TITANIS WALLERI: BONES OF CONTENTION

Gina C. Gould[1] and Irvy R. Quitmyer[2]

Titanis walleri, one of the largest and possibly the last surviving member of the otherwise South American Phorusrhacidae is reconsidered in light of all available data. The only verified phorusrhacid recovered in North America, *Titanis* was believed to exhibit a forward-extending arm with a flexible claw instead of a traditional bird wing like the other members of this extinct group. Our review of the already described and undescribed *Titanis* material housed at the Florida Museum of Natural History suggest that *Titanis*: (1) was like other phorusrhacids in sporting small, ineffectual ratite-like wings; (2) was among the tallest of the known phorusrhacids; and (3) is the last known member of its lineage. Hypotheses of its range extending into the Pleistocene of Texas are challenged, and herein *Titanis* is presumed to have suffered the same fate of many other Pliocene migrants of the Great American Interchange: extinction prior to the Pleistocene.

Key Words: Phorusrhacidae; Great American Biotic Interchange; Florida; Pliocene; *Titanis*

INTRODUCTION

Titanis walleri (Brodkorb 1963), more commonly known as the North American 'Terror Bird', is one of the largest known phorusrhacids, an extinct group of flightless carnivorous birds from the Tertiary of South America, and most likely, the last known member of its lineage (Brodkorb 1967; Tonni 1980; Marshall 1994; Alvarenga & Höfling 2003). *Titanis* was first proposed as a participant in the Great American Interchange by David Webb and his colleagues (Marshall et al. 1982; Webb 1985), because it appears in Florida just after the formation of the Panamanian land bridge (Stelhi & Webb 1985).

In 1961, *Titanis* was discovered from a Blancan site in the Santa Fe River along the Gilchrist/Columbia County line in Florida (Brodkorb 1963; Fig. 1) circa David Webb's arrival at the Florida Museum of Natural History (FLMNH) as the new curator of vertebrate paleontology. At the time, the newly recovered material consisted of a distal end of a tarsometatarsus (the holotype), a phalanx from digit III, and the proximal end of a fibula (never described). Based on the gigantic size of the fossils and the presence of a bifurcated distal foramen on the tarsometatarsus, these specimens were assigned to the Family Phorusrhacidae (Brodkorb 1963) and named after both a Titan Goddess from Greek mythology and Benjamin Waller, the discoverer of the fossils (Zimmer 1997). Since then, isolated *Titanis* material has been recovered from three other localities in Florida (Table 1; Fig. 1; Brodkorb 1963; Carr 1981; Chandler 1994; Hulbert pers com.) and one in Texas (Baskin 1995). Despite considerable effort on the part of the FLMNH and enthusiasts to uncover more complete *Titanis* material, few new remains have been found in the now 30+year search (R. Hulbert pers comm., Table 1). Most of the material is fragmentary, consequently much of it remained undescribed.

Regardless of the scant and incomplete nature of the *Titanis* material, the bird is well known, if not infamous among paleontologists and paleoenthusiasts. *Titanis* has been described as a giant flightless 'terror' bird between two and three meters tall (Brodkorb 1963; Marshall 1994; Feduccia 1999), with a "strong, robust wing, and an extended manus (as in penguins) equipped with a large claw which was used to subdue struggling prey" (Chandler 1994:176). Although published descriptions of this taxon are few (Brodkorb 1963; Chandler 1994; Baskin 1995; Emslie 1998; Alvarenga & Höfling 2003; and one dissertation, Carr 1981; see Table 1), *Titanis* has made its way into the popular literature. In one of the more prominent articles, *Titanis* was described to have had a "three-foot-long wing" which was more

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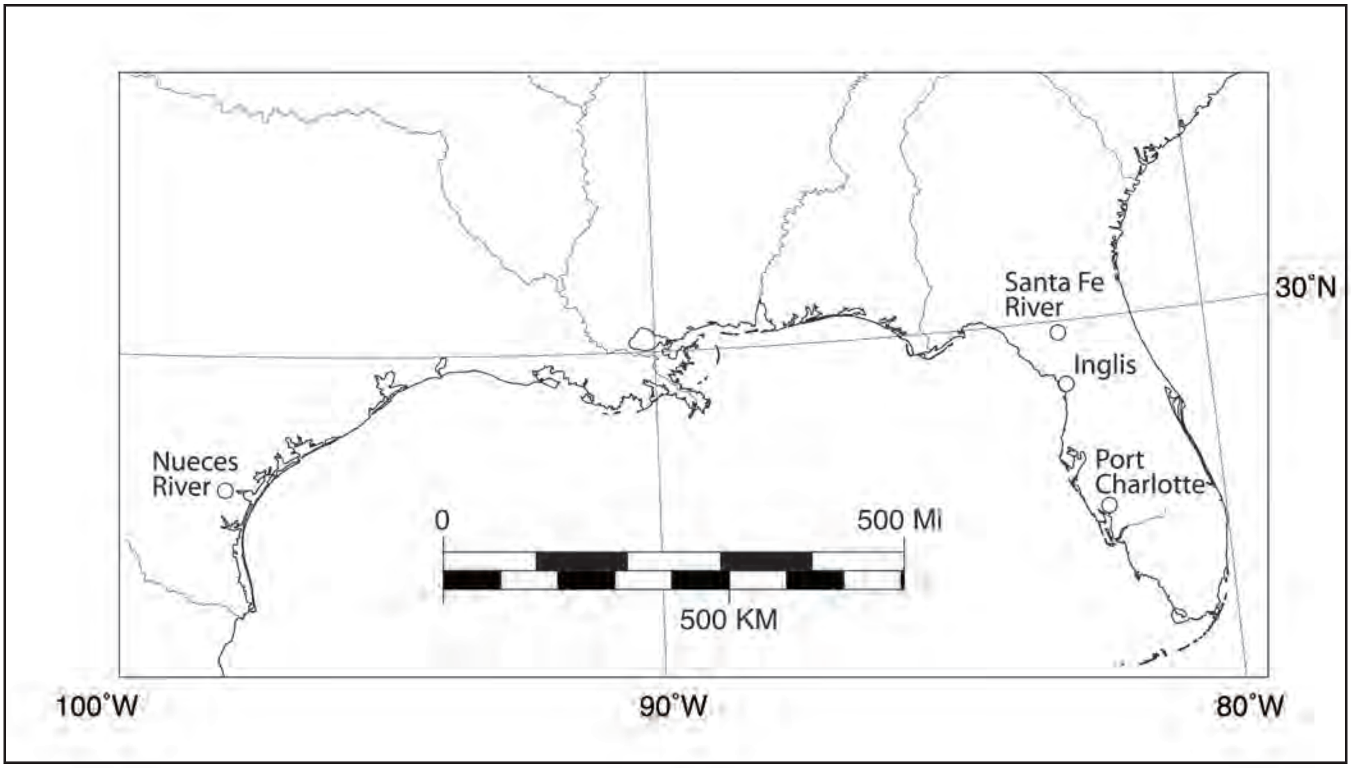

