Journal of Vertebrate Paleontology 27(2):409–419, June 2007

ARTICLE

A NEW PHORUSRHACID (AVES: CARIAMAE) FROM THE MIDDLE MIOCENE OF PATAGONIA, ARGENTINA

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ABSTRACT—The anatomy of a new, enormous phorusrhacid (Aves: Cariamae) from the Middle Miocene Collón Curá Formation of northwestern Patagonia (Río Negro province, Argentina) is described. The new phorusrhacid is known by a single specimen that consists of a nearly complete skull associated with a tarsometatarsus and a pedal phalanx. The new fossil is the largest known phorusrhacid and its morphology resembles more that of taxa traditionally grouped within phorusrhacines. Its skull—by far the best preserved among large phorusrhacids—provides a great deal of previously unknown anatomical information and indicates that reconstructions of the skull of gigantic phorusrhacids based on their smaller relatives are unwarranted.

INTRODUCTION

Although reconstructions of the skull of large phorusrhacids are frequently published in both scientific and popular literature (Feduccia, 1980; Marshall et al., 1986; Tambussi, 1997, 1998), very little information is actually available on the cranial morphology of these Cenozoic flightless birds (Alvarenga and Höfling, 2003). Published reconstructions of these large "terror" birds often highlight their very tall beaks and round, high orbits, but such renderings are extrapolations from the much better known skulls of medium-to-small sized phorusrhacids such as *Psilopterus* (Sinclair and Farr, 1932) and *Patagornis* (Andrews, 1899).

In this article, we describe the cranial and hind-limb material of a new, very large phorusrhacid bird (BAR 3877-11) from the Middle Miocene of Comallo (Río Negro province, Argentina). This article provides the first detailed osteological study of the skull of gigantic phorusrhacids (skulls larger than 600 mm in length) and highlights the significant differences between the cranial morphology of large and small phorusrhacids.

Institutional Abbreviations—BAR, Museo Asociación Paleontológica Bariloche, Río Negro, Argentina; **BMNH**, The Natural History Museum, London, United Kingdom; **MLP** Museo de La Plata, La Plata, Argentina

Anatomical Abbreviations—an, apertura nasi ossea; **ca**, cotyla articularis; **ch**, fossa choanalis; **cl**, cotyla lateralis; **cm**, cotyla medialis; **cme**, condylus medialis; **cns**, crista nuchalis sagittalis; **cnt**, crista nuchalis transversa; **co**, condylus occipitalis; **cp**, corpus phalangis; **cpl**, crista plantaris lateralis; **cpm**, crista plantaris medialis; **cs**, cotyla quadratica squamosi; **ct**, crista temporalis; **dp**, dorsolateral projection of occipital table; **ei**, eminentia intercotylaris; **f**, os frontale; **fa** fenestra antorbitalis; **fc**, fovea ligamenti collateralis; **fh**, foramina nervorum hypoglossi; **fn**, foramen vasculare distale; **fm**, foramen magnum; **fp**?, interpreted as fossa parabasalis; **fs**, fossa subtemporalis; **ft**, fossa temporalis; **h**, hypotarsus; **ima**, impressio M. adductor mandibulae externus; **ips**, attachment area for the M. pseudotemporalis superficialis; **j**, arcus jugalis; **l**, os lacrimale; **msc**, attachment area for the M. splenius capitis; **mx**, os maxillare; **n**, os nasale; **or**, orbita; **p**, os parietale; **pa**, os palatinum; **pm**, os premaxillare; **po**, processus postorbitalis; **pt**, os pterygoideum; **pz**, processus zygomaticus; **rc**, rostral premaxillar grooves; **rm**, rostrum maxillare; **rt**, round tubercle; **se**, sulcus extensorius; **ve**, foramen venae occipitalis externae; **II–IV**, trochleae metatarsi II–IV.

GEOLOGICAL SETTING

The fossil site is located at the southeastern corner of Comallo (41° 01′ 59.4″ S, 70° 15′ 29.7″ W; approximately 100 meters from the railroad), a small village in the northwestern portion of the Province of Río Negro, Argentina (Fig. 1). BAR 3877-11 was discovered in outcrops probably belonging to the pyroclastic Collón Curá Formation, although the stratigraphy of this region has only been preliminarily studied. Comallo and its vicinity are covered by whitish tuffs classically referred as to the Collón Curá Formation (Mazzoni and Stura, 1990; Impiccini and Valles, 2002; Giacosa et al., 2004). This lithostratigraphic unit is contained within the "fosa del río Collón Curá", the northern extension of the Ñirihuau Basin (late Oligocene-Miocene). However, the outcrops of the Collón Curá Formation extend beyond the margins of the morphostructural regions of the Nordpatagonian massif and mountain range (Vucetich et al., 1993). The age of the sediments classically known as the Collón Curá Formation, together with other seemingly equivalent beds, has never been adequately determined. However, the type association of the Friasian SALMA (South American Land Mammal Age) is partially correlated to the fauna of the Collón Curá Formation, and these faunas lay generally above the Santacrucian SALMA (in some instances Friasian beds are contiguous with Santacrucian ones). These faunistic considerations, together with radioisotopic dates from different localities of the Collón Curá Formation (~15.7 Ma; Flynn and Swisher, 1995), indicate that the age of the Conlloncuran SALMA (and BAR 3877-11) is middle Miocene.

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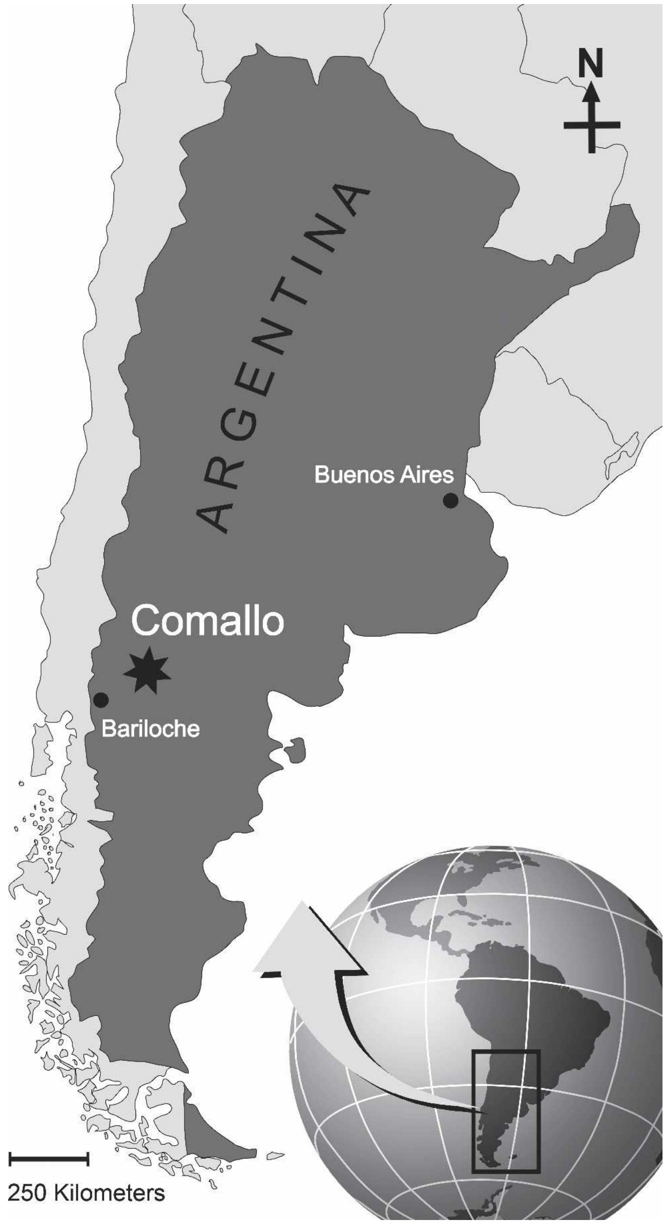

FIGURE 1. Village of Comallo (Río Negro Province, Argentina), where the holotype of *Kelenken guillermoi* (BAR 3877-11) was discovered.

