The youngest record of phorusrhacid birds (Aves, Phorusrhacidae) from the late Pleistocene of Uruguay

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With 2 figures

Abstract: We report the youngest record of a phorusrhacid bird based on a distal portion of a right tarsometatarsus. This fossil comes from late Pleistocene sediments of Uruguay. The age determination was based on lithological features, biostratigraphical studies and absolute dating. The evidence indicates that these groundbirds co-occurred with the typical Pleistocene South American megafaunal mammals. The so far youngest fossils of phorusrhacids stem from the Pliocene or lower Pleistocene of South and North America.

Key words: Giant groundbird, Phorusrhacidae, late Pleistocene, youngest record, South America, Uruguay

1. Introduction

The phorusrhacids, also called “terror-birds”, were carnivorous groundbirds that lived mainly in Cenozoic environments of South America. Probably, evolved to giant sizes due the geographic isolation of South American continent. These birds are amongst the largest birds that have ever existed on the planet, ranging in height from approximately 1 to 3 meters (Marshall 1994; Alvarenga & Höfling 2003). Phorusrhacid birds apparently shared with borhyaenid marsupials the predator niche of grassland ecosystems, and perhaps open areas in dry forest. Because its huge skull with a powerful hooked beak, large curved claws and considerable running abilities (Blanco & Jones 2005), are generally considered as swift cursorial predators. About 13 genera, and 18 species are known for this family, and these are distributed over five subfamilies (Alvarenga & Höfling 2003; Bertelli et al. 2007). The oldest record of this family is from the Paleocene of Brazil (Alvarenga 1985), and the youngest to date may either be a large tibiotarsus assigned to Pliocene or lower Pleistocene of the Raigón Formation in Uruguay (Tambussi et al. 1999) or the various remains of another gigantic species, Titanis walleri, from the Pliocene (late Hemphillian to late Blancan), of Texas and Florida, USA (Brodorb 1963; Chandler 1994; Baskin 1995; Gould & Quitmeyr 2005; MacFadden et al. 2006). These latter discoveries show phorusrhacids to have been part of the Great American Biotic Interchange, and they were the only carnivorous group of South American animals to disperse northward (Marshall 1988, 1994). The present note documents the occurrence of a specimen of terror bird from the late Pleistocene of Uruguay that constitutes the latest geologic occurrence of the Phorusrhacidae.
The material described in this study was collected by Luis Castiglioni in Casil Quarry, Department of Montevideo, about 2.4 km west from the town of La Paz (34º45'24S, 56º15'53W), Uruguay (Fig. 1). It comes from sediment belonging to the Dolores Formation, usually considered to be of middle-late Pleistocene age (ANTÓN & GOSO 1974). This lithological unit is characterized by siltstones, pelites, sandy to gravelly pelites, and sandstones with argillaceous matrix. Calcium carbonate is abundant in various forms (BOSSI & NAVARRO 1991; GUTIÉRREZ et al. 2005). The tarsometatarsus comes from a bone bed in greenish clayish siltstone with sand and gravel clasts. Its color, texture, and degree of abrasion are consistent with those of other fossils from the same bone bed. Taphonomic information, sedimentological features, and mineralogical studies suggest that the depositional event was a high energy deposit such as a mud flow (CORONA et al. 2005, 2007). The associated fauna includes several genera of cingulates (Glyptodon sp., Panochthus sp., Doedicurus sp., Neu ryurus sp., Propraopus sp.); ground sloths (Lestodon armatus and Megatheriinae gen. et sp. indet.); several ungulates (Macrauchenia patachonica, Toxodon cf. T. platensis, Hemiauchenia sp., Ozotocerus cf. bezo articus, Hippidion sp., and Stegomastodon waringii); a rodent (Myocastor sp.), and some indeterminate bird bones. This faunal association, especially the taxa

Fig. 1. Map of Uruguay with solid circle indicating the locality where the specimen. MNHN-1736 was collected.
Macrauchenia patachonica, Lestodon armatus and Stegomastodon waringi, restricts the age of this fauna to middle or late Pleistocene (Perea et al. 2001; Marchesano et al. 2002; Corona et al. 2005). A sample of enamel from a proboscidean molar from the same stratigraphic level was dated to 17620 ± 100 years BP by AMS 14C (see Gutiérrez et al. 2005). Thus, various lines of evidence confirm a late Pleistocene age for this quarry.

3. Material and methods

The specimen consists of the distal portion of a right tarsometatarsus (Fig. 2), lacking the trochlea metatarsi IV. The texture of the periosteum indicates an adult individual. The specimen was compared with the homologous bone of all orders and almost all families of extant non-passerine birds in the osteological collections of the Museu de Historia Natural de Taubaté, Brazil, and the Museo Nacional de Historia Natural y Antropología de Montevideo, Uruguay. Comparisons were also made with published illustrations of extinct families such as Teratornithidae, Diatrymidae, Plotopteridae, Odontopterygidae, and Pseudodontornithidae (Miller 1909, 1910; Matthew & Granger 1917; Olson & Hasegawa 1979; Harrison & Walker 1976). Comparisons were also made with tarsometatarsi attributed to the Phorusrhacidae, using the original data from Alvarenga & Höfling (2003). Anatomical terminology follows Baumel and Witmer (1993). The material described here is deposited in the Museo Nacional de Historia Natural y Antropología, Montevideo (MNHN-1736).

