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Too Much Terror: A Gigantic Terror Bird (Cariamiformes: Phorusrhacidae) from the Middle Miocene of La Venta, Colombia

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Abstract

Phorusrhacids correspond to a group of birds considered to be apex predators, which are a common element of the American fossil Cenozoic avifauna, especially in Argentina, where it is not unusual to find at least two species of terror birds. Nevertheless, the presence of more than one species of terror bird outside Argentina is null. Here we report a second terror bird from the middle Miocene of La Venta locality. The new specimen could reach approximately 180 kg, being about 15% larger than the previous report of a terror bird for the locality. Although it is not possible to completely discard the possibility of these two specimens belonging to a dimorphic species, morphological differences may indicate so. Certainly, the presence of two gigantic terror birds coexisting in the La Venta locality represents an interesting scenario for further studies on their ecology and niche partitioning; this could be an argument for the presence of large open areas within the forests and wetlands of La Venta, further supporting the complex and diverse ecosystems in this region during the Middle Miocene period.

Keywords: Phorusrhacidae; predatory guild; Miocene; South America

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1. Introduction

Large terrestrial birds have often been assigned to the polyphyletic group ratites, a paleognath clade that include emus, cassowaries, kiwis, rheas and ostriches [1,2]. Large terrestrial birds have inhabited Madagascar (*Aepyornis*), Australia (*Dromornis*), New Zealand (*Dinornis*), and Eurasia (*Gastornis* and *Pahystruthio*), amongst other regions around the globe [3]. In South America, *Brontornis burmeisteri*, probably the largest bird that ever

inhabited South America and one of the largest birds to have ever existed, was present throughout the Lower to Middle Miocene of Argentina [1–7]. Undoubtedly, the most iconic group of large terrestrial birds in South America are the phorusrhacids (Cariamiformes: Phorusrhacidae), popularly known as "terror birds" [8], a group of derived Neoaves that evolved a unique hunting technique based on hatching-like strikes with their beaks, only possible due the loss of cranial kinesis [9–11]. This group of cursorial birds [12–14] shared the terrestrial predatory guild during the Cenozoic with large sparrassodonts and Sebecids [15]. The largest of the terror birds have been classified into the subfamily Physornithinae, an evolutionary clade that might have included very large sit-and-wait predators, such as *Physornis* and *Paraphysornis* [16], although the phylogenetic relations of large terror birds still remain unresolved (e.g., [17,18]).

Among phorusrhacids, body size has been often interpreted in relation to niche partitioning, with the smaller taxa (e.g., Psilopterines) probably relying on small mammals and vertebrates in their diets, while the largest Phorusrhacinae and Physornithinae probably consumed larger prey [16,19,20].

Although more than a century of exploration and field research has led to the discovery of a vast paleocommunity of Middle Miocene aquatic and terrestrial vertebrates [21–24], the avifauna from La Venta locality in Colombia is still poorly represented in the fossil record. Nonetheless, these scant avifaunal records can contribute to reconstructing the paleo-environments present at La Venta during this time period. For example, there are specimens referred to as forest-dwelling birds such as jacamars, and birds related to aquatic environments such as limpkins (although see [25] for a different assignation), jabiru, darters, and hoatzins [22,26,27]. More recently, the first record of terror birds for the locality was described, also suggesting the presence of open areas [28]. Clearly, the presence of these birds indicates a humid environment, similar to lowland neotropical wetlands with a mosaic of swamps, large water bodies, forests with arboreal vegetation and open grasslands [24,29].

Recently, one study [30] reported the presence of a large tibiotarsus tentatively assigned to Brontornithidae. Here, we review this same specimen, allowing us to assign it to Phorushracidae. The aim of this study is to describe the second record of a terror bird from the tropical Miocene of La Venta in Colombia (Figure 1), based on the distal portion of a right tibiotarsus (MT-0201); it is a notoriously gigantic bird.