SYSTEMATIC PALEONTOLOGY

AVES Linnaeus, 1758
NEOGNATHAE Pycraft, 1900
CARIAMAE Fürbringer, 1888
PHORUSRHACIDAE (Ameghino, 1889)
KELENKEN GUILLERMOI, gen. et sp. nov.
(Figs. 2–9)

Etymology—The generic name "kelenken" refers to a fearsome spirit of the Tehuelche tribe (native people of Patagonia), represented as giant bird of prey. The species name, "guillermoi" is after the discoverer of the holotype, Mr. Guillermo Aguirre-Zabala.

Holotype—BAR 3877-11, a nearly complete skull (Figs. 2–6) associated with a left tarsometatarsus (Figs. 7–9), a small proximal portion of a pedal phalanx (Fig. 10), and a few indeterminate fragments. The association of these bones to a single specimen is based on these facts: (1) they were collected next to one another, (2) nothing else was collected from this particular site, (3) they agree in their general preservation (color, texture, etc.), and (4) they all correspond morphologically to a large phorusrhacid.

Locality and Horizon—Southeastern corner of Comallo, approximately 100 meters from the railroad (41° 01′ 59.4″ S, 70° 15′ 29.7″ W; 790 meters over sea level), southwestern Rio Negro Province, Argentina (Fig. 1). Collón Curá Formation, Middle Miocene (Rabasa, 1974; Mazzoni and Benvenuto, 1990; Impiccini and Valles, 2002).

Diagnosis—A large phorusrhacid with (1) a very long rostrum (longer than that of *Phorusrhacos longissimus*, Ameghino 1887), (2) a supraorbital ossification fitting into a socket of the postorbital process, (3) an alariform projection and blunt end of the dorsolateral corner of the occipital table, (4) a tall and robust jugal bar (greater than that of *Devicenzia pozzi* Kraglievich, 1931), (5) a subtriangular foramen magnum, (6) a subquadrangular midshaft of the tarsometatarsus (differing from the rectangular and very wide midshaft of brontornithines), (7) a round tubercle—lower in height than the intercotylar eminence—on the medioplantar corner of the lateral cotyla of the tarsometatarsus, (8) a quadrangular trochlea of metatarsal IV (contrasting with the proximodistally rectangular trochlea of *Devicenzia pozzi*), and (9) a centralized position—with respect to the shaft's sagittal plane—of the distal vascular foramen of the tarsometatarsus. This combination of characters is unique among phorusrhacids and characters 1, 2, 5, 7 are distinct autapomorphies of the new taxon, *Kelenken guillermoi*.

ANATOMICAL DESCRIPTION

Anatomical nomenclature follows Baumel and colleagues (1993) except when noted. The Latin terminology used by Baumel and colleagues (1993) is retained for muscles, and osteological structures are described with English equivalents of the Latin terms (although the Latin equivalent is also given).

Skull

Most of the skull of *Kelenken guillermoi* is preserved, although somewhat crushed dorsoventrally. The entire rostrum (rostrum maxillae), much of the orbits, skull roof and braincase, and left quadrate (os quadratum) are preserved, but most palatal bones behind the orbit are missing (see Figs. 2–6).

The skull is very massive, triangular in dorsal view (see Fig. 4), with a dorsoventrally compressed caudal portion (see Figs. 2, 3). The length of the skull—measured from the tip of the rostrum to the center of the sagittal nuchal crest (crista nuchalis sagittalis)—is approximately 716 mm (Table 1). The rostrum is very long. Unlike *Hermosiornis milneedwarsi* (= *Mesembriornis*; Moreno, 1889; Table 2) and *Patagornis marshi* (Moreno and Mercerat, 1891), the rostrum of *Kelenken* exceeds half the total length of the skull. Based on the distance between the external nares (aperturae nasi osseae) and the cranial tip, the ratio between the rostrum and the skull of *Kelenken* is 0.56.

Dorsoventral crushing notwithstanding, the rostrum is high and very robust (Figs. 2 and 3), although it does not appear to have been as high as the rostrum of patagornithines (e.g., *Patagornis*, *Andrewsornis abbotti* Patterson 1941, *Andalgalornis steulletti* [Kraglievich 1931]) (Alvarenga and Höfling, 2003). The cranial end of the premaxilla (os premaxillare) projects prominently as a sharp, ventral hook. Such a strong ventral projection of the rostral end of the premaxilla most closely resembles the condition seen in large-to-medium sized phorusrhacids (e.g., *Phorusrhacos*, *Patagornis*, *Andrewsornis*, *Andalgalornis*) than

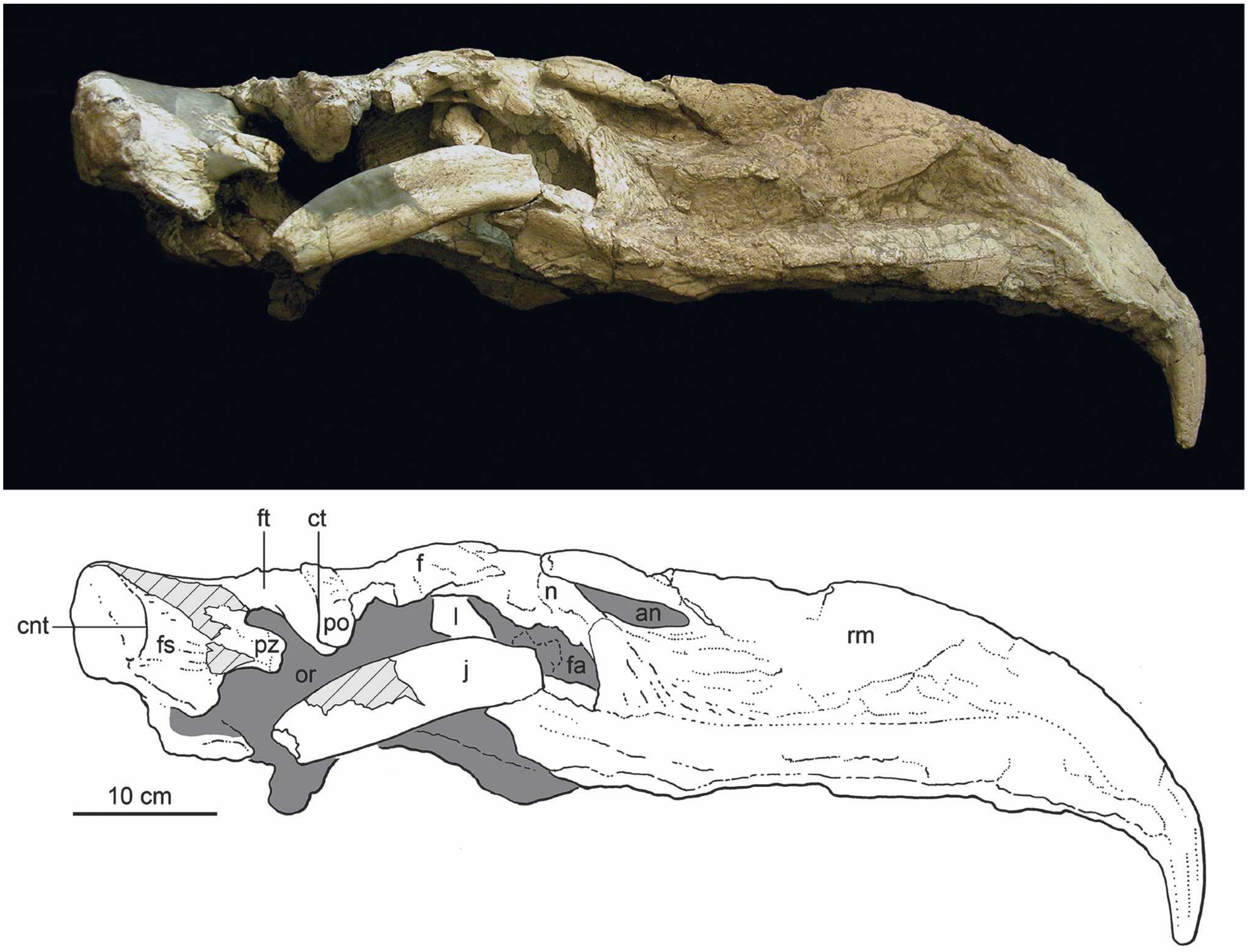

FIGURE 2. Photograph and interpretive drawing of the skull of *Kelenken guillermoi* (BAR 3877-11) in right lateral view.

the weaker projection seen in the smaller psilopterines. Ventrally, the rostral portion of the premaxilla forms a pair of prominent ridges each separated from the tomial margin (crista tomialis) by a groove. A longitudinal groove (rostral premaxillar canal; see Fig. 5) also separates each of these ridges from a broader central portion of the premaxilla. A similar morphology was described by Andrews (1899) for the rostral portion of the palate of *Patagornis*. Much of the lateral side of the rostrum is irregularly scarred by small pits (foramina neurovascularia), exits for the smallest ramifications of the ophthalmic and nasopalatine nerves (nervi ophthalmicus et nasopalatinus). The caudal two-thirds of the rostrum are also excavated by a prominent furrow that runs parallel to the tomial margin.

