *G. giganteus* is known by fragmentary material with eroded intercotylar prominence [49,50]. Because of that, the morphology of this eminence in *G. giganteus* is considered as unknown.

ch#259. *Brontornis burmeisteri* re-scored from 4 to 2. Worthy et al. [24] consider the block-like hypotarsus as a derived trait shared between *Brontornis* and phorusrhacoids. In the same line of thought, Alvarenga and Hofling [2] include as diagnostic of phorusrhacoids a block-like hypotarsus that is subquadrangular in proximal view and subtriangular in posterior view, lacking crests and grooves. However, as recognized by Worthy et al. [24] the hypotarsus of *Brontornis* is distinctive and very different from the condition exhibited by phorusrhacids, (e.g., *Phorusrhacos*, *Tolmodus* [9,24,49]). In *Brontornis* the hypotarsus in proximal view is subtriangular in contour, showing a prominent and thick medial crest, and a slightly pronounced lateral edge, both separated by a longitudinal tendinal groove (Figure 7). This morphology is indistinguishable from that of *Gastornis* [8,45,49], and thus, is codified as such (state 2).

ch#261. *Brontornis burmeisteri* re-scored from 3 to 2. *Brontornis* was scored as having a flat or convex surface between the medial calcaneal ridge and the medial margin of the

shaft. However, in *Brontornis* (FM-P13259) there exists a notable concave surface medial to the medial calcaneal ridge (Figure 7), and thus is scored as “2”.

ch#271. *Gastornis giganteus* re-scored from 0 to ?. The incomplete nature of the distal tarsometatarsus of *Gastornis giganteus* precludes the clear recognition of a surface for articulation with digit I. In this way, this character is coded as “?”.

ch#279. *Brontornis burmeisteri* re-scored from 3 to 1. The tarsometatarsus of *Brontornis* was scored as lacking a distal vascular foramen by Worthy et al. [24]. However, such foramen is present in available specimens [9,19] (Figure 7).

Finally, I included in the data matrix the codifications of characters from 280 to 283. These refer to the shape of pedal phalanges and were scored by Worthy et al. [24] as “?”. Probably, Worthy et al. [24] did not include these scorings because there was no direct evidence indicating the phalanges previously referred to *Brontornis* unambiguously belong to this taxon. However, two phalanges are preserved in the single associated specimen on which *Liornis floweri* (a junior synonym of *Brontornis burmeisteri*) is based (NHMUK PV A580) [9,19]. These phalanges are massive, transversely wide, and ventrally flat, a combination of features that are exhibited by phalanges previously referred to *Brontornis* [2,3,9]. In this way, the specimen NHMUK PV A580 confirms previous referral of pedal phalanges to *Brontornis*, and thus, are coded in the data matrix as such.

4.3. Phylogenetic Results

With the aim to test Worthy et al.’s [24] analysis, only hindlimb material was included in the data matrix. Worthy et al. [24] did not include in their work several bones that have doubtful association with material unambiguously belonging to *Brontornis*. These materials include vertebrae [3,9], quadrate [3], and mandible [2,3,9,18]. These elements, particularly the mandible, show several features reminiscent to giant galloanseres such as dromornithids and *Gastornis* [8,18], and their inclusion in the data matrix may give additional support to the galloanserine affinities of *Brontornis*. In any case, it is preferred to exclude the codification of these elements in the data matrix following Worthy et al. [24].

The phylogenetic analysis here performed resulted in the nesting of *Brontornis* among Anseriforms in a clade formed by gastornithids and dromornithids, in a position similar to that proposed by Agnolin [8] (Figure 1). It is worthy of mentioning that forcing the position of *Brontornis* as a cariamiform results in a tree 1569 in length, having five additional steps.

The clade grouping dromornithids and gastornithids was named by Worthy et al. [24] as Gastornithiformes, to which, based on present analysis, *Brontornis* may belong. In any case, this clade formed by giant graviportal fowls is sustained almost by hindlimb features (characters 202, 211, 215) and it is not improbable that this group may be the result of convergent features related to graviportalness (see discussion in [24]). In their work, Worthy et al. [24] concluded that *Brontornis* resolved as sister to Cariamiformes, but with very low support. They recognized that *Brontornis* was very different from other birds, and indicated in several parts of the text that the position of *Brontornis* in the phylogenetic tree is unstable. Because I agree with Worthy et al. [24] in that *Brontornis* is still incompletely known, it is possible that its inclusion within Gastornithiformes is not strongly warranted.

