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Authors: Degrange, Federico J., Eddy, Drew, Puerta, Pablo, and Clarke, Julia

Source: Journal of Paleontology, 93(6) : 1221-1233

Published By: The Paleontological Society

URL: https://doi.org/10.1017/jpa.2019.53

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Journal of Paleontology, 93(6), 2019, p. 1221–1233
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0022-3360/19/1937-2337
doi: 10.1017/jpa.2019.53

JOURNAL OF PALEONTOLOGY
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New skull remains of *Phorusrhacos longissimus* (Aves, Cariamiformes) from the Miocene of Argentina: implications for the morphology of Phorusrhacidae

Federico J. Degrange,[1]* Drew Eddy,[2,3] Pablo Puerta,[4] and Julia Clarke[2]*

[1]Centro de Investigaciones en Ciencias de la Tierra (CICTERRA), Universidad Nacional de Córdoba, CONICET, Av. Vélez Sársfield 1611, X5016GCA, Córdoba, Argentina <fjdino@gmail.com>
[2]Department of Geological Sciences, University of Texas at Austin, Austin, Texas 78756, USA <julia_clarke@jsg.utexas.edu>
[3]BHP Billiton, 1500 Post Oak Boulevard, Houston, Texas, 77056, USA <drew.eddy@bhp.com>
[4]Museo Paleontológico Egidio Feruglio, Av. Fontana 140-CP9100, Trelew, Chubut, Argentina <ppuerta@mef.org.ar>

Abstract.—The giant carnivorous phorusrhacid bird *Phorusrhacos longissimus* (Aves, Cariamiformes) was first described in 1887 by Florentino Ameghino on the basis of a jaw fragment. The majority of a skull of the species still encased in crumbling rock was preserved only long enough for illustrations to be made by Carlos Ameghino in the field and for a brief description to be written. Skull remains of this species have remained scarce, and few postcranial remains have been figured. Here, we reassess the cranial anatomy of this outstanding 'terror bird' species taking into account data from a newly discovered skull. An additional specimen of a well-preserved dorsal vertebra referable to Phorusrhacinae is also described from a separate locality within the Miocene Santa Cruz Formation (late early Miocene) from Santa Cruz Province in Argentina. The skull includes most of the rostrum, skull roof, and mandible and is compared with material from other members of the Phorusrhacinae. The new data from the skull and vertebra provide morphological features of this clade that benefit future taxonomic and phylogenetic analyses of this iconic group of birds.

Introduction

Phorusrhacidae Ameghino, 1889 is an extinct group of flightless, cursorial carnivorous birds that occupied one of the dominant, large land-predator niches in South America from the lower Eocene to the Pleistocene (Tonni and Tambussi, 1986; Tambussi et al., 1999; Alvarenga et al., 2010; Degrange, 2017; Jones et al., 2018). They dispersed into North America during the Great American Biotic Interchange (~3 Ma; Marshall, 1977; Carr, 1981; Baskin, 1995; Alvarenga and Höfling, 2003; MacFadden et al., 2007). Some remains from Africa and Europe (Mourer-Chauviré et al., 2011; Angst et al., 2013) and the Paleocene of Brazil (Alvarenga, 1985) have been referred to this clade or identified as phylogenetically related to the extant South American seriemas (Cariamidae), but these assignments remain controversial (Agnolín, 2009; Degrange et al., 2015; Mayr, 2017).

With an estimated body mass of more than 100 kg (Degrange, 2012; Degrange et al., 2012), *Phorusrhacos longissimus* Ameghino, 1887 is one of the most iconic fossil birds from South America and part of the early history of paleontology in Argentina. Discovered by Carlos Ameghino in Santa Cruz province, it was described by Florentino Ameghino from an incomplete mandible originally assumed to be from a toothless mammal (Ameghino, 1887; Alvarenga and Höfling, 2003; Buffetaut, 2013a, b). Unfortunately, no illustration accompanied the original description (see Ameghino, 1887).

The avian nature of *Phorusrhacos* was first proposed in 1891 on the basis of comparisons with new remains of the related species *Patagornis marshi* Moreno and Mercerat, 1891 (= *Tolmodus inflatus* according to Ameghino, also originally described as a toothless mammal, Ameghino, 1891a). Moreno and Mercerat (1891) figured the *Phorusrhacos* holotype mandible for the first time (MLP 20-118, Fig. 1; see Acosta Hospitaleche et al., 2001) but erroneously proposed it to be the premaxilla. A subsequent discovery of a skull of *P. longissimus* (NHMUK A529) by Carlos Ameghino could only be described and illustrated (Fig. 2) while it remained in its original sediment matrix in the field, as the specimen was "in such a bad state of conservation that it [was] almost reduced to dust" (Ameghino, 1895, p. 268). Fossil material recovered and deposited from this specimen represents only a small portion of the skull figured by Ameghino (1895), preserving only the rostral tip of the maxilla, fragments of the processus supraorbitalis of the os lacrimale, and part of the mandible (Alvarenga and Höfling, 2003). The illustrations of this specimen of *P. longissimus* have been widely reproduced in textbooks and museums, although a lack of new skull material referable to the taxon has precluded the verification of the morphology illustrated.

The Phorusrhacinae subclade within Phorusrhacidae currently includes *Phorusrhacos longissimus*, *Titanis walleri*

*Corresponding author.

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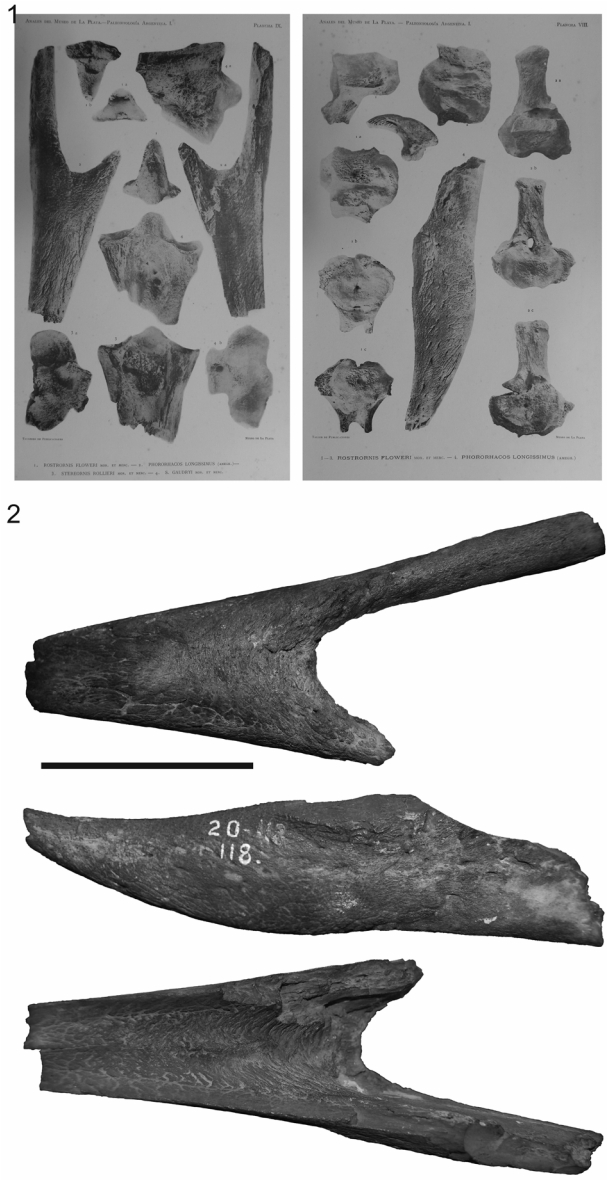


Figure 1. *Phorusrhacos longissimus* holotype MLP 20-122: (**1**) as figured by Moreno and Mercerat (1891); (**2**) photographs in dorsal, ventral, and lateral views. Scale bar = 1 cm.