4. Description and comparisons

Compared with extant birds of South America, the specimen (MNHN-1736) is smaller than the tarsometatarsus of rheas (Rheidae) but larger than that of all other terrestrial birds, including storks. Among the phorusrhacids the specimen is smaller than Mesembriornis incertus (the smallest Mesembriornithinae) but is of similar size to that of Procaria, simplex, the largest of the Psilopterinae (the subfamily that includes the smallest species of Phorusrhacidae). The bone lacks the trochlea metatarsi IV, but the remainder is well preserved and shows some important features. On the lateral side, across the damaged area (Fig. 2D), it is possible to observe the longitudinal section of the canalis interosseus distalis and its ventral branch, which conducts the tendon of Musculus extensor brevis digitii IV and blood vessels into the lateral intertrocchlear incisure (Baumel & Witmer 1993). In dorsal view it is possible to see the foramen vasculare distale located more proximally than the proximal rim of the middle trochlea (Fig. 2A). We can conclude that the specimen came from a large, cursorial bird characterized by: (1) a large and distally expanded trochlea metatarsi III (middle trochlea); (2) a very narrow trochlea metatarsi II (inner trochlea,) with the articular surface transversally convex and without a longitudinal sulcus (in dorsal and distal view); (3) the trochlea metatarsi II in dorsal view is not turned mediad, being almost parallel and much shorter than the middle trochlea, and forming a narrow notch between trochleae II and III. It is important to note that in most extant birds, including some cursorial ones such as Rheidae, Tinamidae, Caripidae, and Otididae, the trochlea metatarsi II is deflected medially; in Teratornithidae, Vulturidae and Ciconiidae, the trochlea II is much wider and reaches almost the same distal size as the trochlea III.

The three features outlined above identify the specimen as a phorusrhacid bird. In addition, the morphology of trochlea II and III in medial view, including the very deep foveae ligamentum col-lateralium, is very typical of the Phorusrhacidae.

Among the terror birds, MNHN-1736 differs from the Psilopterinae in most representatives of which the trochlea metatarsi II is wider and its inner edge is considerably expanded (Sinclair & Farr 1932). It also differs from the Brontornithidae, the largest of the Phorusrhacidae, in lacking the expansion of the dorso-medial extremity of the articular surface of trochlea III (Alvarenga & Höfling 2003). Some features of this specimen are shared with Titanis walleri (see Brodkorb 1963 and Fig. 2) of North America, such as the distally expanded trochlea metatarsi III (dorsal view), which is unlike that in Phorusrhacos or Devincenzia. Likewise, the morphology of the plantar supratrochlear surface and of trochleae II and III in medial view resembles that of Titanis.

5. Discussion

Fossils of Titanis are from temporally mixed faunas associated with Hemphillian (5 Mya) and late Blancan (2.4 to 2.0 Mya) ages in North America (MacFadden et al. 2006). Tambussi et al. (1999) identified a large tibiotarsus of the Phorusrhacinae (MNHN-1563) from Uruguay, to the Pliocene or early Pleistocene of Raigón Formation (Uruguay). Thus the new fossil described here is the youngest occurrence
of the Phorusrhacidae and extends the family into the late Pleistocene of South America.

The three other Phorusrhacidae specimens previously described from Uruguay – a tarsometatarsus MNHN-189 (type of *Devincenzia* pozzi), a distal portion of tarsometatarsus assigned to *Devincenzia* sp. (Museo Municipal “Bautista Rebuffo”, Uruguay, MR-1215) described by Perea and Alfaro (2004), and a tibiotarsus MNHN-1563 (Tambussi et al. 1999) – are all from the Pliocene or lower Pleistocene. All these fossils belong to very large species, different from the smaller and more recent fossil described here. Although the present specimen (MNHN-1736) is insufficient for generic determination, some features (the distally expanded trochlea metatarsi III and a narrow trochlea metatarsi II) are shared with *Titanis walleri* from North America, and other features (as the trochlea metatarsi II not turned mediad, and almost parallel to the middle trochlea and also the absence of a dorsomedial expansion of the trochlea III) preclude a close relationship with the subfamilies Brontornithinae and Psilopterinae suggesting that the last representative of the terror birds may belong to one of the subfamilies Phorusrhacinae, Patagornithinae, or Mesembriornithinae. The extinction of phorusrhacids was presumably due to the invasion into South America of North America flesh-eating placental mammals (see Marshall 1988, 1994; Woodburne et al. 2006). This hypothesis could be precluded because the presence of at least one phorusrhacid

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Fig. 2. Distal end of right tarsometatarsus of a Phorusrhacidae from the late Pleistocene of Uruguay (MNHN-1736) (top) and *Titanis walleri* (holotype, University of Florida, UF-4108) (below). A, dorsal, B, medial, C, planar, D, lateral and E, distal views.
representative in the South American late Pleistocene, coexisting with many predators, even actual species. For these reasons, the extinction causes should be reevaluated in function of this fossil finding.

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