Worthy et al. [24] listed some similarities shared by the hindlimb of *Brontornis* and phorusrhacids, including a lateral excavation at the medial surface of the lateral condyle of femur, and a block-like hypotarsus. The first condition is known to occur in *Gastornis* and dromornithids [50,51], suggesting that it is not only exclusive of phorusrhacids, but is also widespread among giant anseriforms. On the other side, as indicated above and as recognized by Worthy et al. [24], the morphology of the hypotarsus of *Brontornis* is very different from that of phorusrhacids, being very similar to the condition exhibited by *Gastornis* and dromornithids [19,41] (see above, analysis of character 259). Both in *Gastornis* and *Brontornis*, the hypotarsus is subtriangular-shaped in proximal view, with a prominent medial crest and a reduced lateral edge. Further, Worthy et al. [24] recognize that mandibular and hindlimb shape structure of *Brontornis* differ substantially from

phorusrhacids. The same seems to be true for the quadrate bone, as indicated in the descriptive section of the present contribution.

5. Conclusions

A review of the character codifications for *Brontornis burmeisteri* carried out in the comprehensive work of Worthy et al. [24] resulted in a change in the phylogenetic position of this taxon. This change argues against the sentence of Worthy et al. [24] that declares that it was conclusively shown that *Brontornis* is not a galloanserine bird. After few changes in the data matrix, *Brontornis* results as part of a clade composed by the giant anseriforms designated by Worthy et al. [24] as Gastornithiformes. This result is in agreement with recent proposals that excluded *Brontornis* from phorusrhacoid cariamiforms (where it was traditionally nested) and included it among Anseriformes [8,16,18].

Graviportal anseriforms of the clade Gastornithiformes (*sensu* [24]) are represented by Eurasian and North American Paleogene *Gastornis* and kin [17] and by Paleogene and Neogene Australasian members of the Dromornithidae [41,52]. To these, it should now be added the Paleogene-Neogene brontornithes from South America [17,33]. If this phylogenetic grouping is correct, a widespread radiation of giant anseriforms occurred along several landmasses during the Paleogene. The paucity of the fossil record of these giant birds still precludes a detailed framework to understand the palaeobiogeographic history of these birds.

Finally, the nesting of *Brontornis* among herbivorous giant anseriforms [5,17,24,46], together with several aspects of its mandibular morphology [8,18] reinforces previous thoughts that *Brontornis* was herbivorous in habits (Figure 8).