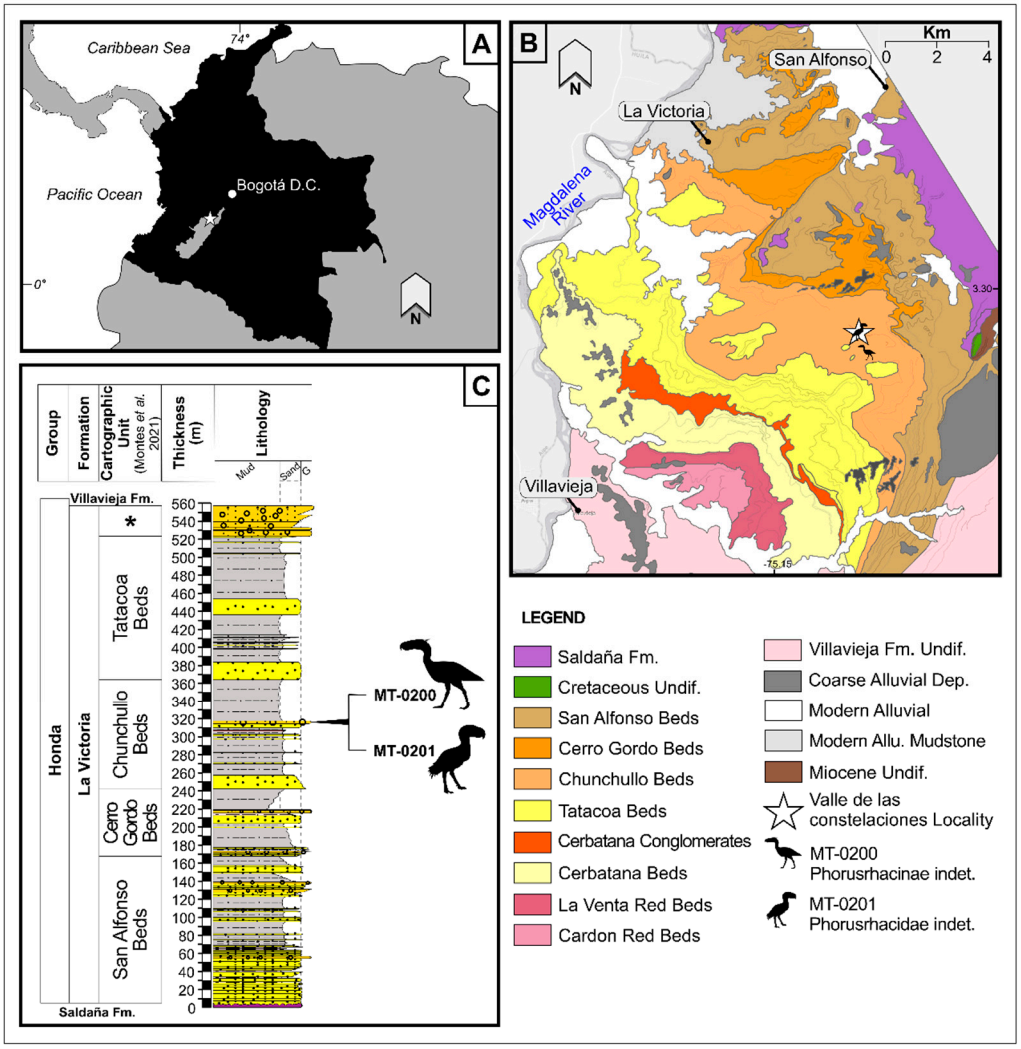

Figure 1. Geographic and stratigraphic occurrence of MT-0201 (Phorusrhacidae indet.). (**A**) Map of Colombia showing the Tatacoa Desert in the Huila department. (**B**) Geological map of the Honda Group highlighting the Valle de las Constelaciones locality and the two occurrences of Phorusrhacidae (Modified from [31]). (**C**) Stratigraphic column from La Victoria Formation illustrating the provenance of MT-0200 and MT-0201 (Modified from [29]). Cartographic Unit marked with an asterisk (*) denotes the Cerbatana Conglomerates.

2. Materials and Methods

If not indicated otherwise, the osteological terminology follows [32] and the arthrological terminology follows [33]. Proportional body size was estimated based on the distal width of the tibiotarsus compared with that of other phorusrhacids.

3. Results

SYSTEMATIC PALEONTOLOGY
Class AVES Linnaeus, 1758
Subclass NEOGNATHAE Pycraft, 1900
Order CARIAMIFORMES Verheyen, 1957
Suborder CARIAMAE Fürbringer, 1888
Family PHORUSRHACIDAE (Ameghino, 1889)
Subfamily 'PHORUSRHACINAE'? Ameghino, 1889
Gen. et sp. indet.

3.1. Material Studied

MT-0201, fragmentary distal portion of right tibiotarsus.

3.2. Geological Setting

MT-0201 was recovered from La Venta, a Middle Miocene fossiliferous deposit currently found within a tropical deciduous woodland area, called "El Desierto de La Tatacoa", located between the Central and Eastern Andean cordilleras in central Colombia (Figure 1). The area is primarily assigned to the Honda Group, which comprises two main geological formations: the older La Victoria Formation (16.0–12.6 Ma) and the younger Villavieja Formation (12.6–10.58 Ma) [29]. This region has yielded one of the most diverse vertebrate assemblages of the Miocene in northern South America [23].

Within this stratigraphic framework, the Chunchullo Beds—a well-defined lithostratigraphic unit of the middle Miocene deposits of the Upper Magdalena Valley [29,31,34]—form part of the La Victoria Formation and reach a total thickness of approximately 120 m (Figure 1C). From base to top, this unit consists of: (1) a basal layer of coarse to very coarse sandstone; (2) an interval of interbedded mudstones and medium- to coarse-grained sandstones; (3) two overlying layers of medium- to coarse-grained sandstone and conglomerates; and (4) an uppermost layer of uniform mudstone [29]. Radiometric and magnetostratigraphic data constrain the age of the conglomeratic layers to approximately 11.81–12.92 Ma in underlying sections [35] and 11.82–12.91 Ma in overlying sections [36], placing them firmly within the Middle Miocene.

The fossil specimen MT-0201 was found at the Valle de las Constelaciones locality (03°16′48.5″ N, 75°07′08.8″ W), west of a small stream, in a gully connected to a drainage channel. It was collected ex situ by one of the authors; however, the composition of the adhering matrix—granule-sized clasts embedded in a sandy matrix—strongly indicates that it originated from the conglomeratic horizon of the Chunchullo Beds (*sensu* [29]), the same layer from which the first documented record of Phorusrhacidae (MT-0200) was recovered [28].