Both external nares are preserved (see Figs. 2, 3). They are small and located on the caudodorsal corner of the rostrum as in patagornithines (e.g., *Patagornis*, *Andrewsornis*; Andrews, 1899; Alvarenga and Höfling, 2003)—the size and position of the external nares is otherwise unknown for the larger phorusrhacines and brontornithines. They appear to be rostrocaudally longer than dorsoventrally high, although this may be exaggerated by dorsoventral crushing, and their caudal margin is formed by the maxillary process of the nasal (os nasale, processus maxillaris). It is not possible to discern whether the nares are connected medially (lacking a septum nasi osseum) as in other phorusrhacids (Andrews, 1899; Alvarenga and Höfling, 2003).

The antorbital fenestra (fenestra antorbitalis) is somewhat crushed on both sides but its quadrangular shape is clearly visible. The rostral border lies approximately at the level of the caudal margin of the external nares. The ventral margin of this opening is straight as viewed from the left side (see Fig. 3). Robust lacrimals (ossa lacrimalia) delimit the antorbital fenestra

TABLE 1. Selected measurements (mm) of BAR 3877-11.

Skull length*	716.00
Distance between external nares (center) and premaxillary tip	404.00
Width at postorbital processes*	225.00
Width at caudal end of skull	312.00
Jugal, maximum height	40.00
Tarsometatarsus, maximum length	437.14
Tarsometatarsus, distal width	90.19
Tarsometatarsus, proximal width	97.70
Tarsometatarsus, midshaft width	48.82
Hypotarsus, proximodistal length	63.56
Trochlea of metatarsal II, width	22.50
Trochlea of metatarsal III, width	41.96
Trochlea of metatarsal IV, width	29.42
Distance between distal foramen and distal end of metatarsal III	75.19

*Calculated by doubling the distance between the left postorbital process and the sagittal plane of the skull.

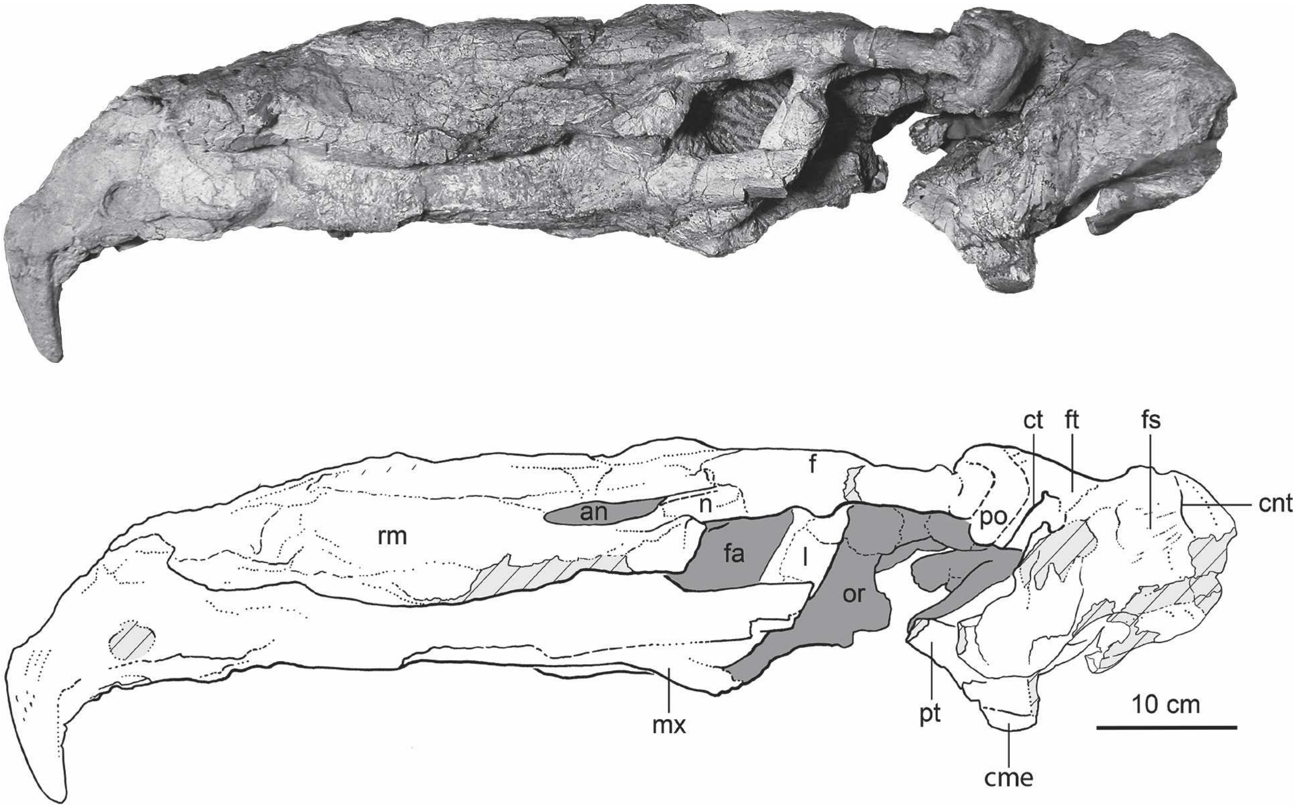

FIGURE 3. Photograph and interpretive drawing of the skull of *Kelenken guillermoi* (BAR 3877-11) in left lateral view.

caudally. These bones are recessed with respect to both the jugal bar (arcus jugalis) and the lateral margin of the frontal (os frontale). The antorbital fenestra of *Kelenken* is proportionally smaller than that of *Patagornis*.

The shape of the orbits may be slightly affected by dorsoventral compression (see Figs. 2, 3). Nonetheless, it is clear that they were low, subrectangular in shape, with a concave dorsal margin and a slightly convex ventral border. Dorsally, the orbit is delimited by a thick and rounded edge; the caudal portion of this supraorbital ossification appears to overhang ventrally as seen on the right side (see Fig. 2). A similar structure was considered by Andrews (1899) to be the supraorbital process of the lacrimal of *Patagornis*. In *Kelenken*, the connection between this supraorbital ossification and the lacrimal is not clear but we follow Andrews (1899) in considering this bone to be an extension of the latter. The supraorbital ossification of *Kelenken* fits within a socket formed by the portion of the frontal that forms the postorbital process. As far as we know, this is not seen in *Patagornis* or any other phorusrhacid. The orbit is ventrally limited by a robust jugal bar (see Fig. 2). The jugal (os jugale) is very tall dorsoventrally (see Table 1), laterally flat, and transversally compressed; at the center of the orbit this bone is approximately four times taller than thick. The dorsoventral height of the jugal is greater than that of other phorusrhacines (i.e., *Devicenzia*) as well as that of patagornithines and psilopterines. Remains of the interorbital septum (septum interorbitale) are visible both at the level of the orbit and the antorbital fenestra.