Figure 1. Distribution of the sites where *Titanis* material has been discovered (illustration by Ian Breheny, FLMNH).

like an "arm with a giant movable claw and two smaller fixed claws" (Zimmer 1997, Discover Magazine). The shear size of *Titanis* and the fantastic nature of its wing pose intriguing questions about the biology and ecology of this extinct bird. An accurate reconstruction of *Titanis* became even more acutely important to researchers and artists at the FLMNH when they wanted to display a full-scale model of it for their new exhibit hall, *Florida Fossils: Evolution of Life and Land*, which opened in 2004.

The *Titanis* material housed in the FLMNH collections is due largely to the efforts of David Webb, his students, and his staff over his 30-year tenure at the FLMNH. It is rumored that the discovery of *Titanis* precipitated Dave's life-long pursuit of understanding and documenting the Great American Interchange that is witnessed in the Florida fossil record (Morgan pers comm.). We thought it befitting that the mysterious nature of *Titanis* be revisited as tribute to Dave Webb's exemplary career in paleontology.

In this paper, it is our objective to compile all of the *Titanis* material housed in the FLMNH's collections into a comprehensive list and describe the more complete specimens. In so doing, we revisit the prevailing hypothesis regarding the morphology of its hand, attempt to more precisely estimate the overall size of *Titanis*, and consider the evidence for *Titanis'* survival into the early Pleistocene.

MATERIALS AND METHODS

As previously mentioned, the only known North American *Titanis* fossils are from Florida and Texas (Table 1). The four sites in Florida are from Santa Fe River IA and IB, Inglis 1A, and Port Charlotte (Fig. 1), all of which are Pliocene in age (Brodkorb 1963; Carr 1981; Chandler 1994; Emslie 1998; Hulbert pers com). The Santa Fe River sites are in-place mid-channel deep-water sediments of Blancan age (Brodkorb 1963; Fig. 1), Inglis 1A is a very late Blancan sinkhole deposit (Carr 1981; Emslie 1998; Fig. 1), and the Port Charlotte site is a canal spoil pile (Hulbert pers comm.; Fig. 1), probably similar in age to Inglis 1A.

The Texas material was recovered from a gravel pit along the Nueces River in San Patricio County (near Corpus Christi), Texas. The age of the material is estimated to be between 5 million and 15,000 years old

(Baskin 1995). This single toe bone (TMM 43060-115) is housed at the Texas Memorial Museum (TMM) in Austin.

Systematic paleontology and specimens reviewed

In total, there are 41 known *Titanis* specimens in North American museums, all but one reside in the FLMNH's collections (Table 1). The fossils, isolated cranial and postcranial material, are fragmentary and can fit in two, maybe three specimen drawers. Of these specimens, only 6 have been described in the literature (5 of which have been photographed and/or illustrated; Brodkorb 1963; Chandler 1994; Baskin 1995; Emslie 1998; Alvarenga & Höfling 2003), and the 11 Inglis specimens were described in Gail Speaker Carr's dissertation (1981). Herein, we review the best-preserved material (see Table 1) and include photographs of each of them (Appendix 1). For comparative material, we relied on the literature and the available phorusrhacid taxa from the collections at the AMNH/Yale University.

Since their initial discovery (Ameghino 1887), more than 20 species within the Phorusrhacidae have been named, renamed, and shuffled among three to four families (Moreno & Mercerata, 1891; Dolgopol de Saez 1927; Sinclair & Pharr 1932; Brodkorb 1967; Cracraft 1968; Tonni 1980; Alvarenga 1985). Despite the murkiness of the interrelationships within this family, it is widely accepted that they form a monophyletic group (Brodkorb 1967; Tonni 1980; Alvarenga & Höfling 2003). The most recent systematic revision (Alvarenga & Höfling 2003) cites the following characters to support phorusrhacid monophyly: (1) large size; (2) laterally compressed skeletal elements (premaxilla, thorax, and pelvis) giving the impression of slimness from frontal view; (3) a robust premaxilla with a large hooked beak; (4) a robust mandibular symphysis; (5) large and pervious nostrils without a septum; (6) a desmognathous palate; (7) well developed basipterygoid processes; (8) presence of an articulation facet for the basipshenoid process on the medial side of the pterygoid; (9) absence of uncinate processes of the ribs; (10) the anterior portion of the pubis is not well developed (as seen in Acciptridae); (11) reduction of the wings and loss of flight; (12) a coracoid with extreme reduction of the procoracoidal and acrocoracoidal processes with a large scapular facet in the form of a grove; (13) a humerus with a prominent medial tuberosity, the proximal portion of the diaphysis strongly curved with a distally prominent processus flexorius; (14) a tarsometatarsus with a triangular shaped hypotarsus in plantar view and the absence of tendon grooves; and (15) strongly curved ungular phalanx.

Phorusrhacid specimens are distributed among various institutions across three continents (South America, Europe, and North America), consequently we had to rely on the literature for descriptions of much of the comparative phorusrhacid material and for the dimensions considered in our allometric analyses (Appendix 2). We used the most recent systematic review of the group (Alvarenga & Höfling 2003) for the nomenclature and classification presented herein (see Table 3). We considered only those measurements that were consistently conserved across the majority of the more complete specimens, and of course, those that correspond to the available *Titanis* material (Table 1; Appendix 2). Forty-one measurements were considered (Table 2) on 16 phorusrhacid taxa, for a total of 26 'individuals' considered in the analyses (Table 3; Appendix 2). It should be noted that composites of the following taxa were used: *Titanis walleri*, *Brontornis burmeisteri* (Moreno & Mercerat, 1881), and *Physiornis fortis* (Ameghino, 1885) (Appendix 2). Although this admission may make some readers wince, we would argue that the determinate growth in birds limits variation in body mass across mature adults within a species (albeit the presence of sexual dimorphism), therefore the margin of variability is minimal. We also chose the largest specimens available to reduce disproportionate composite taxa.