3.3. Description

MT-0201 is a fragmentary distal portion of right tibiotarsus (Figure 2). The distal preserved portion consists of a very stout bone (Table 1), with the condylus medialis craniomedially projected as is typical of phorusrhacids [14,20]. Both cristae limiting the shallow trochlea cartilaginis tibialis are poorly developed and projected caudally. The pons supratendineus seems to have been present, but is quite broken, making the degree of its development impossible to establish. Distal to the pons, there is a very well-marked rounded deep pit present as in all phorusrhacids [28].

Table 1. Measurements (in cm) of the distal tibiotarsi of the La Venta phorusrhacids compared to that of *Brontornis burmeisteri*. Measurements follow [28]. Abbreviations: CLE, condylus lateralis cranio-caudal extension; CME, condylus. medialis cranio-caudal extension; DW, distal width (measured between epicondyli).

Taxon	Specimen	DW	CLE	CME
Phorusrhacidae indet.	MT-0201	11.422	7.897	9.677
Phorusrhacinae indet. *	MT-0200	8.881	~6.2	7.544
Brontornis burmeisteri	MLP 20-88	12.525	10.433	12.977

* Taken from Degrange et al. [28].

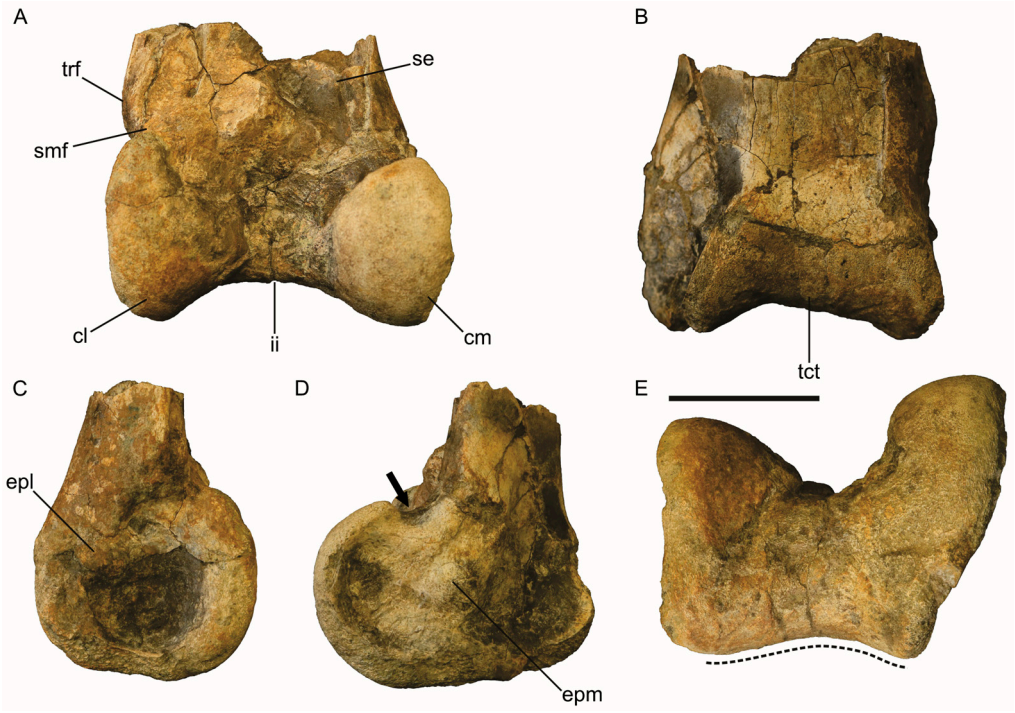

Figure 2. MT-0201, Phorusrhacidae indet., distal extremity of a right tibiotarsus in (**A**) cranial; (**B**) caudal; (**C**) lateral; (**D**) medial; and (**E**) distal views. The black arrow points at the notch located at the base of the condylus medialis, and the black curved dashed line indicates the asymmetric profile of the trochlea cartilaginis tibialis. Abbreviations: cl, condylus lateralis; cm, condylus medialis; epl, epicondylus lateralis; epm, epicondylus medialis; ii, incisura intercondylaris; se, sulcus extensorius; smf, sulcus m. fibularis; tct, trochlea cartilaginis tibialis; trf, tuberculum retinaculi m. fibularis. Scale = 5 cm.