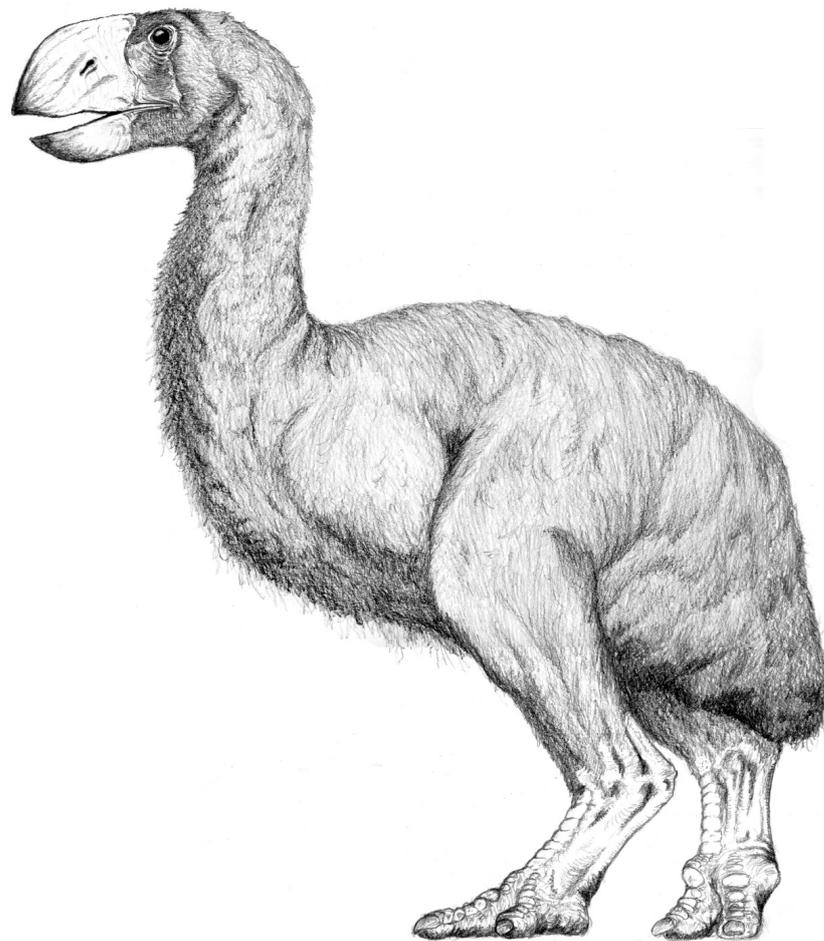


Figure 8. Life reconstruction of *Brontornis burmeisteri*. Artwork by Agustín Agnolin.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Data matrix modified from Worthy et al. [24]. The number of characters and taxa (290 and 48, respectively) as well as character description and states follow Worthy et al. [24]. Scoring modifications are almost restricted to *Brontornis* and *Gastornis* species (see above).

Tinamus_robustus

200010001002200000000000100001200000000- 330000000?00111110000100100100000
0022221100211111001200311100110010010021-110212012110012121111010110101130001
0100021000001010010000022002120000100000000010110100011100001000220000001001
01100011001100010111000110012200311021010010110101100020012000

Vegavis_iaai

??
0010001001000010100?10????0000-1000000001220-000?000????????????????01102011210101?010
1021?0????20????00100000010012001100401101000112001101010020????????????00100??1????
???12200??111

Chauna_torquata

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01200200- 010000011011000000011000000100010010001010000001110000100011000011010
000010121021000020011000122021100101000010010200000010?101

Anhima_cornuta

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1210210000200110011200221001010000000101000000102101

Wilaru_tedfordi

??
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Presbyornis_pervetus

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21000020001001200011100100110020010200?????3?2101

Anseranas_semipalmata

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101101000000000011001101110000110000000010010000100001110000000100000110100001
0011102100002000000000011110000100011000020000002021-0

Dendrocygna eytoni

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 202001000000011011110120110001110000000001001000010110110010000111000011010000
 001210210000200100002101311001011110100112000000302??0

Cereopsis novaehollandiae

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Anser caerulescens

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 0121021000000100012200311001012010210111000000302100

Malacorhynchus membranaceus

021112111102210101111011002210211011111022110111101000110111131001110100111012
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 10111002001210120012021100111000001000110100002011010000000011110001101000000
 12102100001000000120003110000111102101120000?0302100

Tadorna tadornoides

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Leipoa ocellata

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Megapodius reinwardt

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Eulipoa wallacei

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Megapodius eremita

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Alectura lathamii

220010001000101001010101000120110000001010120000110101011101000200110000010
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 011100001010120010110110001111011000010110002100002000021022100

Talegalla fuscirostris

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Macrocephalon_maleo

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Gallus_gallus

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022100

Phasianus_colchicus

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Coturnix_pectoralis

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Acryllium_vulturinum

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Megavitiornis_altirostris

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Crax_rubra

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Ortalis_yetula

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100

Sylviornis_neocaledoniae

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Dromaius_novaeollandiae

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Paracathartes_howardae

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Burhinus_grallarius

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Porphyrio_melanotus

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 01000000002110

Antigone_rubicunda

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 000000110101110110110000001100100010101110100000001000100000010010011000
 11001100000210100000101100110010200110012211221001011110200002000000002110

Brontornis_burmeisteri

??
 ???
 ???
 0000000000112202100010101101001-111102???????

Gastornis_parisensis

?22110??101100?0001?01002100000??????1?????
 ??????1-10-0-----?0??1?????-----0-----?????????
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Gastornis_giganteus

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Tolmodus_inflatus

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Cariama_cristata

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 1110001111012201001010100100001[9]001010111010000000111100001110101110011
 10001011001120100012001100101000200010011221212021012110100101100000002??0

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