The South American Cariamidae (seriemas), an extant group of gruiformes, have been believed to be the sister taxon to the phorusrhacids since the late 1890s (Andrews 1899; Dogopol de Saez 1927; Brodkorb 1967; Cracraft 1968; Livezey 1998; Alvarenga & Höfling 2003). This two-taxon family includes *Chunga burmeisteri* (Harlaub, 1860) (black-legged seriema) and *Cariama cristata* (Linneaus, 1776) (red-legged seriema). Surprisingly, there are only a handful of cariamids in US museum collections, many of which are either incomplete or zoo specimens (Appendix 2), and very little has been published on this group. We included the 7 most complete specimens housed at the Smithsonian (USNM) and the AMNH in our analysis (Appendix 2).

Estimating the size of *Titanis*

One of the most interesting and relevant questions in biology concerns body size (biomass and body dimensions) because it provides useful data to anatomists, ecologists, and biologists (Peters 1983; Schmidt-Nielsen 1984).

Table 1. A comprehensive list of the 40 known fossil elements of *Titanis walleri* housed at the FLMNH. SF = Santa Fe localities, 1A and 1B; I = Inglis 1A; PC = Port Charlotte. Please refer to the map in Figure 1. Fig # = corresponds to figures in Appendix 1; p i = photographed/illustrated in a previous publication; App. 1 = Appendix 1.

Element	Fig.	App. 1	Cat. number	Locality	Date Collected	Publication
Frontal (partial)			UF 137195	SF 1A	1966	
Pterygoid (left; cast)		Fig. 1	UF 162749	I 1A	1995 (donated)	
Narial opening, lower margin		Fig. 2	UF 137193	SF 1B	?	
Quadrate (right), orbital process			UF 137838	SF 1A	1963	
Quadratojugal (left), partial		Fig. 3	UF 57580	SF 1A	1963	Chandler,1994
Quadratojugal (right), partial		Fig. 3	UF 57585	SF 1A	1966	Chandler, 1994
Mandible (right), articular			UF 144179	SF 1B	1993	
Vertebra, 2nd cervical (axis)		Fig. 4	UF 30006	I 1A	1969, 1974	Carr, 1981
Vertebra, 3rd cervical		Fig. 5	UF 30005	I 1A	1969, 1974	Carr, 1981
Vertebra, (partial)			UF 30004	I 1A	1969, 1974	Carr, 1981
Vertebra, thorasic (partial)		Fig. 6	UF 10415	SF 1A	1965	
Coracoid, (partial)			UF 10703	SF 1A	1965	
Coracoid (left), glenoid fossa			UF 144177	SF 1B	1994	
Humerus (left), proximal end	p/I	Fig. 7	UF 137839	SF 1B	1993	Chandler, 1994
Humerus, distal end			UF 10418	SF 1A	1963	
Carpometacarpus (left)	p/I	Fig. 8	UF 30003	I 1A	1969, 1974	Carr, 1981; Chandler, 1994; Alvarenga and Hofling, 2003
Femur, shaft			UF 12207	SF 1B	1966	
Femur, shaft			UF 144181	SF 1B	1966	
Femur, shaft			UF 144182	SF 1B	1966	
Fibula, (left) proximal end		Fig. 9	UF 9051	SF 1A	1963	
Fibula (right), proximal end		Fig. 9	UF 7421	SF 1A	1960-1961	
Limb, shaft			UF 144180	SF 1B	1966	
Tibiotarsus (right), proximal end		Fig. 10	UF 7333	SF 1A	1963	
Tibiotarsus (right)			UF 30002	I 1A	1969, 1974	Carr, 1981
Tibiotarsus, shaft			UF 137196	SF 1A	1965	
Tibiotarsus (left), shaft			UF 12208	SF 1B	1966	
Tarsometarsis (right), distal end	p	Fig. 11	UF 4108 (type)	SF	1961-1962	Brodkorb, 1963; Alvarenga and Hofling, 2003
Tarsometarsis (right), proximal shaft, medial half			UF 137194	SF 1A	?	
Metatarsal (right), I, partial			UF 30007	I 1A	1969, 1974	Carr, 1981
Phalanx			UF 10416	SF 1A	1965	
Digit III (left), phalanx 1		Fig. 12	UF 30001	I 1A	1969, 1974	Carr, 1981
Digit III (left), phalanx 1	p		UF 4109	SF	1961-1962	Brodkorb, 1963
Digit III (right), phalanx 1		Fig. 12	UF 171382	SF 1B	1962	Carr, 1981
Digit III (left), phalanx 2		Fig. 13	UF 30010	I 1A	1969, 1974	Carr, 1981
Digit III (left), phalanx 3			UF 30011	I 1A	1969, 1974	Carr, 1981
Digit IV (left), phalanx, proximal end			UF 124228	PC	(donated 1990)	
Digit IV (left), phalanx 1		Fig. 13	UF 30009	I 1A	1969, 1974	Carr, 1981
Digit IV (right), phalanx 1			UF 30008	I 1A	1969, 1974	Carr, 1981
Digit IV (right), phalanx 1			UF 7332	SF 1A	1963	
Phalanx, distal end (claw)		Fig. 14	UF 10417	SF 1A	1965	

Table 2. Proposed taxonomy for the Phorusrhacidae, after Alvarenga and Höfling, 2003. Those taxa indicated by (*) were included in this study. The taxa that are underlined have preserved wing elements.

- Order Ralliformes Reichenbach, 1852
  - Suborder Cariamae Fürbringer, 1888
    - Family Phorusrhacinae Ameghino, 1889
      - Subfamily Brontornithinae Moreno and Mercerat, 1891
        - **Brontornis burmeisteri* Morena and Mercerat, 1891 (early-middle Miocene)
        - **Physornis fortis* Ameghino, 1895 (middle-late Oligocene)
        - **Paraphysornis brasiliensis* Alvarenga, 1982 (late Oligocene-early Miocene)
      - Subfamily Phorusrhacinae Ameghino, 1889
        - **Phorusrhacos longissimus* Ameghino, 1887 (early-middle Miocene)
        - *Devincenzia pozzi* Kraglievich, 1931 (late Miocene-early Pliocene)
        - **Titanis walleri* Brodkorb, 1963 (late Pliocene)
      - Subfamily Patagornithinae Mercerat, 1897
        - **Patagornis marshi* Moreno and Mercerat, 1891 (early Miocene)
        - *Andrewsornis abbotti* Patterson, 1941 (middle Oligocene)
        - **Andalgalornis steulleti* Kraglievich, 1931 (late Miocene-early Pliocene)
      - Subfamily Psilopterinae Dolgopol de Saez, 1927
        - *Psilopterus affinis* Ameghino, 1899 (middle—late Oligocene)
        - **Psilopterus bachmanni* Moreno and Mercerat, 1891 (middle Miocene)
        - **Psilopterus lemoinei* Moreno and Mercerat, 1891 (middle Miocene)
        - *Psilopterus colzecus* Tonni and Tambussi, 1988 (late Miocene)
        - **Procariama simplex* Rovereto, 1914 (late Miocene-late Pliocene)
        - *Paleopsilopterus itaboraiensis* Alvarenga, 1985 (middle Paleocene)
      - Subfamily Mesembriornithinae Kraglievich, 1932
        - **Mesembriornis milneedwardsi* Moreno, 1889 (late Pliocene)
        - *Mesembriornis incertus* Rovereto, 1914 (late Miocene-early Pliocene)
    - Family Cariamidae Bonaparte, 1853
        - **Cariama cariama* Linnaeus, 1776 (extant)
        - **Chunga burmeisteri* Hartlaub, 1860 (extant)