The frontals appear to have been dorsally flat (see Fig. 4). Damage in the area corresponding to the contact between the frontals and the premaxillae (ossa premaxillae) prevents the identification of sutures between these bones, but the suture of the frontals with either the nasals (ossa nasali) or the parietals is fully fused. The complete fusion between frontals and parietals (ossa parietalia) makes difficult to identify the participation of these bones in the structures of the skull roof. Nonetheless, it is reasonable to follow Andrews (1899) in the claim that the blunt and robust postorbital process was primarily formed by the frontal. Ventrally, each frontal forms a large depression corresponding to the attachment of the M. pseudotemporalis superficialis (see Fig. 5).

The postorbital process is narrowly separated from a well-developed, cranially oriented zygomatic process (processus zygomaticus). These projections enclose a rather narrow temporal fossa (fossa temporalis; see Fig. 2). The postorbital process contains the rostrolateral portion of a distinct temporal ridge (crista temporalis) that delimits the scar left by the origin of the extensive temporal musculature (M. adductor mandibulae externus; see Figs. 2, 3). Such a musculature invaded most of the skull roof at the level of the parietals. The scars left by these massive muscles are separated by only 20 mm along the sagittal plane (see Fig. 4). In addition, the surface for the origin of M. adductor mandibulae externus extends ventrally as a wedge-like scar directed towards the braincase (see Fig. 5). Unlike *Patagornis*, the temporal region of *Kelenken* is characterized by an abrupt transition between the ventromedial surface of the temporal fossa and the flat dorsomedial extension of the temporal musculature. As opposed to *Patagornis*, in *Kelenken* the temporal ridge does not define the medial margin of a deep temporal fossa, but instead the medial extension of the scar left by the temporal musculature (see Fig. 4). Caudal to the robust zygomatic process, along the lateral side of the squamosal (os squamosum), there is a well-developed depression corresponding to the origin of the M. depressor mandibulae. This subtemporal fossa (fossa subtemporalis) is broad and caudally defined by the blunt, lateral extension of the transverse nuchal crest (crista nuchalis transversa; see Figs. 2, 3).

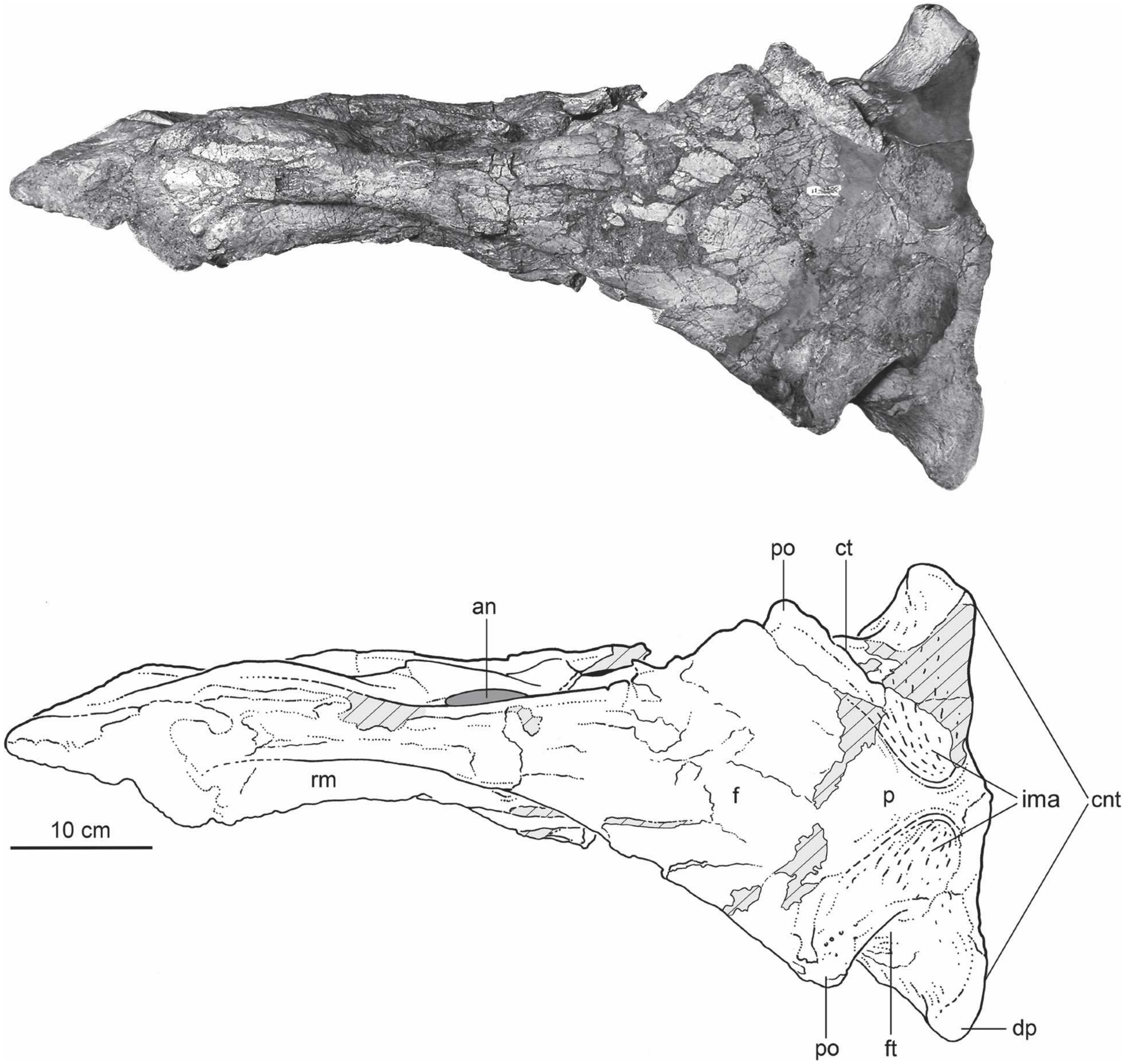

FIGURE 4. Photograph and interpretive drawing of the skull of *Kelenken guillermoi* (BAR 3877-11) in dorsal view.

Most of the palate is preserved, although the pterygoid (os pterygoideum) is represented by only a portion on the left side (see Fig. 5). The boundaries between the premaxillae, maxillae (ossa maxillae), and palatines (ossa palati) are indistinguishable. Both maxillae form an extensive palate, the lateral margins (tomial edges) of which are subparallel over most of the length of the rostrum. The palate becomes wider from the rostral end to the orbital region. As in *Patagornis marshi* (Andrews, 1899), these bones are sagittally separated by a distinct depression that runs for much of their length. Along the caudal half of the palate, this longitudinal depression is flanked by transversally convex portions of the maxillae. Caudally, these bones are broadly connected to the broad palatines, which appear to define much of the long and narrow choanal region (fossa choanalis). The caudolateral margin of the maxilla exhibits a well-defined, sutured contact with the jugal, a condition similar to that seen in *Patagornis* (Andrews, 1899). The only preserved portion of the pterygoid—corresponding to the left side—is detached from the palatine but in articulation with the quadrate. It is a rod-like bone that articulated near the base of the orbital process (processus orbitalis) of the quadrate. The latter is also represented by the poorly preserved left element, which provides minimal anatomical information. Proximally, the quadrate fits into a large squamosal cotyla (cotyla quadratica squamosi), which is clearly visible on the right side; distally, it possesses a rounded, well-developed condyle interpreted as the medial condyle (condylus medialis). Only the orbital process of the quadrate is preserved.