Brodkorb, 1963, *Devincenzia pozzi* Kraglievich, 1931, and *Kelenken guillermoi* Bertelli et al., 2007. Although recent phylogenetic analyses have recovered different relationships among these species and with the rest of phorusrhacids (e.g., Agnolín, 2009; Alvarenga et al., 2011; Degrange et al., 2015), none of the analyses recovered Phorusrhacinae as a natural group. Phorusrhacinae represent fossil birds with gigantic proportions (e.g., body masses greater than 100 kg; Alvarenga and Höfling, 2003; Bertelli et al., 2007; Degrange, 2012), long and narrow mandibular symphyses more than twice as elongate as the width at their base (Alvarenga and Höfling, 2003), and elongated tarsometatarsi (Angst et al., 2015; Degrange, 2017). The majority of these large-bodied phorusrhacid taxa are known from fragmentary skulls and postcrania, with the exception of a nearly complete skull of *Kelenken guillermoi* (Bertelli et al., 2007). This contrasts sharply with the fossil record of smaller and medium-sized phorusrhacids, which is far more complete. An array of nearly intact crania as well as associated postcranial material have been referred to taxa within these clades (i.e., Mesembriornithinae, Patagornithinae, and Psilopterinae; Andrews, 1889; Sinclair and Farr, 1932; Kraglievich, 1946; Alvarenga and Höfling, 2003; Degrange et al., 2015). Reconstructions of larger phorusrhacine skulls have been based on these smaller-bodied phorusrhacid taxa (Bertelli et al., 2007), while the paucity of cranial material continues to limit morphological comparisons within Phorusrhacinae with other phorusrhacids.

Here we present new cranial material referable to the Phorusrhacinae *Phorusrhacos longissimus* comprising a skull roof, rostrum, and partial mandible (MPEF-PV 11356). A thoracic vertebra (MPEF-PV 11355) is also described and tentatively referred to Phorusrhacinae. It is hypothesized to belong to the same taxon due to its size and morphological similarities when compared with other remains of *Phorusrhacos*. Two sites in southern Argentina produced the phorusrhacid material. Both localities (Fig. 3.1) are situated in Santa Cruz Province. The vertebra was discovered as an isolated element at the Puesto Estancia La Costa locality, in sediments typical of the Santa Cruz Formation. The associated cranium and mandible were discovered at the Cerro de los fósiles site, less than 50 km east of the Chilean border, approximately 20 km southeast of Lago Belgrano and slightly lower in section than the vertebra. Santacrucian units in this region are constrained to a late early Miocene age based on comparisons of faunal composition to other early Miocene formations in Argentina dated to the Santacrucian Land Mammal Age (~22.0–16.0 Ma; Marshall, 1976; Marshall et al., 1986; Fleagle et al., 2012; Perkins et al., 2012).

Materials and methods

Unless indicated otherwise, the osteology terminology used in the anatomical description follows Baumel and Witmer (1993) or their English equivalent. Jaw muscles are discussed following Holliday and Witmer (2007).

Repositories and institutional abbreviations.—BAR, Museo Asociación Paleontológica Bariloche, Río Negro, Argentina; DGM, Divisão de Geologia e Mineralogia do Departamento Nacional da Produção Mineral, Rio de Janeiro, Brazil; FM, Field Museum of Natural History, Chicago, United States of America; MLP, Museo de La Plata, La Plata, Argentina; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MPEF-PV, Museo Egidio Feruglio, Trelew, Chubut, Argentina; MPM-PV, Museo Padre Molina, Río Gallegos, Santa Cruz, Argentina; NHMUK, The Natural History Museum, London, United Kingdom.

Systematic paleontology

Class Aves Linnaeus, 1758
Infraclass Neognathae Pycraft, 1900
Order Cariamiformes Verheyen, 1957
Family Phorusrhacidae Ameghino, 1889
Subfamily Phorusrhacinae Ameghino, 1889
Genus *Phorusrhacos* Ameghino, 1887

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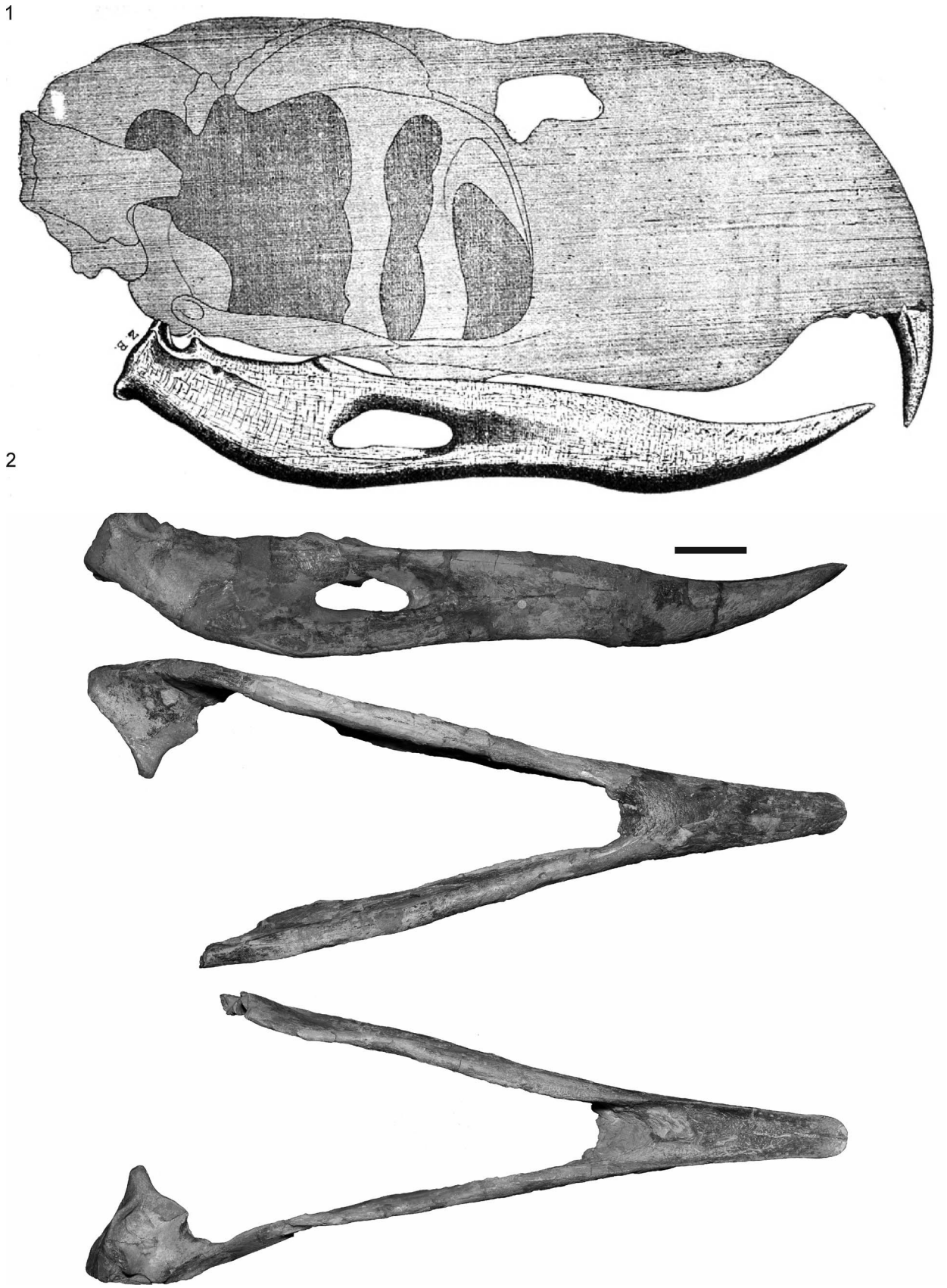


Figure 2. (**1**) The *Phorusrhacos longissimus* specimen discovered by Carlos Ameghino and drawn by Florentino Ameghino (1895) according to the descriptions, sketches, and measurements taken by his brother in the field. (**2**) Photographs of the jaw of that specimen, numbered NHMUK A529, in right lateral, ventral, and dorsal views. Other remains of the same specimen are a fragment of the rostral tip of the maxilla and processus supraorbitalis of the os lacrimale figured by Alvarenga and Höfling (2003, fig. 24). Scale bar = 5 cm.

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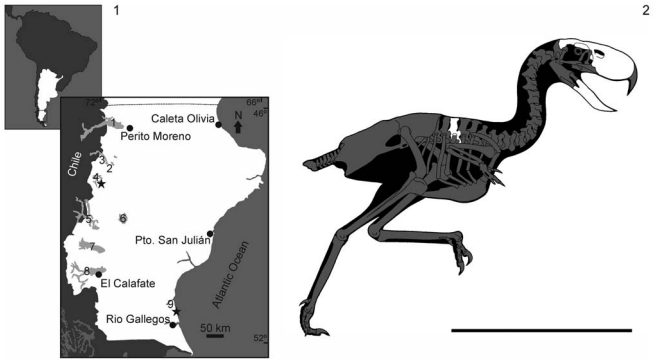


Figure 3. (**1**) Location map of the fossil locality (star), near Lago Belgrano, at southern Patagonia, Argentina. (**2**) Reconstruction of *Phorusrhacos longissimus* skeleton with the preserved bones in white. Scale bar = 1 m. 1 = Lago Buenos Aires; 2 = Lago Posadas; 3 = Lago Pueyrredón; 4 = Lago Belgrano; 5 = Lago San Martín; 6 = Lago Cardiel; 7 = Lago Viedma; 8 = Lago Argentino; 9 = Puesto Ea. La Costa. Reconstruction of *Phorusrhacos* is modified from Paul (2002).