The preserved portion of the sulcus extensorius is proportionally shallow; it is narrow (wider in *Phorusrhacos*) and medially located, as in *Phorusrhacos*, *Devincenzia* and *Patagornis*. The condylus lateralis is rounder and more cranially projected than in MT-0200. The sulcus m. fibularis is wide and shallow, laterally disposed. The depression epicondylaris lateralis is very deep (shallower in MT-0200). The epicondylus lateralis is small and distally located (particularly large in MT-0200, absent in *Devincenzia*). Both condyli are very wide and project cranially, with the condylus medialis markedly more projecting than the lateral, similar to the condition observed in *Paraphysornis*, *Devincenzia*, Mesembriornithinae and Psilopterinae, but unlike Patagornithinae and *Phorusrhacos*, where both condyli are equally projecting. The condylus medialis projects strongly medially, more than in MT-0200 and *Phorusrhacos*, and similar to *Devincenzia*. MT-0201 has a notch located at the base of the condylus medialis, which differentiates it from MT-0200, while closely resembling the condition observed in *Devincenzia* and *Paraphysornis*. The tuberculum retinaculi m. fibularis is very stout, projects strongly laterally (markedly less in *Devincenzia* and *Paraphysornis*) and is proximally located. The lateral scar of the retinaculum m. fibularis is a very well-marked rounded scar, located laterodistally to the pons supratendinueus. This differs from that of MT-0200, in which the lateral scar of the retinaculum m. fibularis is located laterally to the pons supratendineus on the lateral margin of the shaft, and from *Phorusrhacos*, in which the lateral scar of the retinaculum m. fibularis is located laterally on the pons. The incisura intercondylaris is wide as in *Devincenzia*, although shallower (narrow and deep in *Phorusrhacos*). The epicondylus medialis is stout, rounded, extends strongly medially (contrary to *Phorusrhacos*, *Devincenzia* and *Paraphysornis*), is located more caudally on the shaft, and is bounded caudally by a deep fovea and cranially by a shallower fovea. The trochlea cartilaginis tibialis is wide, although shallower than in MT-0200, but it is more

extended proximally than in MT-0200 and *Paraphysornis*. When viewed distally, this trochlea shows an asymmetric profile, being deeper medially (symmetrical in MT-0200), a feature that seems exclusive of this taxon (Figure 2E).

4. Discussion

Although the fossil is fragmentary, preventing a phylogenetic analysis using the most up-to-date proposals (e.g., [16–18]), MT-0201 can unequivocally be assigned to phorusrhacids based on the following characteristics: a craniomedially projected condylus medialis, the quadrangular shape of the distal portion of the tibiotarsus when viewed distally (i.e., poorly developed and projected cristae limiting the almost flat trochlea cartilaginis tibialis), the presence of an oblique and robust pons supratendineus, a medially located sulcus extensorius, a wide and deep incisura intercondylaris, and a wide trochlea cartilaginis [20,28]. Previous assignation of this material indicated that MT-0201 may belong to a Brontornithidae [30]. However, MT-0201 differs from the monospecific family Brontornithidae in having a pons supratendineus (lacking in *Brontornis burmeisteri*; [4,6,7,37]), a slenderer (i.e., more gracile) constitution, a wider incisura intercondylaris (narrow in *Brontornis*), a less extended cranially condylus lateralis, and a medial extension of the condylus medialis (absent in Brontornithidae). Additionally, in Brontornithidae, both condyli are much more extended distally, making the incisura intercondylaris much deeper in cranial view [38], a condition absent in Phorusrhacidae (Figure 3).

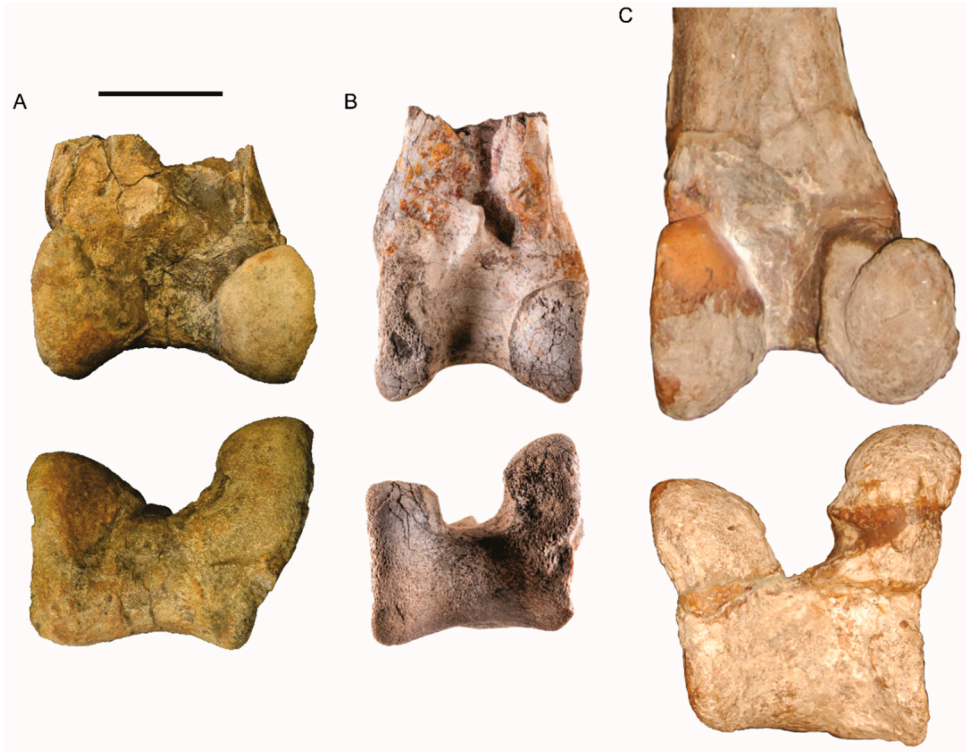

Figure 3. La Venta phorusrhacids. (**A**) Distal portion of right tibiotarsus MT-0201, and (**B**) left tibiotarsus MT-0200 (mirrored for comparisons), compared with (**C**) distal extremity of the left *Brontornis burmeisteri* MLP 20-88 (mirrored). Scale = 5 cm.