The occipital table is very wide, a condition similar to that in *Devicenzia* (see Fig. 6). The occipital condyle (condylus occipitalis) is round, bearing a vertical groove (incisura medialis condylae) originating on its dorsal surface, and reaching nearly the center of the condyle. The foramen magnum is triangular, with a blunt dorsal apex, and slightly smaller than the occipital condyle. The lateral margins of the foramen magnum are recessed with respect to its dorsal margin, which forms an overhanging crest. Dorsal to the foramen magnum is a crest-like prominence (crista

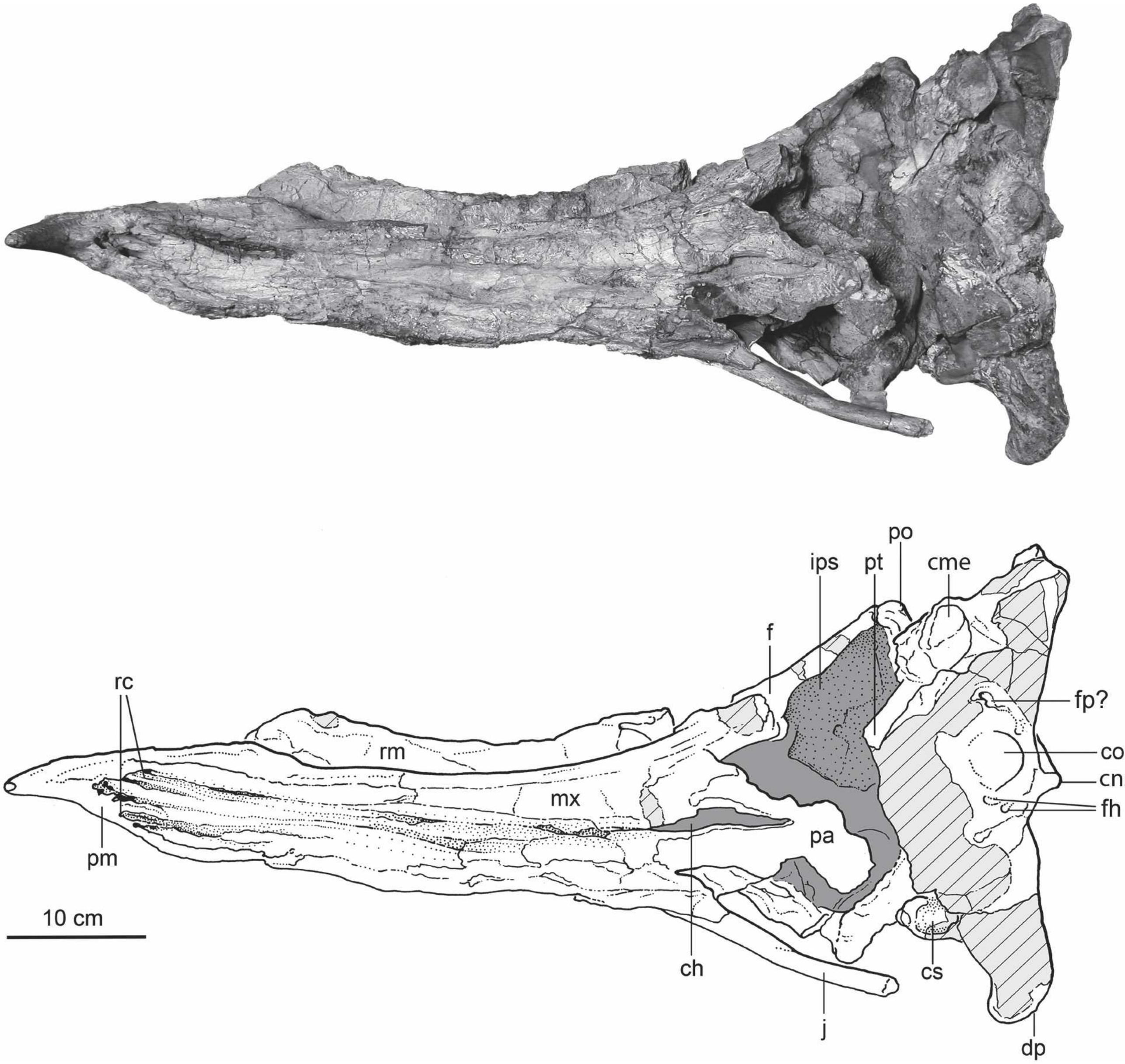

FIGURE 5. Photograph and interpretive drawing of the skull of *Kelenken guillermoi* (BAR 3877-11) in ventral view.

nuchalis sagittalis) that extends vertically from the edge of the foramen to the transverse nuchal crest. The nuchal sagittal crest separates two depressed regions (attachments for the medial part of M. splenius capitis; see Fig. 6). The exit of the external occipital veins (foramen venae occipitalis externae) is visible on each side of the sagittal nuchal crest. A subcondylar fossa (fossa subcondylaris) is not visible on the surface ventral to the occipital condyle, a condition that differs from the distinct subcondylar fossa of *Patagornis* (Andrews, 1899) and *Devicenzia* (see Fig. 5). Two large foramina are vertically aligned on each side of the occipital condyle; these are interpreted as the hypoglossal foramina (foramina nervorum hypoglossi; see Fig. 6). Laterally to these foramina, there is a large and vertically elongated depression (perhaps the parabasal fossa [fossa parabasalis]; see Figs. 5, 6), which contains the openings for the carotid and ophthalmic arteries (arteriae carotis cerebralis et ophthalmica externa). The lateral portions of the occipital table, largely formed by the paraoccipital processes (processus paraoccipitalis), are missing (see Fig. 6).

Tarsometatarsus

The proximal cotylae of the tarsometatarsus (see Figs. 7–9) of *Kelenken* are suboval and deeply concave (see Fig. 9A); the lateral cotyle (cotyla lateralis) is clearly smaller than the medial one (cotyla medialis), and it lies slightly below (in palmar view, see Fig. 7A) the latter. The margins of medial cotyla are much thinner than those delimiting the lateral cotyla and the lateral border of the latter is more angular (see Fig. 9A). The dorsoplantar axis of the medial cotyla is somewhat longer than its transversal axis. As in other phorhusrhacids, the intercotylar eminence (eminentia intercotylaris) is very robust and well developed; its proximal surface is weathered. A distinct, round tubercle—lower in height than the intercotylar eminence—develops on the medioplantar corner of the lateral cotyla. This tubercle does not reach the medial cotyla.

The hypotarsus is broad and robust—its proximal surface lies at the level of the articular cotylae (see Fig. 7B). Intense weathering of the surface prevents determination of the presence or

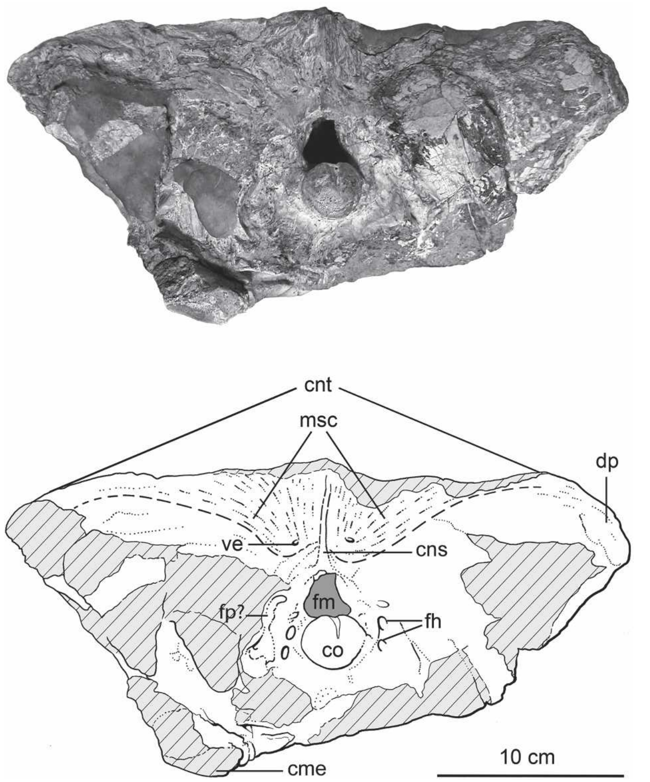

FIGURE 6. Photograph and interpretive drawing of the skull of *Kelenken guillermoi* (BAR 3877-11) in posterior view.

absence of grooves or canals (canales hypotarsi). The lateral surface of the hypotarsus is deeper than its opposite surface, although this may be exaggerated by the apparent lateral crushing of the hypotarsus (see Figs. 8A, B).