Type species.—*Phorusrhacos longissimus* Ameghino, 1887 from Santa Cruz Formation (late early Miocene), Santa Cruz Province, Argentina.

Phorusrhacos longissimus Ameghino, 1887
Figures 3–7

1889 *Phororhacos longissimus* Ameghino, p. 24.
1891 *Stereornis rollieri* Moreno and Mercerat, p. 45, pl. 9, fig. 3, pl. 10, figs. 1, 2, pl. 11, fig. 1.
1891 *Stereornis gaundryi* Moreno and Mercerat, p. 47, pl. 9, fig. 4, pl. 10, fig. 3.
1891 *Mesembriornis studeri* Moreno and Mercerat, p. 48, pl. 4, figs. 2, 3, pl. 7, fig. 4, pl. 10, fig. 4, pl. 11, figs. 2–4, pl. 12, figs. 1–6, lam. 2, fig. B.
1891 *Mesembriornis quatrefragesi* Moreno and Mercerat, p. 50, pl. 18, figs. 1–6, pl. 16, fig. 3.
1891 *Darwinornis copei* Moreno and Mercerat, p. 60, pl. 17, figs. 1, 2.
1891 *Darwinornis zittelli* Moreno and Mercerat, p. 63, pl. 17, figs. 3, 4.
1891 *Darwinornis socialis* Moreno and Mercerat, p. 63, pl. 17, fig. 5.
1891 *Owenornis affinis* Moreno and Mercerat, p. 64, pl. 17, fig. 6, pl. 18, fig. 1.
1891 *Owenornis lydekkeri* Moreno and Mercerat, p. 64, pl. 18, figs. 2–5.
1891a *Phororhacos shenensis* Ameghino, p. 258.
1891b *Phororhacos sehuensis* Ameghino, p. 451.
1891b *Phororhacos platygnathus* Ameghino, p. 452.
1893 *Titanornis mirabilis* Mercerat, p. 5.
1895 *Callornis giganteus* Ameghino, p. 574, figs. 28, 29.
1901 *Eucallornis giganteus* Ameghino, p. 78.
1927 *Liornis minor* Dolgopol de Saez, p. 158, pl. 4.

Type specimen.—Lower jaw (MLP 20-122) from Santa Cruz Formation (late early Miocene), Santa Cruz Province, Argentina (Moreno and Mercerat, 1891, pl. 8, fig. 4, pl. 9, fig. 2).

Occurrence.—Cerro de los fósiles locality, NW of Santa Cruz Province, Argentinean Patagonia, santacrucian SALMA (late early Miocene) of Santa Cruz Formation.

Description.—Cranial material of MPEF-PV 11356 (Figs. 4–6) is represented by a large part of the rostrum (including the ossa premaxillaris, ossa nasalis, and a small portion of the right os maxillare) and part of the skull roof and orbit (right os lacrimale, ossa frontalia, and ossa parietalia). Although most of the braincase (e.g., occipital region) and palatal elements are not preserved in MPEF-PV 11356, the internal surface of the dorsal cranium is in good condition, preserving the outline of the rostrodorsal portion of the brain cavity (Fig. 6). The dorsal surface of the rostrum is abraded along most of its length (Fig. 5), and damage continues along the curved rostral surface of the premaxilla. The shape of the bill tip has not been preserved, but it can be inferred from preserved remnants of the ventral margin that the typical downturned hook was present as in other *Phorusrhacos* specimens (e.g., NHMUK A535).

The rostrum of MPEF-PV 11356 is dorsoventrally tall (14.1 cm at its preserved midpoint, with an estimated maximum height at midlength of the nares of 17.3 cm) and narrow (~6 cm width) with the thick, heavy premaxillary construction typical of larger phorusrhacids. It is proportionally shorter (estimated length of 52 cm) relative to skull length than illustrations of the skull referred to *Phorusrhacos longissimus* by Ameghino (1895; 65 cm) and proportionally shorter than that of the phorusrhacine *Kelenken guillermoi* (71.6 cm according to Bertelli et al., 2007). The shape of the rostrum of MPEF-PV 11356 most closely resembles those of the smaller patagornithines *Patagornis marshi* Moreno and Mercerat, 1891 (NHMUK A516) and *Andalgalornis steulleti* (Kraglievich, 1931) (FM-P14357). The lateral surfaces of the rostrum are characterized by an extensive meshwork of grooves and pits (i.e., neurovascular foramina). These small channels served as exits for the ophthalmic and nasopalatine nerves (Bertelli et al., 2007), and their presence is widespread throughout Phorusrhacidae (e.g., Degrange and Tambussi, 2011; Degrange et al., 2015).

The tomium of the premaxilla is mostly broken, and a small portion of the os maxillare is visible as an irregularly shaped, paired element surrounded by matrix (Fig. 4). Rostrally, the os maxillare follows the preserved outline of the rostrum and curves dorsally, where it would have contacted the os premaxillare. MPEF-PV 11356 is interpreted to have a slightly upturned ventral margin of the rostrum immediately caudal to its beak tip, which contrasts with that of *Kelenken* in which the tomium is almost straight (although this could be the result of the dorsoventral crushing present in the holotype). This feature, characterized by a falcated tomia, is typical of the 'Terror Bird' skull type (Degrange, 2012) and is present in Patagornithinae and most Phorusrhacinae and contrary to the Psilopterinae type, in which the tomial margin is nearly straight. Upturning of the ventral premaxillary margin is exaggerated in the reconstructed Mesembriornithinae *Mesembriornis milneedwardsi* Moreno, 1889 (see Kraglievich, 1946) and in the illustration of the skull of the phorusrhacine *Phorusrhacos longissimus* (Ameghino, 1895).

A sutural contact between the processus premaxillaris of the os nasale and the processus frontalis of the os premaxillare

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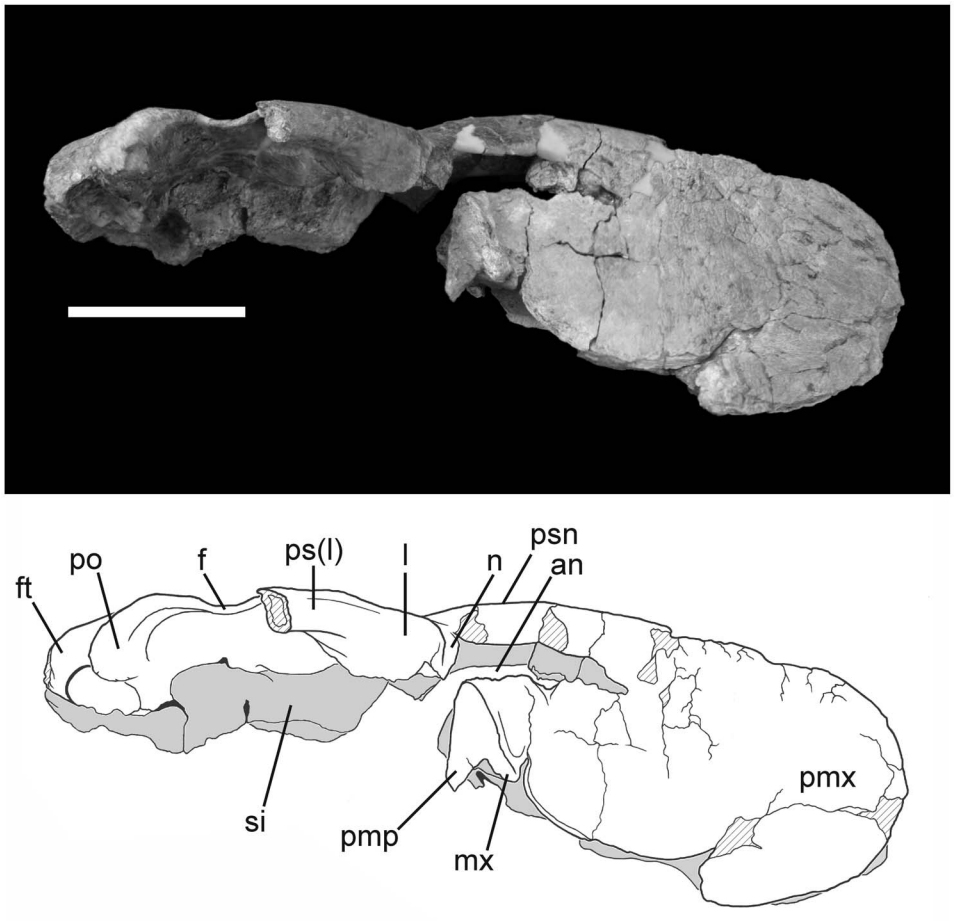