With fossil taxa, these estimates are even more critical for accurately reconstructing animals that are often represented by only a few skeletal fragments. Such is the case with *Titanis*, which as mentioned, is represented by extremely fragmentary material. Estimating its size consequently, is not a straightforward matter.

Of first concern is the algorithm itself: body mass is what is commonly calculated, not the height of the animal. Body mass in birds has been estimated using the least shaft circumference of either the tibiotarsus (Campbell & Tonni 1983), or more preferably, the length of the femur (Campbell & Marcus 1988). In the case of *Titanis*, neither of these elements is preserved in their entirety (Table 1), nor are they preserved consistently in other phorusrhacid taxa. The most recent attempt at estimating the body mass of other phorusrhacids used the least circumference of the distal end of the femur and tarsometatarus which were then compared to ratites and other large birds of known weights (Alvarenga & Höfling 2003). It is not clear however, how the authors arrived at these height estimates, no algorithm was provided. In this study, we estimate the size of selected skeletal components of *Titanis*; the length of the skull, the standing height of the bird, and the femur-tibiotarsus-

Table 3. Allometric constants used to predict the skull length, leg length (femur length + tibiotarsus length + tarsometarsus length), and standing height of the bird *Titanis walleri*.

Independent Variable X Measurement (mm)	*Titanis walleri* Dependent Variable Y Predicted (mm)	N	r^2	b Slope	a Intercept	X Measurement (mm)	Y Predicted (mm)	Range of X (mm)
Q-Jugal (L)	Skull (TL)	12	0.70	1.19	0.08	170.0	542.3	42.0 - 101.6
Q-Jugal (H)	Skull (TL)	10	0.91	0.42	1.98	23.0	359.9	1.0 - 20.3
Axis (L)	Skull (TL)	12	0.86	0.64	1.37	127.0	520.5	8.8 - 114.3
Tibiotarsus distal width	Femur (L)+Tibiotarsus (L) +Tarsometatarsus (L)	17	0.85	0.74	1.77	88.9	1631.3	14.3 - 63.0
Tarsometatarsus trochlea (W)	Femur (L)+Tibiotarsus (L) +Tarsometatarsus (L)	13	0.70	0.52	2.09	76.0	1184.6	8.0 - 105.0
Tarsometatarsus trochlea (W)	Standing Height of the Bird	5	0.75	0.60	2.03	76.0	1444.0	20.0 - 105.0
Tibiotarsus distal width	Standing Height of the Bird	8	0.87	0.76	1.80	88.9	1870.0	18.5 - 63.0

Formula is $Y = aX^b$
where X is the independent variable (measured skeletal element, mm); Y is the dependent variable (e.g., skull length, mm); a is the Y-intercept and b is the slope.

Q-Jugal = quadratojugal; L= length; H= height; W= width; TL= total length tarsometatarsus length (leg length) using comparative measurements of other phorusrhacids and seriemas and the least-squares regression model commonly used in biology to predict body size relationships (Huxley 1927; 1932, Peters, 1983). We use this method because most animal body size relations can be accurately predicted by the equation ($Y = aX^b$) (Peters 1968). The technique is regarded as a simple and robust approach in describing body size relations (Peters 1983; Schmidt-Nielsen 1984; Reitz et al. 1987). It is also ideally suited to estimating body size relationships of incomplete fragmentary fossil and subfossil materials (Reitz et al 1987).

It is well known that allometry reflects the regular and orderly change of shape, structure, and or function of size among similarly shaped animals (Huxley 1932; Prang et al. 1979; Peters 1983; Schmidt-Nielson 1984; Reitz et al. 1987). Growth is a nonlinear process through ontogeny, and this allometric relationship is described by a mathematical power function $y = aX^b$ (Schmidt-Nielson 1984). This is transformed using the common log in order to produce a straight-line regression. The resulting formula is $\log y = a + b(\log X)$ with b as the slope of the line, a the y intercept, x the independent variable (skeletal measurement), and y the dependent variable, size estimate of skeletal elements.

Allometric analyses generally require a robust sample size and completeness of data (Peters 1983). In our analysis, the data are limited because of the paucity and fragmentary nature of *Titanis* and phorusrhacid fossils, and our inability to take measurements on the taxa that reside in collections outside of the United States. To further complicate the application of least-squares allometry as the predictive tool is the fact that *Titanis* is one of the largest of the phorusrhacids**,** consequently, the measurements of the independent variables (X) of the preserved elements (e.g., quadratojugal length) exceeds the calculated regression line based on the smaller phorusrhacid taxa used in the analysis (Table 4). In such instances the confidence limits deteriorate toward the extremes of the regression line.

These caveats leave us with the difficult decision of whether or not to continue with an analysis that is known to be compromised *a priori* or abandon the attempt to estimate the size of *Titanis*. In light of a full-scale reconstruction of *Titanis*, an expression of Dave Webb's legacy in vertebrate paleontology, being built for permanent exhibition at the time we conducted this study, we accepted the vagaries of the fossil record and persevered in our attempt to more accurately estimate its size. And our only practical option to estimating the body relationships of *Titanis* is through the use of least squares regression.

In Table 3 we present the allometric constants used to estimate the total length (TL) of *Titanis'* skull (dependent variable Y) from the length (L) and width (W) of the largest quadratojugal (independent variable X) preserved. Since the quadratojugal is one of the few cranial elements preserved in *Titanis*, we had little other options for skull length predictors. As a secondary analysis, we also estimated its total skull length (Y) using the axis length (X). Our working assumption being that since the axis vertebra supports the head, its overall size would be a reflection of the skull size it was supporting.