The center of the dorsal surface of the proximal end is deeply excavated by a longitudinal depression corresponding to the extensor groove (sulcus extensorius, see Fig. 7A). At the bottom of this depression are several cracks and pits that likely represent the proximal vascular foramina (foramina vascularia proximalia) but which cannot be determined with precision. Regardless, the proximal foramina exit through the plantar surface of the bone at both sides of the hypotarsus.

The shaft is moderately slender with a subquadrangular mid-section; this approaches the condition seen in *Phorusrhacos* (Alvarenga and Höfling, 2003; see Figs. 7, 8). The upper two-thirds of the dorsal surface are concave; the distal third is flatter. In plantar view, the mid-section of the shaft exhibits two robust ridges (cristae plantares lateralis et medialis) that bound a central, longitudinal depression corresponding to the flexor groove (sulcus flexorius). The lateral and medial plantar crests give the tarsometatarsal shaft a convex appearance when viewed in either lateral or medial view (see Fig. 8).

Distally, the plantar supratrochlear surface is rather flat, similar to that in *Titanis walleri* Brodkorb, 1963 (see Fig. 7B). The dorsal excavation of the distal vascular foramen (foramen vasculare distale) is large and funnel-shaped. It is placed between the third and fourth trochleae (trochleae metatarsi III et IV), and above the proximal end of these trochleae (see Fig. 7A). The plantar exit of the distal foramen is centrally located, proximal to the lateral rim of the third trochlea (see Fig. 7B). The distal trochleae are somewhat distorted by transversal compression. The latter trochlea is much bigger than the other two and also projects much more distally (see Fig. 9B). This trochlea forms a gynglimous structure, whose median groove is deeper plantarly than dorsally. The fourth trochlea is wider than the second one and it is also more distally projected. This trochlea develops a median groove on the plantar surface only, and the lateral rim of this trochlea is much more plantarly projected than its medial rim. Other than size and the extension of its distal projection, the morphology of the second trochlea (trochlea metatarsi II) is comparable to that of the fourth trochlea. The plantar extension of its medial (outer) rim is nonetheless weathered out. The outer surfaces of the second and fourth trochleae as well as both sides of the third trochlea exhibit deep ligamental pits (foveae ligamentum collateralium).

TABLE 2. List of junior and senior synonyms of phorusrhacid species (in bold) recognized by Alvarenga and Hofling (2003). These species are classified according to the traditional systematics of the group.

Brontornithinae
Brontornis burmeisteri
Rostrornis floweri
Brontornis platyonyx
Physornis fortis
Physornis brasiliensis
Paraphysornis brasiliensis
Aucornis euryrhyncus
Patagornithinae
Patagornis marshi
Tolmodus inflatus
Phororhacos inflatus
Paleociconia cristata
Andrewsornis abbotti
Andalgalornis steulleti
Phororhacos steulleti
Phororhacos deautieri
Andalgalornis ferox
Mesembriornithinae
Mesembriornis milneedwardsi
Paleociconia australis
Driornis pampeanus
Hermosiornis milneedwardsi
Hemosiornis rapax
Phophororhacos australis
Mesembriornis incertus
Prophororhacos incertus

Psilopterinae
Psilopterus bachmanni
Psilopterus communis
Patagornis bachmanni
Psilopterus intermedius
Phororhacos delicatus
Pelecyornis pueyrredonensis
Psilopterus lemoinei
Patagornis lemoinei
Pelecyornis tubulatus
Phororhacos modicus
Staphylornis gallardoi
Staphylornis erythacus
Pelecyornis tennuirostris
Psilopterus australis
Psilopterus affinis
Phororhacos affinis
Psilopterus colzecus
Procariama simplex
Paleopsilopterus itaboraiensis

Phorusrhacinae
Phorusrhacos longissimus
Phororhacos longissimus
Phororhacos sehuensis
Phororhacos platygnathus
Stereornis rollieri
Stereornis gaundryi
Mesembriornis studeri
Mesembriornis quatrefragesi
Darwinornis copei
Darwinornis zittelli
Darwinornis socialis
Owenornis affinis
Owenornis lydekkeri
Titanornis mirabilis
Callornis giganteus
Eucallornis giganteus
Liornis floweri
Liornis minor
Devincenzia pozzi
Phororhacos pozzi
Phororhacos l. mendocinus
Onactornis depressus
Titanis walleri

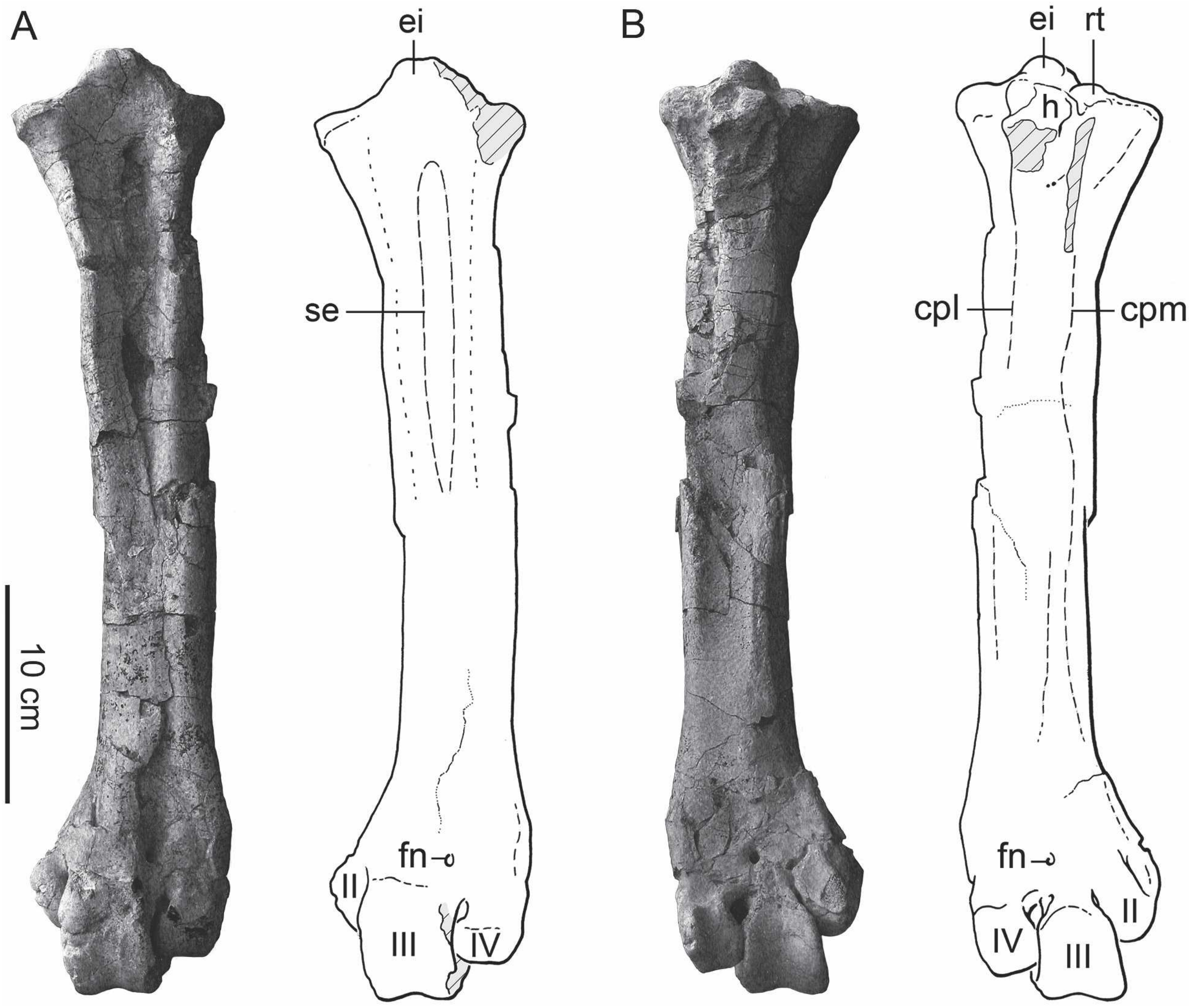

FIGURE 7. Photograph and interpretive drawing of the left tarsometatarsus of *Kelenken guillermoi* (BAR 3877-11) in dorsal (**A**) and plantar (**B**) views.