Figure 4. Photograph and interpretive drawing of the skull of *Phorusrhacos longissimus* MPEF-PV 11356 in right lateral view. an = aperture nasi ossea; f = os frontale; ft = fossa temporalis; l = os lacrimale; mx = os maxillare; n = os nasale; pmp = processus maxillopalatinus; pmx = os premaxillare; po = processus postorbitalis; ps(l) = processus supraorbitalis of the os lacrimale; psn = pila supranasalis; si = septum interorbitale. Scale bar = 10 cm.

is visible in dorsal view and extends caudal to the opening of the apertura nasi ossea (Fig. 5). The nasopremaxillary contact becomes difficult to trace rostrally due to breakage and the fusion between both bones typical of phorusrhacids (Degrange, 2012); however, holorhiny can be confirmed in *Phorusrhacos* (Ameghino, 1895). The pila supranasalis delimits a bow shape when viewed laterally that is not as marked as in *Llallawavis* or *Patagornis*. This condition is not observed in *Kelenken*, although absence could be a consequence of the deformation in the latter. The morphology of the external naris is somewhat obscured by breaks surrounding the opening on both sides of the skull. Only the dorsal margin of the external naris is well defined in MPEF-PV 11356. The general shape of the external naris is inferred to be rostrocaudally elongated, similar to that observed in *Kelenken guillermoi* (Bertelli et al., 2007), although the dorsal surface of the nares seems straight in *Kelenken* and curved in MPEF-PV 11356. This suggests that the preserved shape of the naris in *Kelenken guillermoi* (BAR 3877-11) may not be an artifact of dorsoventral crushing of the skull, although it appears to be shorter in *Phorusrhacos*. The external naris illustrated for *Phorusrhacos longissimus* (Ameghino, 1895) is more squared in appearance, as seen in the patagornithines *Andalgalornis steulleti* and *Patagornis marshi*.

Caudoventral to the external naris, the os premaxillare flares laterally to its contact with the processus maxillaris of the os nasale, which is not clearly distinguishable in MPEF-PV 11356. Rostral to this contact point, the premaxilla exhibits a shallow, bowl-shaped depression that opens to accommodate an accessory fossa of the external naris. It is unclear from Ameghino's (1895) illustrations whether early specimens of *Phorusrhacos longissimus* preserved this depression, although it is present (although shallower) in *Kelenken guillermoi* and the patagornithines *Andalgalornis steulleti* and *Patagornis marshi.* The smaller Psilopterinae also preserves a large accessory fossa to the external naris (Sinclair and Farr, 1932; Agnolín, 2009; Degrange and Tambussi, 2011). The depression angles rostroventrally and is proportionally smaller in MPEF-PV 11356 than in Psilopterinae. Although most of the ventral margin of the external naris is broken in MPEF-PV 11356, the narial floor is preserved and slopes caudoventrally. At the base of the curved surface of the narial floor, two small, broken processes slope ventromedially, preserving either the rostroventral portion of the maxillary process of the os nasale or part of the processus maxillopalatinus.

The skull roof of MPEF-PV 11356 is dorsoventrally flattened, wide (estimated width of 24 cm, calculated by doubling the distance between the right postorbital process and the sagittal

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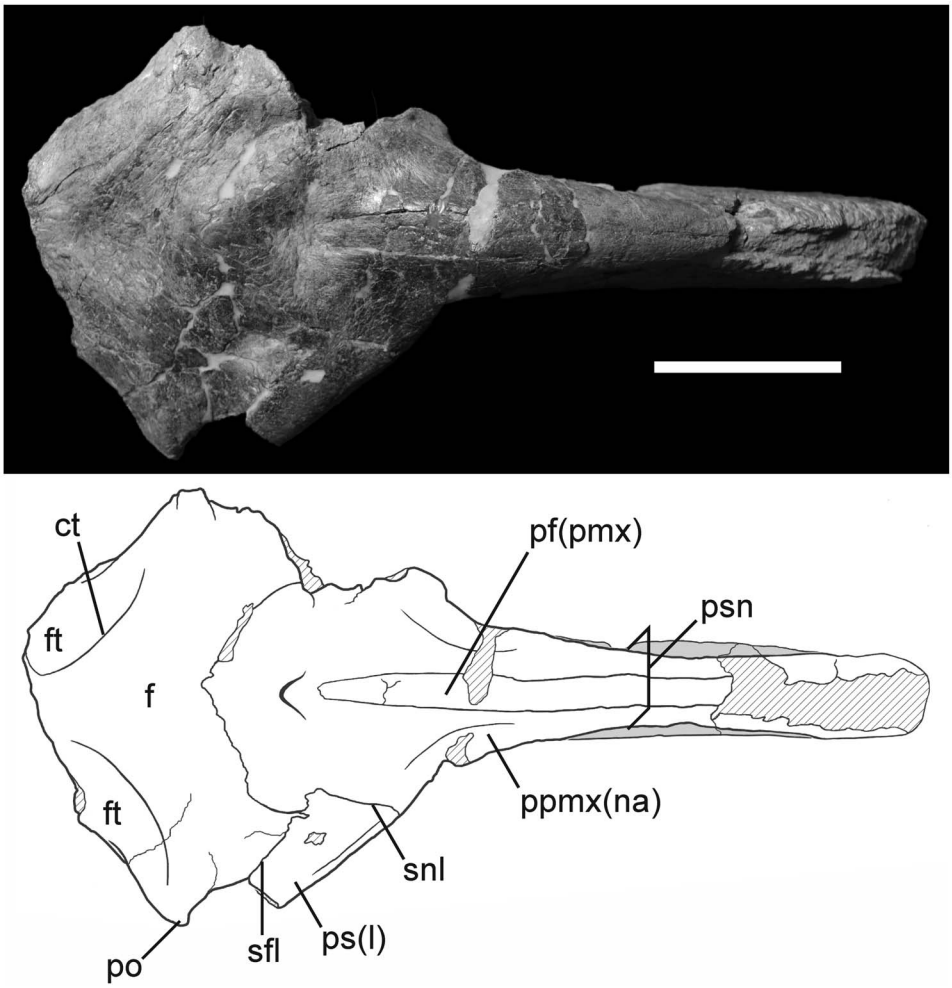


Figure 5. Photograph and interpretive drawing of the skull of *Phorusrhacos longissimus* MPEF-PV 11356 in dorsal view. ct = crista temporalis; f = os frontale; ft = fossa temporalis; pf(pmx) = processus frontalis of the os premaxillare; po = processus postorbitalis; ppmx(na) = processus premaxillaris of the os nasale; ps(l) = processus supraorbitalis of the os lacrimale; psn = pila supranasalis; sfl = sutura frontolacrimalis; snl = sutura nasolacrimalis. Scale bar = 10 cm.