MT-0201 corresponds to the second phorusrhacid reported for the La Venta locality, with MT-0200 being the first and considered one of the largest terror birds that have ever existed [28]. With MT-0201 being markedly larger and stouter, the question of both specimens corresponding to the same species or to different species arises. Differences in size between individuals of the same species can be related to age, sexual dimorphism, or polymorphism. As far as we know, there is only one record of a juvenile phorusrhacid, which belongs to

Patagornis marshi (FM-P13213), for which partial hind limb bones were unearthed, including one fragmentary tibiotarsus. Unfortunately, this bone is quite damaged in the known juvenile specimen, but ontogenetic differences with adult specimens assigned to *Patagornis* can be appreciated, including the width and depth of the trochlea cartilaginis tibialis as well as its proximal extension, being poorly extended, wide and shallow in the juvenile, and deeper, more marked and extended proximally in the adult. Moreover, the distal portion of the tibiotarsus is poorly ossified in juvenile stages (e.g., [39–41]), which is certainly not the case for the smaller phorusrhacid (MT-0200) recovered from the same locality at La Venta [28]. Both MT-0200 and MT-0201 correspond to adult specimens.

Given the fragmentary nature of the available records of terror birds at La Venta, we cannot provide definitive evidence as to whether MT-0200 and MT-0201 represent different sympatric species or if differences in size can be attributed to intra-specific variation. It is worth noting, however, that there is a 15% difference in size between them (see [28]: Table 1). Differences in size among conspecific terror birds are only larger for specimens known from *Patagornis marshi*—about 16% [14,28]. In *Mesembriornis milneedwardis*, the largest differences among adult specimens is 9%; in *Procariama simplex*, it is 8%, in *Psilopterus lemoinei*, 12%, and, in *Phorusrhacos longissimus*, about 8%. There are also several differences in the shape of the tibiotarsus between the two phorusrhacid specimens that have been found at La Venta (Figure 3). In MT-0201, the condylus lateralis is markedly wider, and the condylus medialis is more medially projecting. Although the distal pit is present in both phorusrhacids, it is not as markedly rounded in MT-0200 as in MT-0201. The tuberculum retinaculi m. fibularis is stouter, more laterally projecting and more proximally located in MT-0201. The epicondylus medialis is rounder and more projected medially in MT-0201, the epicondylus lateralis is small, the fovea lateralis is deeper in MT-0201, the trochlea cartilaginis tibialis is proportionally shallower, showing an asymmetric profile distally, and the sulcus m. fibularis is laterally disposed (faces mainly cranially in MT-0200). All these factors together seem to indicate that MT-0200 and MT-0201 are specimens belonging to different species.

The specimen MT-0201 has some similarities with *Phorusrhacos* (e.g., the placement of the sulcus extensorius and the strong medial projection of the condylus medialis), but it seems to be more similar to *Devincenzia* and *Paraphysornis*, terror bird species belonging to Phorusrhacinae and Physornithinae, respectively. *Paraphysornis brasiliensis* was a markedly sturdy phorusrhacid from the Oligocene of Brazil [42,43]. As in the case of MT-0200, the markedly more medially and less cranially projected condylus medialis, the more proximally extended trochlea cartilaginis tibialis, and the asymmetric profile of this trochlea precludes the assignment of MT-0201 to *Paraphysornis brasiliensis* (see [28]). When compared to *Devincenzia*, a large phorusrhacid from the Miocene of Argentina [5,18], MT-0201 has a condylus medialis that is markedly more cranially projecting and is strongly medially projecting, and the incisura intercondylaris is wide. However, the marked medial extension of the epicondylus medialis and the asymmetric profile of the trochlea cartilaginis tibialis differ in MT-0201 from *Devincenzia*. Therefore, overall, based on general similarities, MT-0201 seems more similar to the Phorusrhacinae *Devincenzia* than to the rest of the terror birds (see [28]: Figure 3). However, while Phorusrhacinae are characterized by having an elongated craniodistally slanted epicondylus medialis, this feature is rounded and markedly medially protruding in MT-0200. This, together with the sturdier constitution of the tibiotarsus, makes the assignation to Phorusrhacinae difficult to fully assess. At present, the fragmentary nature of the fossil remain precludes a more precise assignation than that of a Family level.

5. Conclusions

Phorusrhacids are a fairly common element of the fossil Cenozoic avifauna, especially in Argentina, where it is not unusual to find at least two species of terror birds belonging to different species and with contrasting body sizes [20]. Nevertheless, throughout their known geographical distribution, there are no records of two species of gigantic terror birds living together. The finding of a second specimen that can be assigned to a terror bird that may belong to a different species at La Venta in the tropical lowlands of the Middle Miocene of Northern South America has important ecological and biogeographical implications. From an ecological perspective, the potential presence of two extremely large phorusrhacid species at La Venta suggests the terrestrial predatory guild was more diverse that previously proposed [15]. This is particularly relevant considering that these two terror birds might have coexisted, as they were found (MT-0200 and MT-0201) in the same stratigraphic layer and in relatively close proximity to each other (<1 km apart).