DISCUSSION

The enormous size of the specimen, in combination with the laterally compressed, strongly hooked rostrum and convex culmen identifies *Kelenken guillermoi* as a member of the Phorusrhacidae, an extinct clade of large predatory birds (Andrews, 1899; Sinclair and Farr, 1931; Livezey, 1998; Alvarenga and Höfling, 2003). Traditional studies of phorhusrhacids have classified the known diversity of taxa within five subgroups (brontornithines, phorusrhacines, patagornithines, mesembriornithines, and psilopterines), which altogether describe the observed spectrum of corpulence, from the massive, graviportal brontornithines to the small, very gracile psilopterines (Tonni, 1980; Tambussi and Noriega, 1996; Alvarenga and Höfling, 2003). The monophyly of these groups is yet to be supported through cladistic analyses—a task that is beyond the scope of the present article—but the morphology of *Kelenken* indicates a relationship with taxa traditionally grouped as phorusrhacines.

Minimal cranial information is available for bronthornithines (Alvarenga and Höfling, 2003), but the moderately slender tarsometatarsus of *Kelenken* can be easily discriminated from the stout, short, and dorsoplantarly flattened tarsometatarsus of these birds, and the new Patagonian phorusrhacid also differs by lacking the dorsoproximal spreading that characterizes the trochlea of metatarsal III of brontornithines. The skull of *Kelenken* differs from that of more gracile groups (i.e., patagornithines, mesembriornithines, and psilopterines) in a number of aspects (Chiappe and Bertelli, 2006). The postorbital process of these birds is acuminated and ventrally directed (as opposed to blunt and rounded) and the rostrum is proportionally shorter than that of the new Patagonian bird (the rostrum of *Mesembriornis* is heavily reconstructed in a 'vulture-like' style). Furthermore, the tall jugal bar of *Kelenken* is dorsoventrally greater than that of patagornithines and psilopterines, and its small external nares differ from the large, elliptical nares of psilopterines (Sinclair and Farr, 1932) and apparently mesembriornithines (Alvarenga and Höfling, 2003). *Kelenken* also differs from the more gracile groups in the longer and more slender nature of the tarsometatarsus of all these birds. The tarsometatarsus of *Kelenken* also lacks the subequal cotyla, the ligamental pit at the base of the intercotylar prominence, the distinct projection of the lateral margin of the lateral cotyle of patagornithines and psilopterines

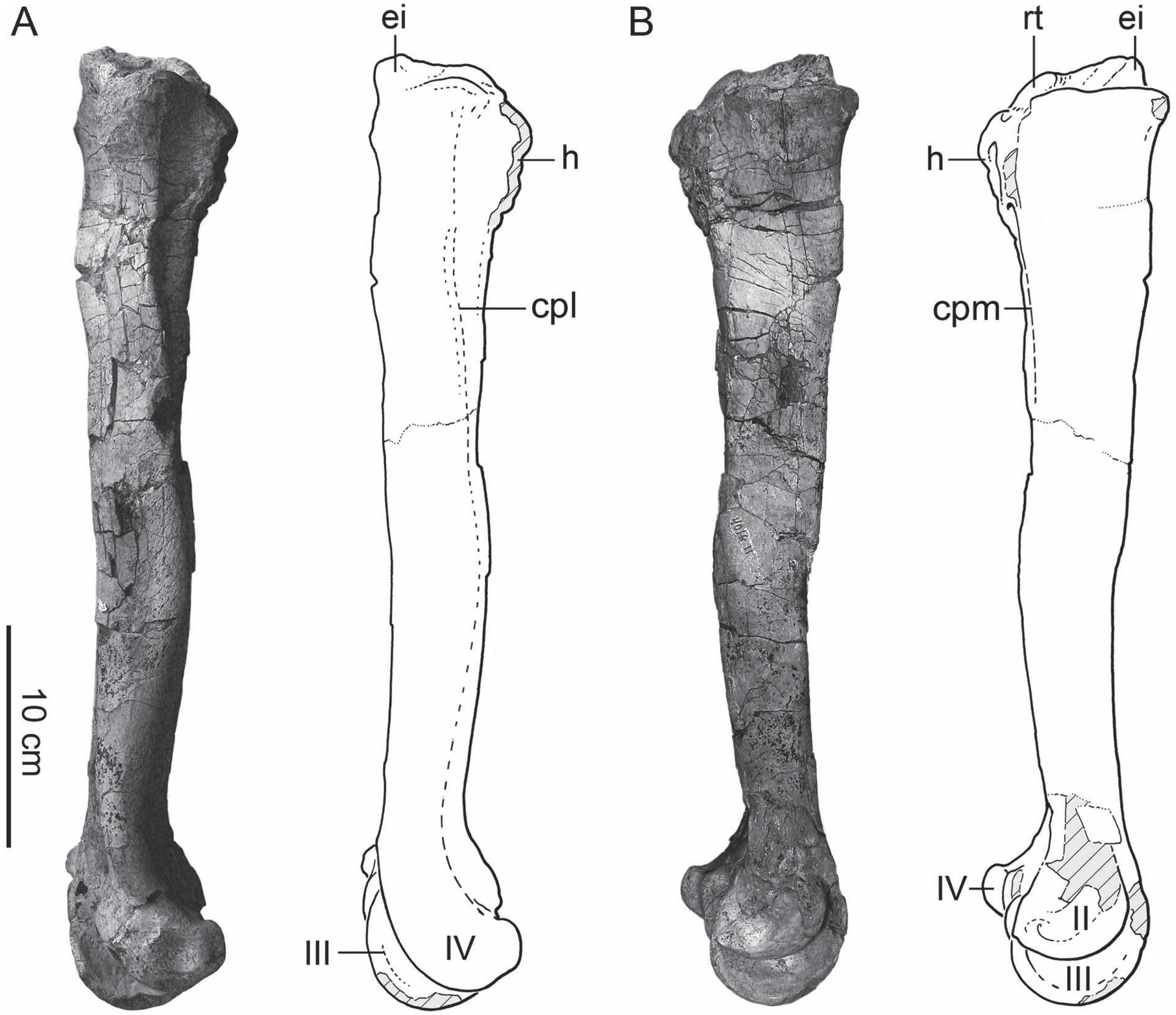

FIGURE 8. Photograph and interpretive drawing of the left tarsometatarsus of *Kelenken guillermoi* (BAR 3877-11) in lateral (**A**) and medial (**B**) views.

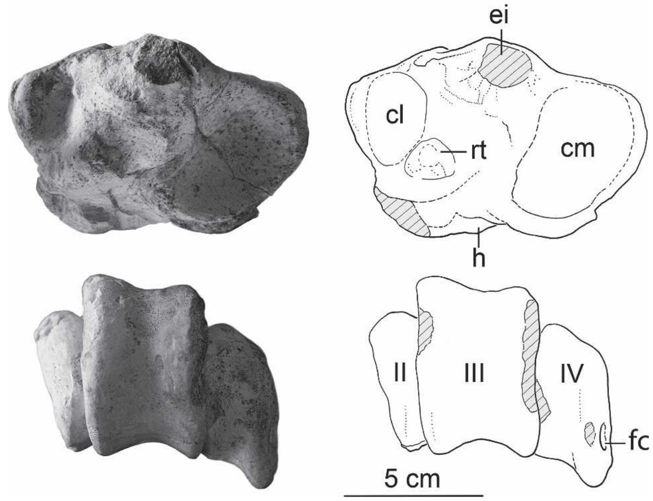

FIGURE 9. Photograph and interpretive drawing of the left tarsometatarsus of *Kelenken guillermoi* (BAR 3877-11) in proximal (**A**) and distal (**B**) views.