plane of the skull), and would have been roughly triangular in shape when intact (Fig. 5). A shallow depression marks the caudal extent of the nasopremaxillary contact and is bordered by a small, raised knob directly caudal that is crossed by the nasofrontal suture. The wide nasofrontal contact curves rostrolaterally to meet the os lacrimale, at which point the suture divides into nasolacrimal contact rostrolaterally and frontal-lacrimal contact caudolaterally (suturae lacrimofrontalis et lacrimonasalis). The nasolacrimal contact meets the lateral margin of the orbit, and breakage along the ventral margin of the os lacrimale demarcates the missing processus orbitalis of the os lacrimale. In lateral view, the processus supraorbitalis of the os lacrimale forms a thick orbital brow that comprises the lateral borders of the skull roof, although this feature is broken caudally on the right side of the skull of MPEF-PV 11356. *Phorusrhacos longissimus* shares this prominent processus supraorbitalis with the patagornithines *Patagornis marshi* and *Andalgalornis steulleti*, meanwhile this feature is comparatively reduced in the os lacrimale of Psilopterinae. Nevertheless, the tip of this process seems separated from the orbital rim in MPEF-PV 11356, as in *Devincenzia pozzi* (Cabrera, 1939). This condition is not seen in Patagornitinae, in which the processus supraorbitalis is in contact with the orbital rim through its entire length. According to Bertelli et al. (2007), in the phorusrhacinae *Kelenken* the contact between the processus supraorbitalis of the os lacrimale and the orbital rim of the os frontale is not clear. However, they also state that "The supraorbital ossification of *Kelenken* fits within a socket formed by the portion of the frontal that forms the postorbital process" (Bertelli et al., 2007, p. 402). So it seems likely that in *Kelenken* the processus supraorbitalis of the os lacrimale is fused with the os frontale, forming the orbital rim. This condition represents an exclusive feature of *Kelenken*, different from any other Phorusrhacidae. The processus supraorbitalis runs approximately parallel to the roof of the cranium in MPEF-PV 11356 (Figs. 4, 5). An illustration of the skull of *Phorusrhacos longissimus*, NHMUK A529 (Ameghino, 1895), shows this process slightly caudoventrally deflected relative to the plane of the skull roof. It is unclear whether this morphology is due to distortion. It is not present in MPEF-PV 11356.

The processus postorbitalis forms a point that constitutes the greatest width of the preserved skull of MPEF-PV 11356 in dorsal view. However, the missing parietal region was likely wider, as in other phorusrhacines. Although the left processus

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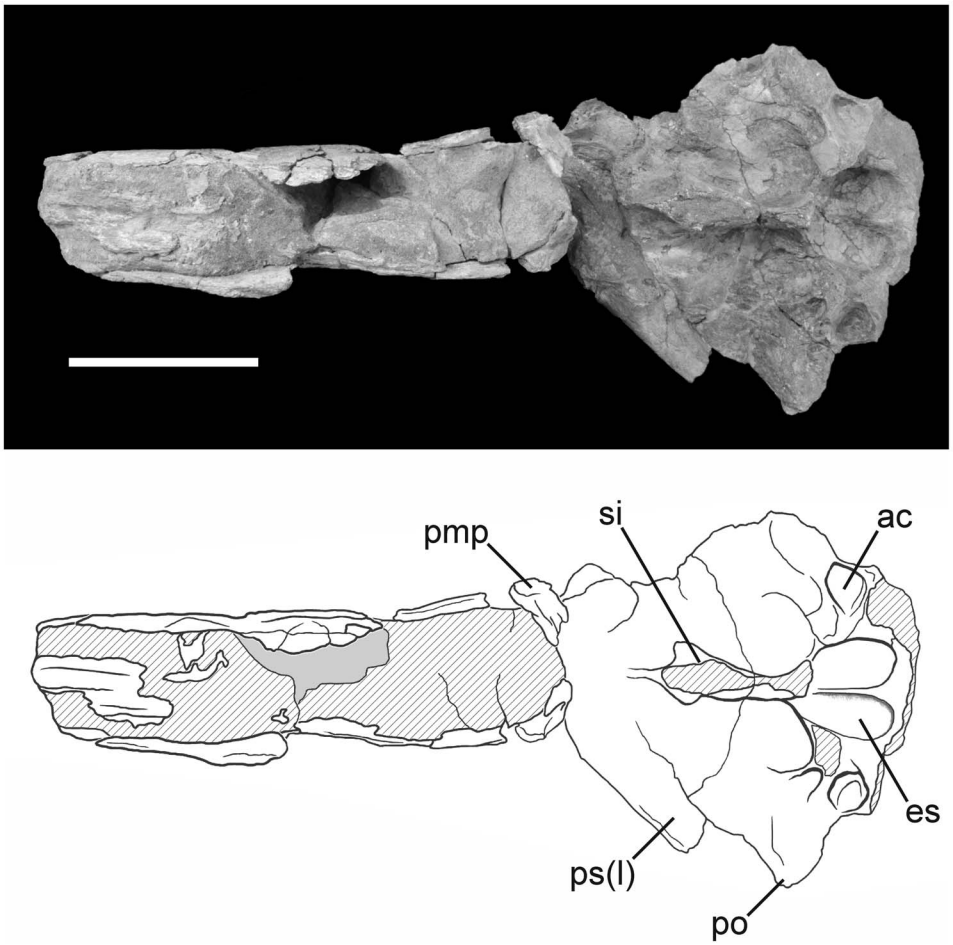


Figure 6. Photograph and interpretive drawing of the skull of *Phorusrhacos longissimus* MPEF-PV 11356 in ventral view. ac = accessory cotyla for m. adductor mandibulae externus profundus attachment; es = eminentia sagittalis; pmp = processus maxillopalatinus; po = processus postorbitalis; ps(l) = processus supraorbitalis of the os lacrimale; si = septum interorbitale. Scale bar = 10 cm.

postorbitalis is broken, the right is deflected only slightly ventrally. This is not the condition in *Devincenzia* and *Kelenken*, in which the processus is more deflected ventrally or in patagornithines and psilopterines, in which a strong ventral deflection is present. The lateralmost point of the postorbital serves as the origin for a crescent-shaped crista temporalis that extends caudomedially to near the midline (Fig. 5), as in *Kelenken* (not preserved in *Devincenzia*). Caudolateral to this ridge, the skull roof slopes ventrally and displays a distinct depression, the fossa temporalis, which corresponds to the origin for the m. adductor mandibulae externus profundus. The crista nuchalis sagittalis (that separates both fossae temporalis) is hourglass shaped. It is much wider between the fossae temporalis than in *Devincenzia pozzi, Kelenken guillermoi*, *Andalgalornis steulleti*, and the Psilopterinae and somewhat wider than that in the NHMUK A529 specimen of *Phorusrhacos longissimus*. Only a small portion of the caudal margin of the temporal fossa is visible to the left of the midline.

The septum interorbitale is quite robust and is broken at approximately midheight of the skull (Figs. 4, 6). It is lateromedially compressed, expanding caudally to the cranial border of the braincase. Its rostral margin is intact, forming a sharp ridge. The lateral wall of the septum is steep and shows a narrow, longitudinal sulcus olfactorii preserved on the right side of the skull. Caudally, a heart-shaped fossa cranii rostralis indicates the space occupied by the telencephalon, and more specifically by well-developed eminentia sagittalis, a feature present and developed in all phorusrhacids (Degrange et al., 2016a, b). Small crenulations of the brain are visible on the roof of the braincase (Fig. 6) and may represent impressions of the vena cerebralis dorsorostralis and vena cerebralis dorsocaudalis. This region of the braincase is divided medially by a low, rounded crista frontalis interna, which widens caudally near its contact with the missing rostral ridge for the fossa cerebelli. Lateral to the fossa cranii rostralis, an accessory fossa, interpreted here as an accessory attachment site for the m. adductor mandibulae externus profundus, opens ventrolaterally and slightly caudally (Fig. 6). This feature is absent in Psilopterinae, Mesembriornithinae, and other Phorusrhacinae such as *Kelenken* and *Devincenzia*, but is present, although shallower, in *Patagornis*.

Although the mandible of MPEF-PV 11356 is incompletely preserved, it includes most of the rostrum mandibulae and pars symphysialis and both left and right rostral portions of rami mandibulae (pars intermedia) (Fig. 7). The right ramus preserves the rostral margin of the fenestra mandibulae.