Moreover, the potential coexistence of these two large terror birds immediately raises the idea of inter-specific competition and niche partitioning, in a scenario that would entail the first record of two large phorusrhacids living in sympatry. Although it has been hypothesized than a prey-size selection occurred based on predator size [20], separating predator niches, this hypothesis has been based on the presence of markedly different size phorusrhacids, as is evident in the Santacrucian, where small (*Psilopterus lemoinei* and *P. bachmanni*), medium (*Patagornis marshi*) and gigantic-sized (*Phorusrhacos longissimus*) phorusrhacids coexisted [44–46]. The estimated body mass of MT-0200 is about 156 kg [28]. With MT-0200 being ~15% larger, this would mean that this terror bird may have reached approximately 180 kg. Certainly, the presence of two gigantic terror birds coexisting in the La Venta locality represents an interesting scenario for further studies on their ecology and niche partitioning. Finally, the existence of very large terror birds would further suggest the presence of large open areas within the forests and wetlands of La Venta, further supporting the complex and diverse ecosystems in this region during the Middle Miocene period [29].

From a biogeographic and evolutionary perspective, the presence of two large phorusrhacid taxa in the tropical environments of La Venta, in Northern South America, is of significant interest, as it reaffirms the presence of large phorusrhacids in tropical environments and suggests a broad distribution throughout South America; it also opens the debate for novel hypotheses about the colonization of tropical environments by possibly several clades of terror birds. These debates will need to be resolved with additional paleontological evidence from La Venta and other tropical fossil sites in South America.

Finally, we cannot completely disregard the possibility of these two specimens belonging to a dimorphic species or even one with significant developmental changes through their life histories, which would raise new interesting ideas regarding intra-specific competition for resources and mates within these iconic terrestrial predators of South America. In conclusion, we note that the evolutionary history and ecological interactions of terror birds are not completely understood, and every new discovery sheds light on the evolution and natural history of terror birds in the Americas.

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Data Availability Statement: All the data are provided in the text.

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

Abbreviations

FM-P	Field Museum of Natural History, Chicago, IL, USA
LT	Museo La Tormenta, Villavieja, Huila, Colombia
MLP	Museo de La Plata, La Plata, Argentina

References

1. Harshman, J.; Braun, E.L.; Braun, M.J.; Huddleston, C.J.; Bowie, R.C.; Chojnowski, J.L.; Hackett, S.J.; Han, K.-L.; Kimball, R.T.; Marks, B.D.; et al. Phylogenomic evidence for multiple losses of flight in ratite birds. *Proc. Natl. Acad. Sci. USA* **2008**, *105*, 13462–13467. [CrossRef]
2. Yonezawa, T.; Segawa, T.; Mori, H.; Campos, P.F.; Hongoh, Y.; Endo, H.; Hasegawa, M. Phylogenomics and morphology of extinct paleognaths reveal the origin and evolution of the ratites. *Curr. Biol.* **2017**, *27*, 68–77. [CrossRef]
3. Maderspacher, F. Flightless birds. *Curr. Biol.* **2022**, *32*, R1155–R1162. [CrossRef] [PubMed]
4. Moreno, F.P.; Mercerat, A. Catálogo de los pájaros fósiles de la República Argentina conservados en el Museo de La Plata. *An. Mus. Plata* **1891**, *1*, 7–71.
5. Alvarenga, H.M.F.; Höfling, E. Systematic revision of the *Phorusrhacidae* (Aves: Ralliformes). *Pap. Avul. Zool.* **2003**, *43*, 55–91. [CrossRef]
6. Agnolín, F.L. *Brontornis burmeisteri* Moreno y Mercerat, un *Anseriformes* (Aves) gigante del Mioceno Medio de Patagonia, Argentina. *Rev. Mus. Argent. Cienc. Nat.* **2007**, *9*, 15–25. [CrossRef]
7. Agnolín, F.L. Reappraisal on the phylogenetic relationships of the enigmatic flightless bird (*Brontornis burmeisteri*) Moreno and Mercerat, 1891. *Diversity* **2021**, *13*, 90. [CrossRef]
8. Marshall, L. The Terror Birds of south America. *Sci. Am.* **1978**, *14*, 82–89. [CrossRef]
9. Degrange, F.J. A revision of *Phorusrhacidae* (Aves, Cariamiformes) skull morphology. *J. Vertebr. Paleontol.* **2021**, *40*, e1848855. [CrossRef]
10. Degrange, F.J.; Tambussi, C.P.; Moreno, K.; Witmer, L.M.; Wroe, S.; Turvey, S.T. Mechanical Analysis of Feeding Behavior in the Extinct "Terror Bird" *Andalgalornis steulleti* (Gruiformes: Phorusrhacidae). *PLoS ONE* **2010**, *5*, e11856. [CrossRef]
11. Degrange, F.J.; Tambussi, C.P.; Witmer, L.M. Reversing the trend: The evolution of cranial akinesis in the Terror Birds (Cariamiformes, Phorusrhacidae). *Foss. Stud.* **2025**, *3*, 12. [CrossRef]
12. Andrews, C. Remarks on the Stereornithes, a group of extinct birds from Patagonia. *IBIS* **1896**, *7*, 1–12. [CrossRef]
13. Dolgopol de Saez, M. Las aves corredoras fósiles del Santacrucense. *An. Soc. Ci. Arg.* **1927**, *103*, 145–164.
14. Degrange, F.J. The hind limb morphometry of terror birds (Aves, Cariamiformes, Phorusrhacidae): Their functional implications for substrate preferences and locomotory lifestyle. *Earth Environ. Sci. Trans. R. Soc. Edinb.* **2017**, *106*, 257–276. [CrossRef]
15. Wilson, O.E.; Parker, A.K. Low predator competition indicates occupation of macropredatory niches by giant Miocene reptiles at La Venta, Colombia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **2023**, *632*, 111843. [CrossRef]
16. LaBarge, T.W.; Gardner, J.D.; Organ, C.L. The evolution and ecology of gigantism in terror birds (Aves, Phorusrhacidae). *Proc. R. Soc. B* **2024**, *291*, 20240235. [CrossRef]
17. Degrange, F.J.; Tambussi, C.P.; Taglioretti, M.L.; Dondas, A.; Scaglia, F. A new *Mesembriornithinae* (Aves, Phorusrhacidae) provides new insights into the phylogeny and sensory capabilities of terror birds. *J. Vertebr. Paléontol.* **2015**, *35*, e912656. [CrossRef]
18. Agnolín, F.L.; Chafrat, P.; Álvarez-Herrera, G.P. New specimens of *Patagorhacos terrificus* Agnolín and Chafrat, 2015 (Aves) shed light on the phylogeny and evolution of the *Phorusrhacidae*. *Hist. Biol.* **2025**, *37*, 1744–1756. [CrossRef]
19. Tonni, E.P. El rol ecológico de algunas aves fororracoideas. *Ameghiniana* **1977**, *14*, 316.
20. Degrange, F.J. Morfología Del Cráneo y Complejo Apendicular en Aves Fororracoideas: Implicancias en la Dieta y Modo de Vida. Ph.D. Thesis, La Plata University, La Plata, Argentina, 2012; pp. 1–390.
21. Hirschfeld, S.E.; Marshall, L.G. Revised faunal list of the La Venta fauna (Friasian-Miocene) of Colombia, South America. *J. Paleontol.* **1976**, *50*, 433–436.