The total length of the leg (femur+tibiotarsus +tarsometatarsus) (Y) and the standing height of the bird was estimated from the width of the distal tibiotarsus and the width of the tarsometatarsus trochlea (Table 3). Our presumption is that these elements must be large enough to support the mass and movement of the animal (Schmidt-Nielsen 1984). The mechanics are similar to engineering supports for flag poles; a 5-foot flag pole requires a much smaller base than does a 100-foot flag pole. It should be noted that we estimated the width of the tarsometatarsus trochlea of *Brontornis burmeisteri* (Moreno & Mercerat, 1891), believed to be the largest known phorusrhacid, from the sum of the single measurements for each trochlea of specimen (FM-P13259) (Alvarenga & Höfling 2003) and is most likely underestimated.

RESULTS AND DISCUSSION

Since our primary intent is to further describe the most complete *Titanis* specimens which are indicated by an asterix (*) in Table 1, we felt that the descriptions should be closely associated with their photographs. Please refer to Appendix I for full descriptions and images of the selected elements.

Although we are reluctant to hypothesize about the phylogenetic relationships of *Titanis* due to our inability to adequately compare it to other phorusrhacids, we nonetheless present a cursory review of the only preserved characters proposed by Alvarenga and Höfling (2003) that support the placement of *Titanis* within the Phorusrhacidae: its gigantic size, the morphology of the pterygoid and tarsometatarsus, and the loss of flight.

TITANIS, A PHORUSRHACID? A PHORUSRHACINE?

There is a beautifully preserved left pterygoid (UF

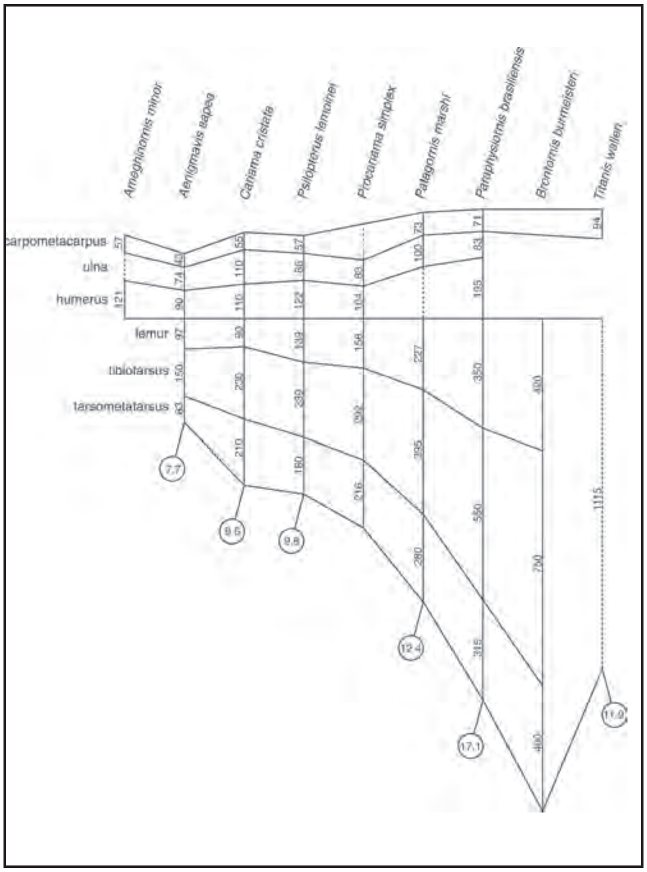

Figure 2. Graph depicting wing and hind leg lengths for several phorusrhacid taxa (after Alvarenga, and Höfling, 2003).

162749) from the Inglis 1A site, which is represented by a cast (the original resides in a private collection; Appendix 1, Fig. 1). It is 75 mm in length and 15 mm in width with a medially placed facet for articulation of the basipterygoid process (Appendix 1, Fig.1b). The extraordinarily large size of the pterygoid in conjunction with the presence of a medially placed articulation facet, are consistent with the characters cited for the family (Alvarenga & Höfling 2003). The distal portion of the tarsometatarsus of *Titanis* (Appendix 1, Fig. 13c), when viewed from a plantar perspective, is triangular in shape, another cited synapomorphy for the Phorusrhacidae (Alvarenga & Höfling 2003).

Alvarenga and Höfling (2003) placed *Titanis* within the Phorusrhacinae, together with *Phorusrhacos longissimus* (Ameghino, 1887) and *Devincenzia pozzi* (Kraglievich, 1932). The characters they submitted as evidence of monophyly are; a [relatively] long mandibular symphysis that is twice as long as the width of its base, and a [relatively] long and narrow tarsometatarsus that is approximately 60% of the length of the tibiotarsus. Only fragments of the leg are preserved in *Titanis*, consisting of only the proximal or distal ends of the tarsometatarus and tibiotarsus (Table 1; Appendix 1, Figs. 13-16). We submit that the placement of *Titanis* within this subfamily is tenuous until further fossils are recovered (see Table 3).

A Big Bird

The length of the largest of the two preserved quadratojugals (UF 57585) measures 170 mm and estimates a total skull length of 542 mm ($r^2 = 0.70$) (Table 3). The total height of quadratojugal (UF 57580) is 23 mm and predicts a skull length of 360 mm ($r^2 = 0.91$) (Table 3).

It should be noted that the predicted skull length from the length of the quadratojugal is underestimated because the most distal portion is missing (Appendix 1, Fig. 3). We believe that approximately 25 mm of the bone was not preserved. Regardless, the r^2 value for this predictor is not as strong as the height of the quadratojugal, so the missing portion might be a moot point. The axis maximum length of UF 30006 is 127

Figure 3. Photo of the reconstructed foot of *Titanis*, the carpometacarpus, the distal portion of the humerus, and the carpometacarpus of a wild turkey included for scale (photo by Tammy Johnson, FLMNH).

mm, and predicts a total skull length of 521 mm (r^2 = 0.86) (Table 3). The allometric predictions of the three equations seem to show that the skull length of *Titanis* lays somewhere between approximately 360 mm and 542 mm.

The width of tarsometatarsus trochlea (UF 4108) is 76 mm and predicts a total leg length (femur+tibiotarsus+tarsometatarsus) of 1185 mm (r^2 = 0.70), while the predicted leg length of the distal tibiotarsus width (88.9 mm) yields a value of 1631 mm (r^2 = 0.85) (Table 3).

The standing height of the bird is predicted to be 1444 mm (r^2 = 0.75) based on tarsometarsus trohclea width. The distal width of the tibiotarsus predicts a standing height of 1870 mm (r^2 = 0.87). Previously, *Titanis* had been described as "similar in size to *Phorusrhacos longissimus*, although differing in proportions … smaller than *Devincenzia*…" (Brodkorb 1963:115) and between two and three meters tall (Marshall 1994; Feduccia 1999). Our estimate of standing height ranges between 1444 mm and 1870 mm or over 1.5 meters with respect to previous hypotheses of its height.