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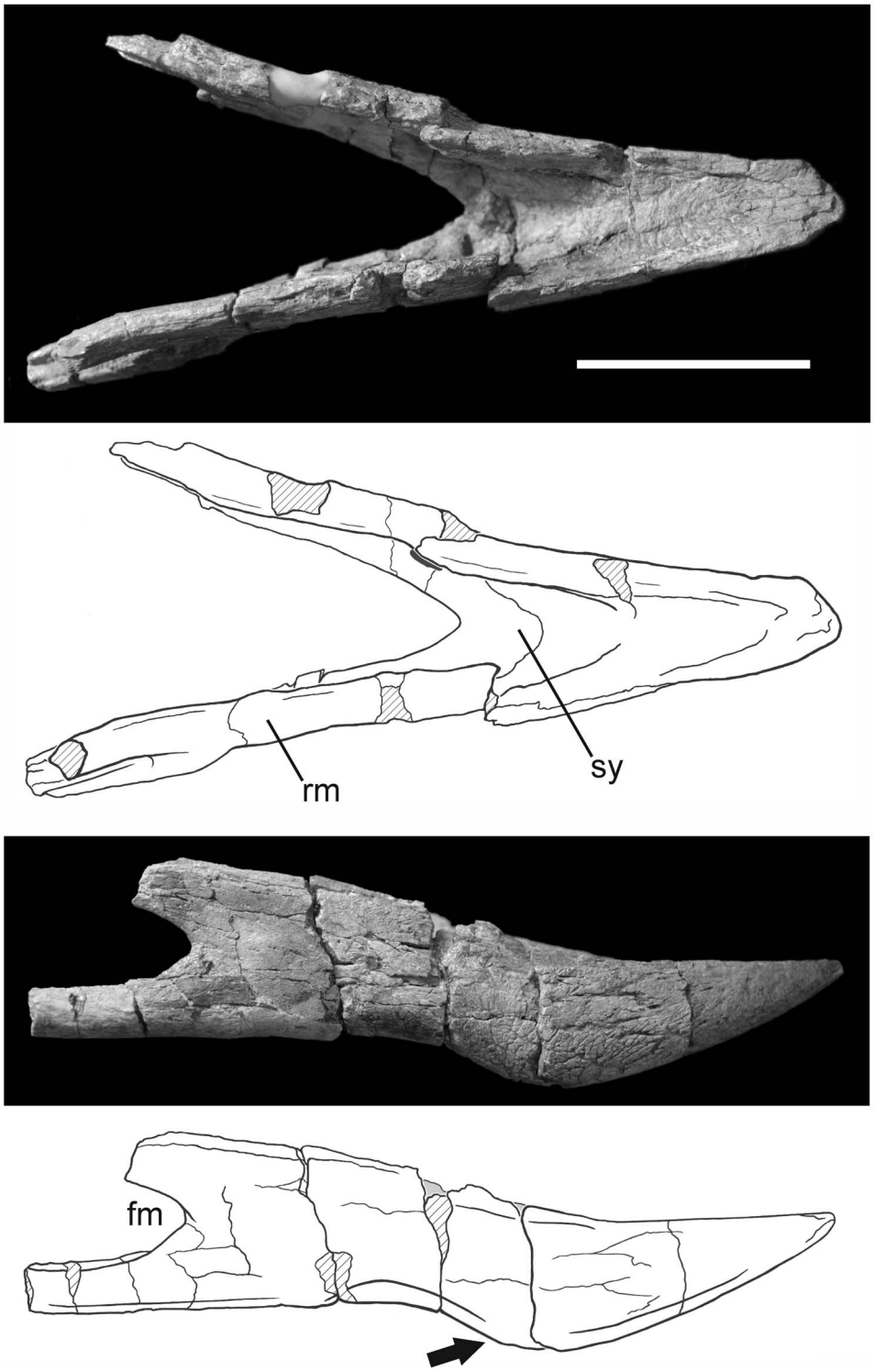


Figure 7. Photograph and interpretive drawing of the jaw of *Phorusrhacos longissimus* MPEF-PV 11356 in dorsal and right lateral views. fm = fenestramandibulae; rm = ramus mandibulae; sy = symphysis mandibulae. The arrow points to the ventral extension of the caudal portion of the symphysis. Scale bar = 10 cm.

The mandibular symphysis is robust (Table 1), and crushing has shifted the rostral portion to the right in dorsal view. The rostral tip of the symphysis is broken but preserves several small openings for the foveae corpusculorum nervosorum that probably housed sensory corpuscles within the rhamphotheca (Baumel and Witmer, 1993). The margo dorsalis of the symphysis are textured with scars similar to those observed in the rostrum. In dorsal view (Fig. 7), the mandibular symphysis is bordered by lateral ridges that caudally become more elevated with respect to the symphysis floor. The floor of the mandibular symphysis slopes caudoventrally and terminates in a V shape along its caudal margin, which is dissimilar to what it is observed in other

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Table 1. Measurements of MPEF-PV 11356 jaw symphysis and specimens referred to *Phorusrhacos longissimus* compared with other phorusrhacids. Parentheses indicate estimates based on incomplete elements. H = height; L = length; W = width.

Specimen	H	L	W	L/W
Phorusrhacos longissimus MPEF-PV 11356	57.2	~148.8	70.6	~2.11
Phorusrhacos longissimus NHMUK A529	62	179	67	2.67
Phorusrhacos longissimus NHMUK A530	57	—	66	—
Phorusrhacos longissimus NHMUK A684	54	—	60	—
Phorusrhacos longissimus MLP 20-118	53	(160)	67	(2.38)
Andalgalornis steulleti FM-P14357	39.5	108.7	47.3	2.29
Patagornis marshi NHMUK A516	29.5	89.6	32.9	2.72
Llallawavis scagliai MMP5050	16.0	52.7	19.2	2.74

Phorusrhacos longissimus specimens (e.g., NHMUK PV A529, A530, MLP 20-118, MPM-PV4241). The preserved rostral portion of the fenestra mandibulae exhibits a wide rounded edge, indicating the presence of an oval-shaped fenestra. The position of the rostral limit of the fenestra relative to the caudal limit of the symphysis exhibits variation among *Phorusrhacos* specimens. In NMHUK A529, the distance between the rostral margin of the fenestra and the caudal limit of the symphysis is substantial, whereas in MPM-PV4241 these features are positioned much closer to one another. MPEF-PV 11356 shares similarities with the latter specimen. An obvious feature of MPEF-PV 11356 is the extension of the ventral margin of the symphysis caudally, which accentuates the sigmoid shape of the jaw. This feature is quite similar to that of MNHUK A530 but is even more pronounced in MPEF-PV 11356. A rostrocaudally elongated furrow excavates the ventral and cranial margin of the fenestrae mandibulae (Fig. 7), penetrating them rostrally. This opening represents the rostral opening of the Meckelian canal.

Materials.—Partial skull (MPEF-PV 11356; Fig. 4) including a large part of the rostrum, skull roof, and orbit, as well as the distal portion of the mandible. The roof of the skull is incomplete, with the occiput and large part of the fossae temporales missing. The mandibular symphysis is preserved as well as partial rami mandibulae; however, the mandibulae are broken caudal to the rostral margin of the external mandibular fenestra.

Remarks.—Several features preclude MPEF-PV 11356 from assignment to other taxa for which skull material has been reported within Phorusrhacinae. In MPEF-PV 11356, the separation between the fossae temporales is less than that of *Devincenzia* but greater than that of *Kelenken*. The pila supranasalis has a bow shape when viewed laterally, a condition absent in *Kelenken*. The processus supraorbitalis of the os lacrimale is not completely fused with the orbital rim of the os frontale as in *Kelenken*. The processus postorbitalis is less developed (Fig. 4) than in either *Devincenzia* or *Kelenken*, and MPEF-PV 11356 presents an accessory fossa for the insertion of the m. adductor mandibulae extrenus profundus that is absent in *Devincenzia* and *Kelenken*. Supporting this assessment, the material proceeds from a Santacrucian locality from which only a single species of *Phorusrhacos* has been described, *Phorusrhacos longissimus*, and the size of MPEF-PV 11356 is consistent with the known size range of *P. longissimus*. Fragmentary cranial remains housed at AMNH and assigned to *P. longissimus* (AMNH 9158) are strikingly similar in size and morphology to the material presented here.

Phorusrhacinae indeterminate

Occurrence.—Puesto Estancia La Costa locality, SE of Santa Cruz Province, Argentinean Patagonia, santacrucian SALMA (late early Miocene) of Santa Cruz Formation.