22. Rasmussen, T. Birds. In *Vertebrate Paleontology in the Neotropics: The Miocene Fauna of La Venta, Colombia*; Madden, R.H., Cifelli, R.L., Flynn, J.J., Eds.; Smithsonian Institution Press: Washington, DC, USA, 1997; pp. 171–184.
23. Carrillo, J.D.; Jaramillo, C.; Abadía, F.; Aguilera, O.; Alfonso-Rojas, A.; Billet, G.; Zapata, S. The Miocene La Venta Biome (Colombia): A century of research and future perspectives. *Geodiversitas* **2023**, *45*, 739–767. [CrossRef]
24. Kay, R.F.; Madden, R.H. Mammals and rainfall: Paleoecology of the middle Miocene at La Venta (Colombia, South America). *J. Hum. Evol.* **1997**, *32*, 161–199. [CrossRef]
25. Contreras Roqué, J.R.; Aguilar, H.A.; Piloni, G.; Agnolín, F.L.; Delpino Aguayo, M.A.; Giacchino, A.; Bertonatti, C.; Tubaro, P.; Gasparri, B.; Davies, Y.E. *Historia Natural de Carau (Aramus guarauna)*; Fundación de Historia Natural Félix de Azara: Buenos Aires, Argentina, 2019.
26. Miller, A.H. A fossil hoatzin from the Miocene of Colombia. *Auk* **1953**, *70*, 484–489. [CrossRef]
27. Pelegrin, J.S.; Acosta Hospitaleche, C.; Link, A.; Cooke, S.; Cortés, D.; Jaramillo, C. Ensamblaje de Aves del Mioceno Medio de La Venta (Desierto de la Tatacoa), Colombia: Implicaciones paleoecológicas y paleobiogeográficas. In *Libro de Resúmenes del II Congreso Colombiano de Paleontología*; Universidad del Rosario: Rosario, Colombia, 2023; p. 72.
28. Degrange, F.J.; Cooke, S.B.; Ortiz-Pabón, L.G.; Pelegrin, J.S.; Perdomo, C.A.; Salas-Gismondi, R.; Link, A. A gigantic new terror bird (Cariamiformes, Phorusrhacidae) from Middle Miocene tropical environments of La Venta in northern South America. *Pap. Palaeontol.* **2024**, *10*, e1601. [CrossRef]
29. Mora-Rojas, L.; Cárdenas, A.; Jaramillo, C.; Silvestro, D.; Bayona, G.; Zapata, S.; Ibañez, M. Stratigraphy of a middle Miocene neotropical Lagerstätte (La Venta Site, Colombia). *Geodiversitas* **2023**, *45*, 197–221. [CrossRef]
30. Ortiz-Pabón, L.G.; Cooke, S.B.; Degrange, F.J.; Link, A.; Pelegrin, J.S.; Perdomo, C.A.; Salas-Gismondi, R. Implicaciones paleoecológicas de la presencia de grandes aves terrestres (Phorusrhacidae y Brontornithidae) en el Mioceno de La Venta en Colombia. In *XII Congreso Latinoamericano de Paleontología: Memorias*; Benemérita Universidad Autónoma de Puebla: Puebla, México, 2025; pp. 209–210.
31. Montes, C.; Silva, C.A.; Bayona, G.A.; Villamil, R.; Stiles, E.; Rodriguez-Corcho, A.F.; Von Quadt, A. A middle to late Miocene trans-Andean portal: Geologic record in the Tatacoa Desert. *Front. Earth Sci.* **2021**, *8*, 587022. [CrossRef]
32. Baumel, J.J.; Witmer, L.M. Osteologia. In *Handbook of Avian Anatomy: Nomina Anatomica Avium*, 2nd ed.; Baumel, J.J., King, A.S., Breazile, J.E., Evans, H.E., Vanden Berge, J.C., Eds.; Publications of the Nuttall Ornithological Club: Cambridge, MA, USA, 1993; pp. 45–132.
33. Baumel, J.J.; Raikow, R. Arthrologia. In *Handbook of Avian Anatomy: Nomina Anatomica Avium*, 2nd ed.; Baumel, J.J., King, A.S., Breazile, J.E., Evans, H.E., Vanden Berge, J.C., Eds.; Publications of the Nuttall Ornithological Club: Cambridge, MA, USA, 1993; pp. 133–188.