Alvarenga and Höfling (2003) offered estimates of the height of other phorusrhacids, standing height to the top of the back (SHB), and the maximum standing height to the top of the head (MSH), as well as their estimated weights in kilograms:

Psilopterus lemoinei (*Moreno* & Mercerat, 1891)
~ 60cm SHB/80cm MSH, 5 kg

P. bachmanni (Moreno & Mercerat, 1891)
~ 60cm SHB/70cm MSH, 5 kg
Procariama simplex (Rovereto, 1914)
~ 70cm SHB, 10 kg

Patagonis marshi (Moreno & Mercerat, 1891)
~ 90cm SHB, 45 kg

Andalgalornis steulleti (Patterson & Kraglievich, 1960) ~ 100cm SHB, 50 kg

Mesembriornis milneedwardsi (Moreno, 1889)
~ 110cm SHB/170 cm MSH, 70 kg

Phorusrhacos longissimus (Kraglievich, 1931)
~ 130cm SHB/2.4m MSH, 130 kg

Paraphysiornis brasiliensis (Alvarenga, 1982)
~ 140cm SHB/240cm MSH, 130 kg

Figure 4. Images of carpometacarpii (in palmar view) of, from right to left, *Titanis walleri*, (b) *Meleagris gallopavo* (turkey), (c) *Gallus gallus* (chicken); photo by Tammy Johnson, FLMNH).

Brontornis brumeisteri
~ 175cm SHB/280cm MSH, 350 kg

The sister taxa, the seriemas are much smaller, *Cariama cariama* (Linnaeus, 1776) stands approximately 90 cm at the head, reaching weights of 1.5 kg. *Chunga* (Hartlaub, 1860) is even smaller, standing at only 50-70 cm at the head and weighing less than 1 kg (Gonzaga, 1996).

Based on the estimates of Alvarenga and Höfling (2003), *Titanis* was one of the taller phorusrhacids, and was probably similar in the size to *M. milneedwardsi* and *A. steulleti*, although as we mentioned, our estimate is most likely low, hence *Titanis* could have reached the dimensions of *P. longissimus.*

For relative comparisons, the largest living terrestrial bird, the ostrich (*Struthio camelus* Linneaus 1758) reaches heights of 200 cm and weighs approximately 130 kg. The largest flying bird known, *Argentavis magnificens* is estimated to have been weighted between 72 and 79 kg (Campbell & Tonni 1983; Campbell & Marcus 1998). Although the ostrich and *Brontornis* were similar in height, *Brontornis* was considerably stockier than the living ostrich. Certainly, much of the weight in phorusrhacids was concentrated in their skulls, which were massive, while the ostrich skull is somewhat puny compared to its overall size.

Due to the limitations of the preserved specimens, we were unable to estimate the body mass of *Titanis* using any of the possible body size relationships (Appendix 2). This remains a an intriguing question for future research

Our estimates for the size of *Titanis* are as rigorous as feasibly possible given the lack of preserved specimens. We caution readers not to lose sight of the fact that our analyses were compromised by a small sample size and incomplete of data.

A Unique Wing?

As mentioned, one of the characters that support phorusrhacid monophyly is the loss of flight and reduction of the wing. A review of the maximum lengths of phorusrhacid appendages (i.e., legs and wings) suggests that there is an inverse relationship between the overall size of the bird and the size of its wing (Fig. 2, taken from Alvarenga & Höfling 2003, Fig. 3; Appendix 2). A comparison of the left carpometacarpus, the proximal end of the left humerus, and a reconstruction of the right foot of *Titanis* illustrate this phenomenon (Fig. 3). The scale used in this image is that of the carpometacarpus of a wild turkey (*Meleagris gallopavus* Linneaus 1758), their carpometacarpii are approximately the same size!

The published descriptions of *Titanis'* wing describe it as being a "strong, robust wing (unlike the paedomorphic wings of ratites) … like its closest relatives … with a rigid wrist and flexible fingers … on a manus that was held extended, as in penguins" (Chandler 1994:176). We agree that *Titanis* retained a rigid wrist, which is a plesiomorphic state in birds (the ulnare and radiale restrict the movement of the manus in *all birds* in order to keep primary feathers in alignment [Vasquez 1992]). With respect its robustness, our data suggest otherwise. Figure 2 illustrates the ratio of known phorusrhacid wings to their total leg length; the wing of *Titanis* is the smallest known with respect to its body size, being approximately 6 times smaller than its leg length, whereas *Psilopeterus* has a wing length that is only 3 times smaller than its leg length.

The hypothesis that the hand of *Titanis* was "held extended, as in penguins" is purportedly evidenced by an "almost vertical carpal trochlea of the carpometacarpus" (Chandler 1994:176). The carpometacarpus is directed postero-laterally in (most) birds, with the alula pointed downward. Necessarily, the facet on which the carpometacarpus articulates with the ulnare and radiale is vertically oriented. We are unclear as to what the author meant by "almost vertical" because we found that in most birds, the orientation of the articulation facet is very similar in morphology, this state is even noted in chicken and turkey wings (Fig. 4; Appendix 1, Fig. 9; see also Gilbert et al. 1981:figs. 123-146).

The "presence of a ball joint on the facet of the metacarpal I" instead of an actual (pollix) facet is offered as evidence of a flexible claw on the hand of *Titanis* and its close relatives (Chandler 1994:176). The most recent review of the morphology of the carpometacarpii of phorusrhacids (Alvarenga & Höfling 2003) indicates that the only well preserved phorusrhacid wings are from *Titanis*, *Paraphysiornis*, *Patagornis*, *Psilopterus australis*, and *Mesembriornis* (Alvarenga & Höfling 2003; Table 3). All of them exhibit a protuberance, or 'ball and joint articulation on the carpometacarpus', as suggested by Chandler (1994). Within most birds, this joint articulates with digit I, or the alula. The first digit in a bird's hand, although seemingly insignificant, is actually critical in preventing stalling during low-speed flight. The alula, which consists only of phalanx 1, moves independently of the rest of wing and acts as a wing slot to increase lift. Essentially, the alula and associated feathers direct airflow over the upper surface of the wing at a steep angle. As seen in the comparative presentation of carpometacarpii across 64 taxa (Gilbert et al. 1981:figs. 52-59), the morphology of the pollical facet varies interspecifically and can be represented by either a facet or some kind of protruding articulating surface. In fact, a facet for the alula is more common among birds than the retention of a ball joint as seen in *Titanis*. Presumably, there is a relationship between the morphology of the wing and how the bird makes a living, a question that is outside the scope of this study. We do know, however that this ball-joint morphology is also exhibited in seriemas (Alvarenga & Höfling 2003), the closest-living taxon to Phorusrhacidae (see also Gilbert et al. 1981). Neither of the two living seriemas express a flexible claw in lieu of the small single-phalanx finger. Our review of the existing *Titanis* material did not recover evidence to suggest that the expressed phenotype of *Titanis* and other phorusrhacids was vastly different than that seen in seriemas today (Fig. 5).