Description.—The vertebra is strongly mediolaterally compressed and shows pronounced muscular scars on the cranial and caudal face of the processus spinosus as well as other morphological similarities with described thoracic vertebrae of the patagornithine *Andalgalornis steulletis* (Patterson and Kraglievich, 1960; Tambussi et al., 2012) and those of the phorusrhacine *Titanis walleri* (see Gould and Quitmyer, 2005). It is narrower and taller than thoracic vertebrae of the Mesembriornithinae *Mesembriornis milneedwardsi* (Kraglievich, 1940), and the processus spinosus is relatively longer. Direct comparison with the nearly complete vertebral series from the patagornithine *Andalgalornis steulleti* suggests the vertebra of MPEF-PV 11355 may correspond to the second or third thoracic vertebra. The corpus vertebra is short (Fig. 8). In cranial view, the facies articularis cranialis of MPEF-PV 11355 is wide and saddle-shaped with a low ridge on its lateral margin. This facies is continuous at its base with a tall processus ventralis corporis that displays an asymmetrical, laterally expanded kink. The processus spinosus is very high and notably expanded dorsally. The foramen vertebrale is oval in shape. In lateral view, the processus ventralis corporis is rounded at its distal end; proximally, it spans nearly the length of the centrum. Placed on the ventrolateral surface of the stout processus transversi, the fovea costalis for the articulation with the tuberculum costae can be observed; meanwhile laterocaudally to the facies articularis cranialis, the fovea costalis for the articulation with the capitulum costae are present as a dorsoventrally oriented, oval shallow depression. Ventral to this fovea, a large pneumatic foramen penetrates the centrum. The opening for the foramen is of similar size and shape to the fovea costalis but is craniocaudally oriented. Dorsal to this large foramen, two smaller accessory pneumatic foramina penetrate the ventral surface of the processus transversi where it attaches to the centrum. The facies articularis caudalis is narrower and taller than the facies articularis cranialis.

Materials.—A nearly complete thoracic vertebra (MPEF-PV 11355; Fig. 8).

Remarks.—The identification of the vertebra MPEF-PV 11355 past the level of Phorusrhacinae is less certain, owing to a paucity of described or figured comparable material. It cannot definitively be referred to the species *Phorusrhacos longissimus* barring detailed postcranial diagnoses of species within phorusrhacine. Thus, it is here considered as Phorusrachinae indet. At 17.4 cm in height, it is smaller than the only undescribed thoracic vertebra for *Titanis walleri* but larger than complete vertebrae known from any other clades of phorusrhacids (e.g., Mesembriornithinae, Patagornithinae, and Psilopterinae).

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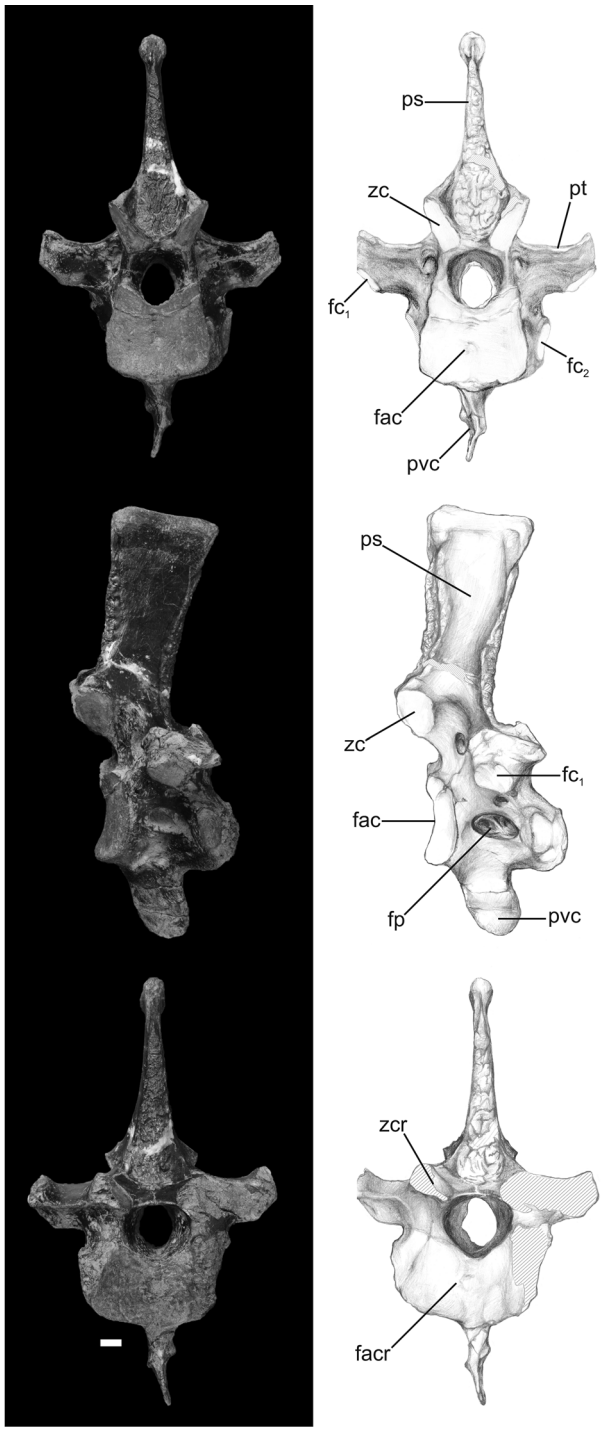


Figure 8. Photograph and interpretive drawing of the thoracic vertebra of Phorusrhacinae MPEF-PV 11355 in caudal, right lateral, and cranial views. fac = facies articularis caudalis; facr = facies articualris cranialis; fc_1 = fovea costalis for articulation with tuberculum; fc_2 = fovea costalis for articulation with capitulum; fp = foramen pneumaticum; ps = processus spinosus; pt = processus transversus; pvc = processus ventralis corporis; zc = zygapophysis caudalis; zcr = zygapophysis cranialis. Scale bar = 1 cm.

Discussion

The cranial material (MPEF-PV 11356) is consistent with the mediolaterally compressed and dorsoventrally high terror bird skull type of Degrange (2012), characterized by triangular ossa frontalia, processus supraorbitalis of the os lacrimale partially fused with the orbital rim, robust premaxillae, nares relatively small compared with the beak size, absence of the premaxillary fossa, and a dorsoventrally sigmoidal mandible. Although vertebra remains from other Phorusrhacinae have been reported, they have not been described in detail. Such is the case for a partially restored thoracic vertebra referred to *Titanis walleri* (see Gould and Quitmyer, 2005) and a fragmentary undescribed thoracic vertebra assigned to *Devincenzia* only on the basis of its size (Noriega and Agnolín, 2008). However, the lack of postcranial characters identified to diagnose distinct Phorusrhacinae species limits our referral of the recovered vertebra. We conclude its morphologies and size are consistent with referral to *Phorusrhacos longissimus* or a similarly sized phorusrhacine species.

The skull is referred to Phorusrhacinae because of its large skull size and the morphology of the mandible, specifically, the ratio of mandibular symphysis length to width at the base (~2.11), although a small amount of material missing from the tip of the mandible of MPEF-PV 11356 artificially decreases this ratio. These ratios are 2.38 in the holotype and 2.67 in the referred specimen NHMUK A529. Mandibular symphyses of bulkier phorusrhacids such as Physornithinae are shorter and wider at the base, with a ratio of 1.5 for *Physornis fortis* Ameghino, 1895 (FM-P13340). However, it is worth noting that comparative mandibular material is not known for several other named species of Phorusrhacinae (i.e., *Kelenken guillermoi*, *Titanis walleri*, and *Devincenzia pozzi*). Smaller phorusrhacids such as *Llallawavis scagliai* Degrange et al., 2015 have slightly bigger ratios (2.74).

Within Phorusrhacinae, skull remains are generally limited, which complicates comparisons; those so far known are deformed (*Kelenken*), deformed and heavily artificially reconstructed (*Devincenzia*), or limited to fragmentary remains (*Titanis*). However, the nares of MPEF-PV 11356 appear to be less elongated than those present in *Kelenken*. The width of the skull roof between the fossae temporalis is greater in *Phorusrhacos* and *Devincenzia* than in *Kelenken*. In addition, in *Phorusrhacos* the processus postorbitalis is weakly projected ventrally when compared with the rest of Phorusrhacinae. Finally, the suturae frontolacrimalis and nasolacrimalis delimit an 'L' shape when viewed dorsally in the new specimen, while in *Kelenken* those suturae are not marked due to fusion of the bones (see the following). In this character, the condition observed in *Phorusrhacos* is more similar to that of the much smaller 'Psilopterine' skull type of Degrange (2012) (e.g., *Psilopterus* and *Llallawavis*).

Several characters described in the preceding support the placement of MPEF-PV 11356 within Phorusrhacinae to the exclusion of other phorusrhacid groups and will likely benefit future analyses upon the recovery of more complete specimens. Although there is a comparative lack of cranial material among Phorusrhacinae specimens (Fig. 8), we propose the specimen MPEF-PV 11356 presented here is referable to *Phorusrhacos longissimus*.