34. Guerrero, J. Stratigraphy, sedimentary environments, and the Miocene uplift of the Colombian Andes. In *Vertebrate Paleontology in the Neotropics: The Miocene Fauna of La Venta, Colombia*; Madden, R.H., Cifelli, R.L., Flynn, J.J., Eds.; Smithsonian Institution Press: Washington, DC, USA, 1997; pp. 15–43.
35. Anderson, V.; Horton, B.; Saylor, J.; Mora, A.; Tesón, E.; Breecker, D.; Ketchan, R. Andean topographic growth and basement uplift in southern Colombia: Implications for the evolution of the Magdalena, Orinoco, and Amazon River systems. *Geosphere* **2016**, *12*, 1235–1256. [CrossRef]
36. Flynn, J.J.; Guerrero, J.; Swisher, C.C. Geochronology of the Honda Group. In *Vertebrate Paleontology in the Neotropics: The Miocene fauna of La Venta, Colombia*; Madden, R.H., Cifelli, R.L., Flynn, J.J., Eds.; Smithsonian Institution Press: Washington, DC, USA, 1997; pp. 44–59.
37. Worthy, T.H.; Degrange, F.J.; Handley, D.; Lee, M.S. The evolution of giant flightless birds and novel phylogenetic relationships for extinct fowl (Aves, Galloanseres). *Roy. Soc. Open Sci.* **2017**, *4*, 170975. [CrossRef]
38. Buffetaut, E. A brontornithid from the Deseadan (Oligocene) of Bolivia. *Contrib. Mus. Argent. Cienc. Nat.* **2017**, *7*, 39–47.
39. Picasso, M.B.J. Postnatal ontogeny of the locomotor skeleton of a cursorial bird: Greater rhea. *J. Zool.* **2012**, *286*, 303–311. [CrossRef]
40. Picasso, M.B.J.; Degrange, F.J.; Mosto, M.C.; Tambussi, C.P. Un individuo juvenil de *Pterocnemia pennata* (Aves, Rheidae) en el Pleistoceno de la Región Pampeana: Implicancias ontogenéticas y ambientales. *Rev. Mex. Cienc. Geol.* **2011**, *28*, 192–200.
41. Watanabe, J. Ontogeny of macroscopic morphology of limb bones in modern aquatic birds and their implications for ontogenetic ageing. *Contrib. Mus. Argent. Cienc. Nat.* **2017**, *7*, 183–220.
42. Alvarenga, H. Uma gigantesca ave fóssil do Cenozóico brasileiro: *Physornis brasiliensis* sp. n. *An. Acad. Bras. Ciênc.* **1982**, *54*, 697–712.
43. Alvarenga, H. *Paraphysornis* novo gênero para *Physornis brasiliensis* Alvarenga, 1982 (Aves: Phorusrhacidae). *An. Acad. Bras. Ciênc.* **1993**, *65*, 403–406.
44. Ameghino, F. Enumeración de las aves fósiles de la República Argentina. *Rev. Arg. Hist. Nat.* **1891**, *1*, 441–453.

45. Degrange, F.J.; Noriega, J.I.; Areta, J.I. Diversity and paleobiology of the Santacrucian birds. In *Early Miocene Paleobiology in Patagonia: High-Latitude Paleocommunities of the Santa Cruz Formation*; Vizcaíno, S.F., Kay, R.F., Bargo, M.S., Eds.; Cambridge University Press: Cambrideg, UK, 2012; pp. 138–155.
46. Diederle, J.M.; Noriega, J.I. New records of birds from the Santa Cruz Formation (Early–Middle Miocene) at the Río Santa Cruz valley, Patagonia, Argentina. *Publicación Electrónica Asoc. Paleontológica Argent.* **2019**, *19*, 55–61.

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