Chandler (1994) suggested that previous reconstructions of phorusrhacid wings were based on the smaller psilopterine taxa, hence the misinterpretation of wing structure in *Titanis* and other phorusrhacines. We would argue that, based on the known wing elements (Table 3; Appendix 2) for this group, there is a considerable range in the ball joint morphotype, suggesting ho-

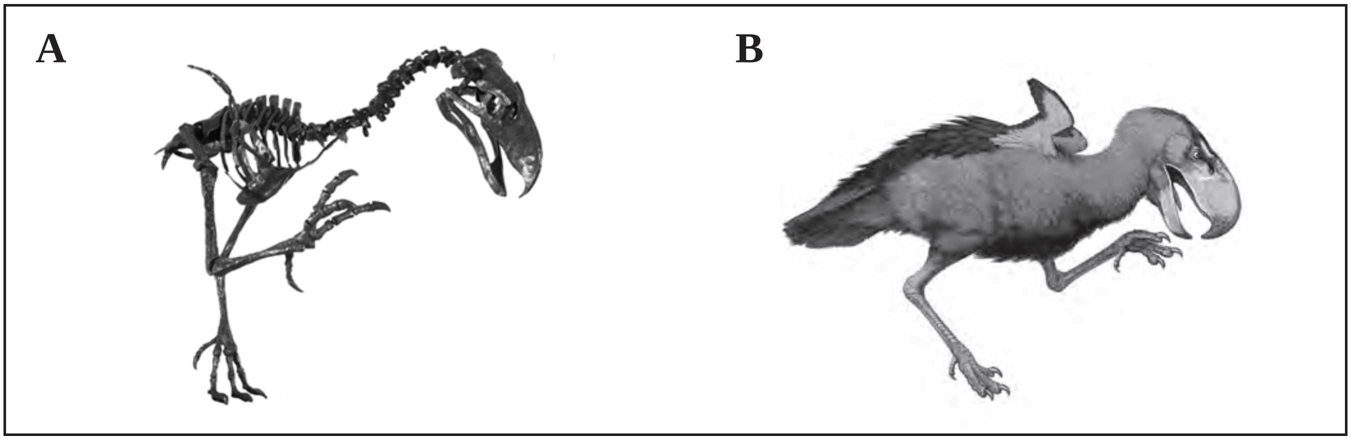

Figure 5. (a) A sculpture of *Titanis* at the Florida Museum of Natural History, (b) A reconstruction of *Titanis* after Gould & Quitmyer (artwork by Carl Buell, 2002)

moplastic behavior of this particular character within the Phorusrhacidae.

Stratigraphic Range

Paleontologists, enthusiasts, and rock companies alike have been actively prospecting and excavating the Florida fossil record for 80+ years. To date, there are approximately 460 documented Pleistocene deposits in Florida (FLMNH sites only) and approximately 86,000 Pleistocene vertebrate specimens currently catalogued in the collections at the FLMNH (+/- 2,500 uncatalogued; Hulbert, pers comm). Despite the magnitude of the Pleistocene collections, there is no evidence of *Titanis* in the Florida Pleistocene. *Titanis* is incredibly rare in the abundant Pliocene collections in Florida, which is not unexpected because large predatory animals are far less abundant in a given ecosystem.

The Texas site, however, is not as clear-cut. It is reported to be "anywhere from late Hemphillian to late Rancholabrean in age" (Baskin 1995:843) containing early Pliocene horses as well as late Pleistocene vertebrates (Baskin 1995). "The source head for these Hemphillian deposits are unknown but probably eroded from older, undip sediments from the Upper Goliad Formation and then transported …" and redeposited (Baskin 1995:842). Based on a lack of "definitive Blancan or Irvingtonian taxa" from the site and similarity in color and preservation of the Pleistocene fauna, it was suggested that *Titanis* might have survived into the Rancholabrean (Baskin 1995). Presuming this to be true, it would imply that *Titanis* was roaming the grasslands of the North American Gulf Coast for more than a million years since its first known appearance in the fossil record, anywhere. Its location in Texas, and its presumed Rancholabrean age would then suggest that *Titanis* was heading south. If that were the case, one would still expect to find *Titanis* in the Florida Pleistocene record because, like many other large animals, it would have sought a tropical haven during the ice age. Given the extensive Florida Pleistocene collections, one would expect to find at least some evidence of its existence.

An alternative hypothesis is that the *Titanis* material in Texas is late Pliocene in age, but the formation from which it came has not yet been identified nor aged appropriately. We would expect to see *Titanis* in the Pliocene in Texas because certainly, as a migrant in the Great American Interchange, it would have had to pass through Texas to reach Florida; at that time it was a 1,100-mile journey along the Gulf Coast. Unfortunately there are few Pliocene-Pleistocene Gulf sites outside of Florida (Baskin 1995).

As depicted in the photographs of the Florida specimens in Appendix 1, there is a considerable range in the preservation color of the *Titanis* elements even in from a single site, as with most Florida Pliocene material. Given the rapid and extreme changes in global sea level during that time (Hulbert 2001), one would expect great perturbations in local Gulf environments coinciding with these sea level changes. Based on these data, we question the use of color as an indicator for geological age.

The only definitive evidence for *Titanis* is in the Blancan/Irvingtonian of Florida. We reject the use of negative fossil data to support a Pleistocene survival hypothesis of *Titanis* in Texas (i.e., "lack of definitive Blancan taxa" [Baskin 1995]). We prefer the scenario of a yet-to-be discovered Blancan-aged site in Texas in which *Titanis* bones were deposited, reworked, and re-deposited somewhere down stream. This hypothesis is the most parsimonious given the available data because it does not beg the question as to why *Titanis* is absent in the Pleistocene record in Florida or why it is not in the Blancan in Texas. And it does further corroborate the faunal interchange hypothesis (Stehli and Webb 1985).