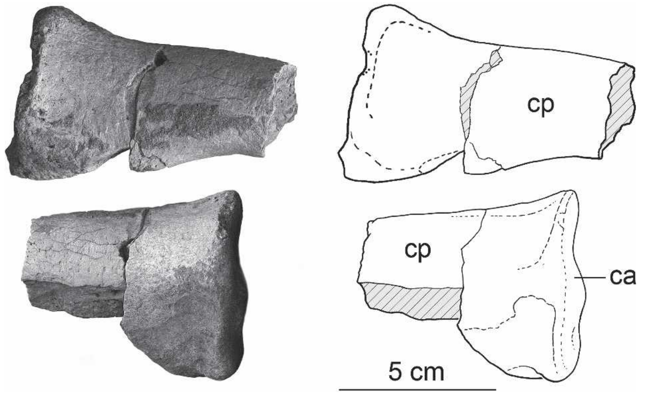

FIGURE 10. Photograph and interpretive drawing of the proximal half of a pedal phalanx of *Kelenken guillermoi* (BAR 3877-11) in side views.

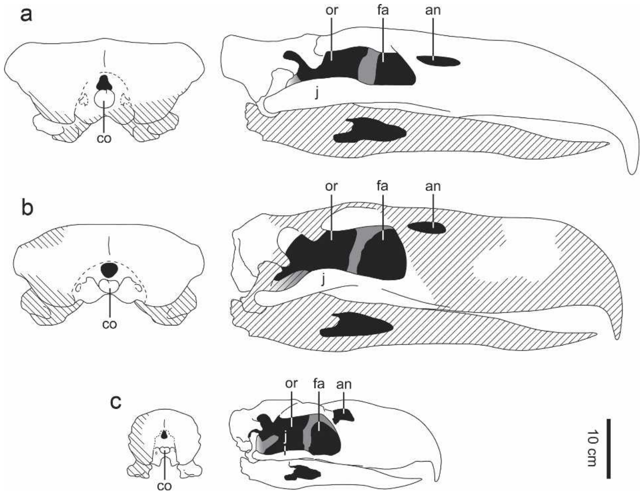

FIGURE 11. Reconstruccions of *Kelenken guillermoi* (BAR 3877-11) (**A**), *Devicenzia pozzi* (MLP 37-III-7-8) (**B**), and *Patagornis marshi* (BMNH A517) (**C**) in occipital (left) and lateral (right) views.

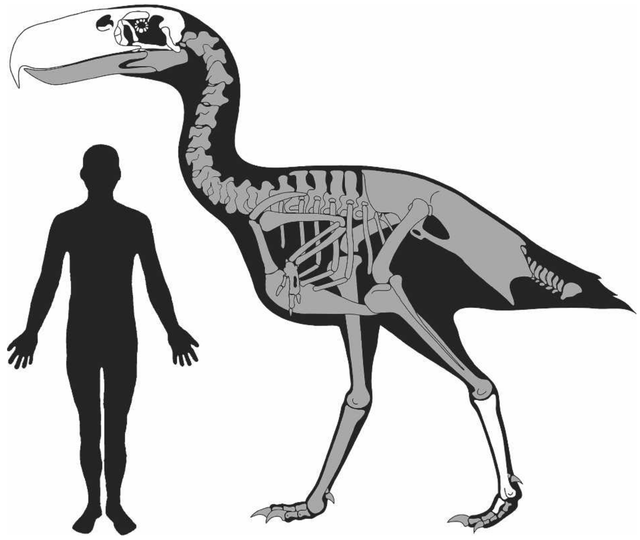

FIGURE 12. Reconstruction of *Kelenken guillermoi* scaled for comparison to a human. Preserved bones are in white.

(Andrews, 1899; Sinclair and Farr, 1932), and the prominent plantar projection of the medial rim of the trochlea of metatarsal II of the latter (Sinclair and Farr, 1932). *Kelenken* also differs from mesembriornithines, whose tarsometatarsus is dorsally excavated by a groove that extends throughout the shaft (Kraglievich, 1946).

The morphology of *Kelenken* not only agrees with the relative proportions of the phorusrhacines, but it also shows similarity in the presence of several features: (1) the caudal portion of the skull is low and dorsoventrally compressed (Patterson and Kraglievich, 1960), (2) the occipital table is very wide (the width exceeds twice the height of the occiput; Patterson and Kraglievich, 1960), (3) the postorbital process is blunt as opposed to the rostrally hooked process of psilopterines (Sinclair and Farr, 1932; Patterson and Kraglievich, 1960). The postorbital process also appears to be blunt in patagornithines; Andrews, 1899), and (4) the tarsometatarsus is similar to the phorusrhacine *Titanis* in having a flat supratrochlear surface on the plantar side of the distal end.

Comparisons between *Kelenken* and taxa traditionally grouped as phorusrhacines are hampered by the minimal anatomical information available for the skull of these birds. Indeed, the cranial morphology of phorusrhacines is largely limited to the poorly preserved caudal half of the skull of *Devicenzia* (Cabrera, 1939; Alvarenga and Höfling, 2003)—the frequently reproduced skull of *Phorusrhacus* is based either on *P. longissimus*, the skull of which virtually disintegrated during collection (only the tip of the beak has survived; Ameghino, 1895), or *P. inflatus*, now interpreted as a junior synonym of the patagornithine *Patagornis marshi* (Alvarenga and Höfling, 2003). These limitations notwithstanding, the cranial morphology of *Kelenken* resembles that available for *Devicenzia*, particularly in the low and rectangular-shaped orbit, and the remarkable width of the occipital table (Chiappe and Bertelli, 2006). However, the jugal bar of *Kelenken* appears to be taller and more robust than that of *Devicenzia*, the former taxon has a triangular foramen magnum (unlike the round one of *Devicenzia*), and it lacks the strong rim that borders the parabasal fossa of the occipital area dorsally. The tarsometatarsal morphology of *Kelenken* also differs from that of all other phorusrhacines. When viewed cranially, the trochlea IV of *Kelenken* is quadrangular as opposed to the proximodistally rectangular trochlea IV of *Devicenzia*, *Phorusrhacus*, and *Titanis*, and the vascular distal foramen of the former lies more medially (the foramen is leveled with the lateral margin of trochlea III in *Kelenken* and the intertrochlear incisure [incisura intertrochlearis lateralis] in other phorusrhacines). The tarsometatarsal trochlea of *Kelenken* is also less divergent than in *Devicenzia*—in this design it resembles more *Phorusrhacus* and *Titanis*.

CONCLUSIONS

The new species *Kelenken guillermoi* is the largest known phorusrhacid, and its skull represents the largest known among birds (Chiappe and Bertelli, 2006). Beyond the superlative, the new fossil provides critical anatomical information given the paucity of well-preserved skulls of large-bodied phorusrhacids. Indeed, the discovery of *Kelenken* has shown that significant differences in cranial morphology (e.g., much lower and longer rostrum, rectangular orbit, notable height of the jugal bar, flat cranial roof, and low and rectangular-shaped occipital table) distinguished gigantic phorusrhacids from their smaller and more gracile relatives (Fig. 11). Before the discovery of *Kelenken*, the cranial morphology of large-bodied phorusrhacids—with skull length exceeding 600 mm—was largely limited to those observed in the fragmentary *Devicenzia pozzi*. Influenced by the frequently reproduced sketch of the destroyed skull of *Phorusrhacos longissimus* (in itself based on the much smaller *Patagornis marshi*), the skull of gigantic phorusrhacids has been frequently reconstructed as a scaled version of the better-preserved skulls of their much smaller relatives. However, the skull morphology of *Kelenken* suggests that this widely accepted notion is unwarranted.

ACKNOWLEDGMENTS

We are especially grateful to Guillermo Aguirre-Zabala—who also discovered the specimen—for the preparation of BAR 3877-11. We are also very grateful to Helga Smekal and the Asociación Paleontólogica Bariloche for making the specimen available for study and to Pablo Puerta and the preparation laboratory of the Museo Egidio Feruglio for preparation assistance. We give special thanks to Enrique Guanuco and Stephanie Abramowicz for creating the illustrations and to Adrian Tejedor for his help with the reconstruction of BAR 3877-11. Don Glut and Jack Tseng provided editorial assistance. This project was supported by the Fundación Antorchas and the Natural History Museum of Los Angeles County.

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Submitted November 8, 2006; accepted February 4, 2007.