The illustration of a skull of *Phorusrhacos longissimus* (Fig. 2, NHMUK A529; Ameghino, 1895) differs substantially from that of MPEF-PV 11356 in the following ways: (1) the rostrum of MPEF-PV 11356 is dorsoventrally shorter and

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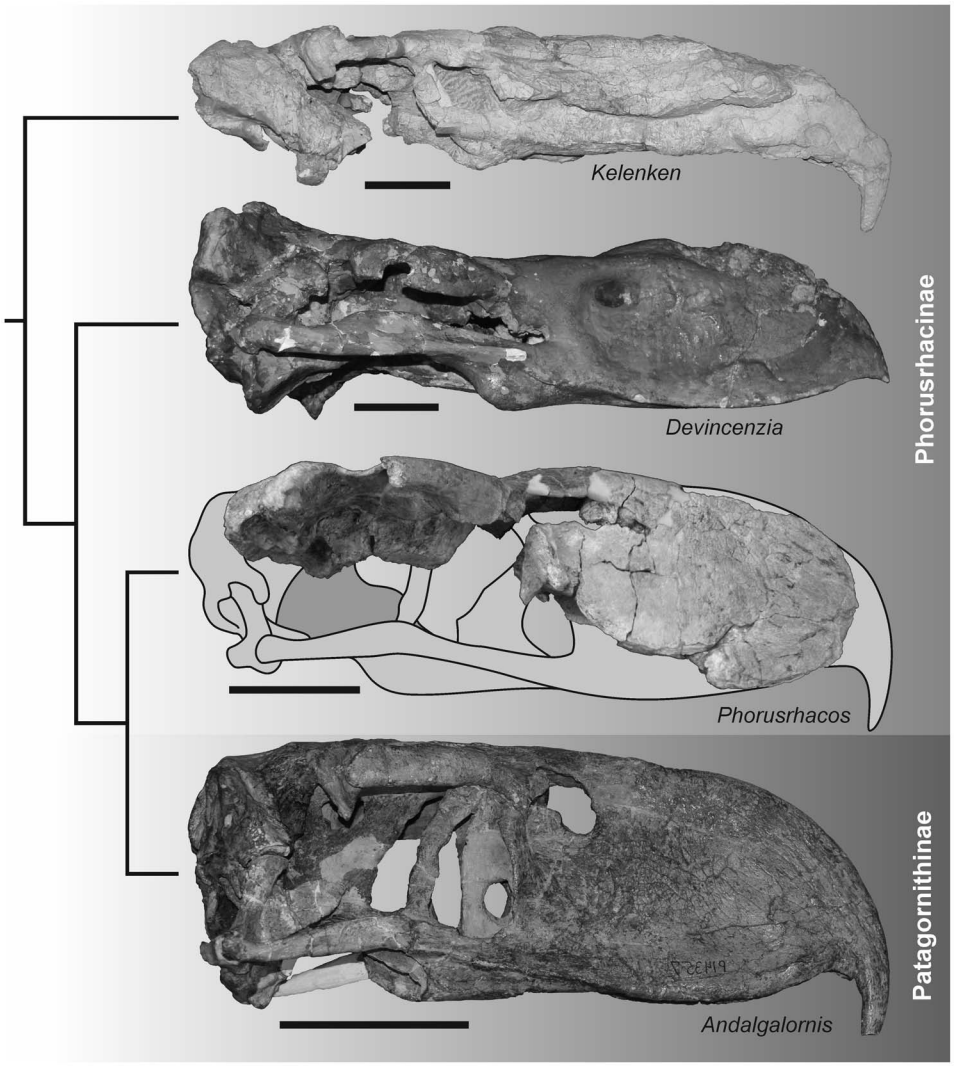


Figure 9. Lateral views of the skulls of the Phorusrhacinae *Kelenken guillermoi* BAR 3877-11, *Devincenzia pozzi* MLP 37-III-7-83, and *Phorusrhacos longissimus* MPEF-PV 11356 and the Patagornithinae *Andalgalornis steulleti* FM-P14357 displayed in a phylogenetic framework simplified from Degrange et al. (2015). Skulls of *Kelenken*, *Devincenzia*, and *Andalgalornis* are mirrored for comparison. Scale bar = 10 cm.

more elongated; (2) the external nares are elongated in MPEF-PV 11356 and are instead shown to be more quadrangular in the illustrated *Phorusrhacos longissimus*; (3) the ventral margin of the rostrum shows a strongly sigmoidal shape in the illustrated *Phorusrhacos longissimus*, while it is shallow and not as prominent in MPEF-PV 11356; and (4) the processus supraorbitalis of the os lacrimale is parallel to the plane of the skull roof in MPEF-PV 11356, whereas the caudal edge of this processus is ventrally deflected in the illustrated *Phorusrhacos longissimus*. It is important to consider here that the material depicted by Florentino Ameghino represents a field illustration of a skull that was highly fragmented. Commendable in its attempt, this illustration nevertheless was based on proportions of the jaw and beak hook, field measurements of length and width, in-person descriptions provided by his brother Carlos Ameghino, and references to the skull of *Patagornis marshi* (= *Tolmodus inflatus*; see specimen NHMUK A516). The problematic nature of this reconstruction is made clear by examination of the nares, as the nares illustrated for *Phorusrhacos* appear to be scaled-up versions of those seen in *Patagornis marshi* NHMUK A516 (see Ameghino, 1895, fig. 1).

The associated jaw presented here is also quite similar in morphology to that of *P. longissimus*. The only mandibles confidently referred to a taxon within Phorusrhacinae are from *Phorusrhacos longissimus*, although this element is well represented in other members of Phorusrhacidae, for example, *Paraphysornis brasiliensis* (Alvarenga, 1982), *Andrewsornis abbotti* Patterson 1941, *Patagornis marshi*, *Andalgalornis steulleti*, *Llallawavis scagliai*, and various psilopterines. Potential sexual dimorphism or ontogenetic variation notwithstanding, the mandible of MPEF-PV 11356 is similar in both size and shape to specimens of *Phorusrhacos longissimus* (including the holotype specimen) and specifically shares with that taxon a mandibular symphysis more than twice as long as its width at the symphysis base. This feature is the only character of the skull reported as diagnostic for Phorusrhacinae by Alvarenga and Höfling (2003) and distinguishes MPEF-PV 11356 from specimens

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referred to taxa within Physornithinae that possess a shorter, wider symphysis.

Conclusions

The new cranial material presented here is assignable to *Phorusrhacos longissimus*, one of the largest terror birds from Patagonia. The new vertebra, referred to Phorusrhacinae indet., calls attention to the paucity of described postcranial diagnoses for species in this clade. In light of the new cranial material, it is clear that some features previously described or mentioned that were based on the field drawings of Ameghino (1895) must now be revised. The new material allows us to state confidently that the skull of *Phorusrhacos longissimus* has the following previously unknown features: (1) narial openings are elongated; (2) the pila supranasalis forms a bow shape in lateral view; (3) the processus supraorbitalis of the os lacrimale is parallel to the orbital rim and caudally detached from the orbital margin; (4) the suturae frontolacrimalis and nasolacrimalis delimit an 'L' shape when viewed dorsally; (5) the processus postorbitalis is stout, although less developed than the rest of phorusrhacids; and (6) an accessory cotyla for the attachment of the m. adductor mandibulae externus profundus is present. The new specimens provide data critical to filling existing gaps in the knowledge of the evolutionary history of the most iconic fossil giant predatory birds. This description provides further key cranial comparisons among closely related phorusrhacine taxa and calls attention to the need for the identification of new cranial and postcranial morphological characters needed to better understand the phylogenetic relationships among phorusrhacines, and phorusrachids more generally.

Acknowledgments

We thank E. Ruigomez from the Museo Egidio Feruglio (Trelew) for granting access to the material. Our thanks to the following for allowing and facilitating the consultation of the collections under their management: W. Simpson, J. Holstein, and K. Lawson from the Field Museum of Natural History (Chicago); C. Norris, D. Brinkman, and M. Fox from Yale Peabody Museum (New Haven); C. Mehling from the American Museum of Natural History (New York); M. Reguero and A. Scarano from the Museo de La Plata (La Plata); and M. Taglioretti and F. Scaglia from the Museo Tradicional Lorenzo Scaglia (Mar del Plata). Phoebe Wang is thanked for her skillful drawings of the vertebra. Thanks to the editor D. Ksepka and three anonymous reviewers for their helpful comments. This research was supported by Jackson School of Geosciences to DE and JC.

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Accepted: 7 June 2019

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