CONCLUSIONS

Our least squares regression estimates suggest that *Titanis* stood over 1.5 meters tall (range = 1.4 m – 1.9 m) tall with a skull estimated to have been between 359 mm and 560 mm in length that had a proportionately large beak. As with other phorusrhacids, *Titanis* most likely had a laterally-compressed physique, long 'running' legs and diminutive wings without a claw. The localities in which *Titanis* has been recovered suggest that it lived in a fairly open grassland environment in which karst sinks and springs were present very much like Florida today. From these sites, a diverse array of taxa have been recovered (Olsen 1965; Scott & Allman 1992; Emslie 1998; Hulbert 2001), to include *Xenosmilus hodsonae* (sabertooth cat), *Eremotherium eomigrans* (giant sloth), *Glyptotherium arizonae* (glyptodont), *Rhyncotherium praecursor* (proboscidean), *Chasmoporthetes ossifragus* (hyena), *Arctodus pristinus* (bear), *Erethizon kleini* (porcupine), rails, ducks, condors, and other small birds, rodents, lizards, snakes, alligators, turtles, and arthropods.

This type of environment is not much different than the environment inhabited by seriemas today. We suspect that *Titanis*, like the seriemas, was an opportunistic feeder that preyed on anything that it could run down and subdue. We also believe that the prey of choice for *Titanis* was probably anything that it could swallow in its entirety, much like behavior of the seriemas (Gonzaga 1996).

As with many other Florida Pliocene taxa, there is no compelling evidence to date that *Titanis* survived into the Pleistocene, and the Texas evidence is suspect.

ACKNOWLEDGEMENTS

We gratefully acknowledge the following institutions for providing access to their vertebrate paleontology and ornithology collections: FLMNH, AMNH, and USNM. Specifically, we thank Richard Hulbert for making FLMNH collections available to us, as well as his recollections, and Carl Mehling and Mark Norell of the AMNH for allowing access to the phorusrhacid material to us and our artists. We are also very grateful to Bruce MacFadden and the FLMNH's Exhibits and Public Programs for subsidizing much of this research. A number of people were instrumental in the formation of this work; Ian Breheny for helping us to lay out the images in the body of the text, Tammy Johnson and Jeff Gage of the FLMNH for taking wonderful photographs of *Titanis* and *Cariama*, Tara Odorizzi for Photoshop work with the figures, Kurt Auffenberg for helping with the interlibrary loans, Richard Webber who did the skeletal reconstruction of *Titanis* for the FLMNH's new fossil hall exhibit, Carl D. Buell for the illustration reconstructions of *Titanis* for this publication and the exhibit, Steve and Suzan Hutchens for reconstructing *Titanis*' foot and donating the pterygoid (UF 164729), and Steve Martin of Natural Encounters for allowing us to take images of his seriemas. We also thank Julia Clarke for early discussions of phorusrhacid systematics and morphology, and a rigorous review of this article. And if it were not for the help of Herculano Alvarenga and his dissertation, this work would have been greatly impaired. We also thank Luis Chiappe for a thoughtful review of our initial manuscript. We gratefully acknowledge the late Ben Waller who discovered the first *Titanis* fossil remains and brought them to the attention of the Florida Museum of Natural History. Continued paleontological research by Pierce Brodkorb, Steve Emslie, Robert Chandler, Dave Webb and others have kept the research of this most interesting bird alive. Dick Franz, Gary Morgan, Richard Hulbert, John Baskin, and Bruce MacFadden are to be commended for their efforts in putting together this volume.

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Appendix 1. The following are images and descriptions of the more complete specimens of *Titanis* that reside at the FLMNH (photos by Tammy Johnson, FLMNH**).** Refer to Table 1 for the discovery and publication history of each element listed and Appendix 2 for selected measurements.

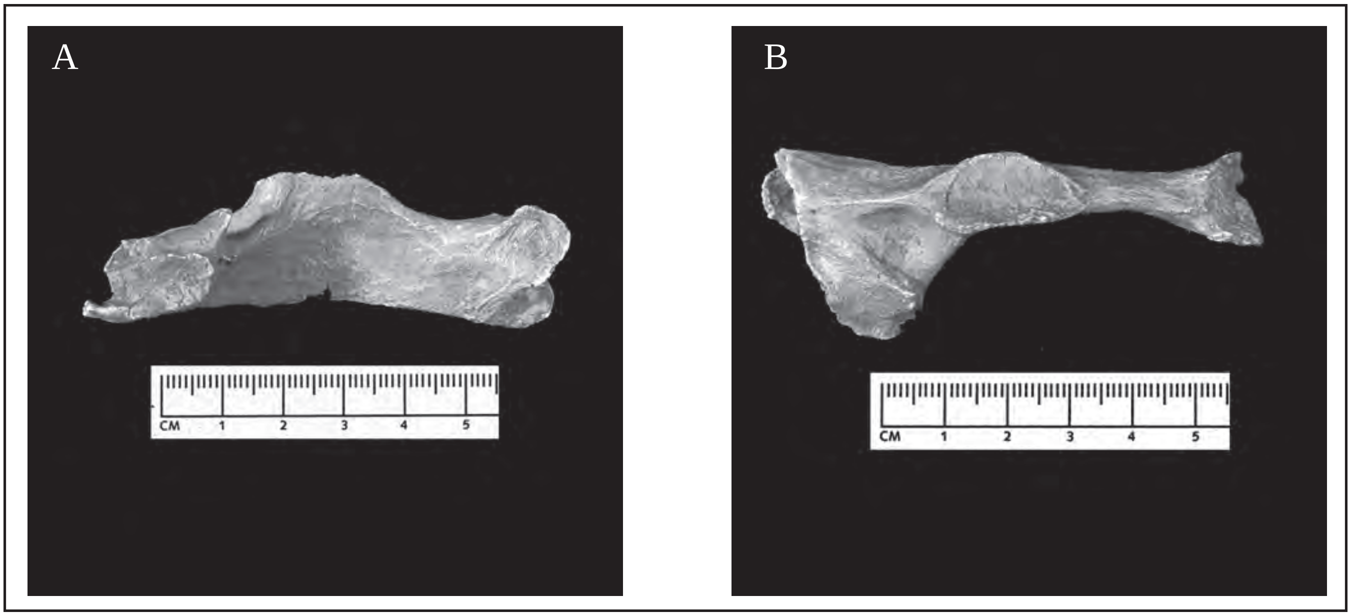

Figure 1. Pterygoid (right), UF 162749: (a) anterior view; (b) medial view. Almost complete, missing a small portion of its articulation facet for the quadrate. Length is 75mm and its depth, from the lateral edge to articulation facet for the basisphenoid, is 15mm. The articulation facet for the basisphenoid is medially placed, consistent with other phorusrhacids.

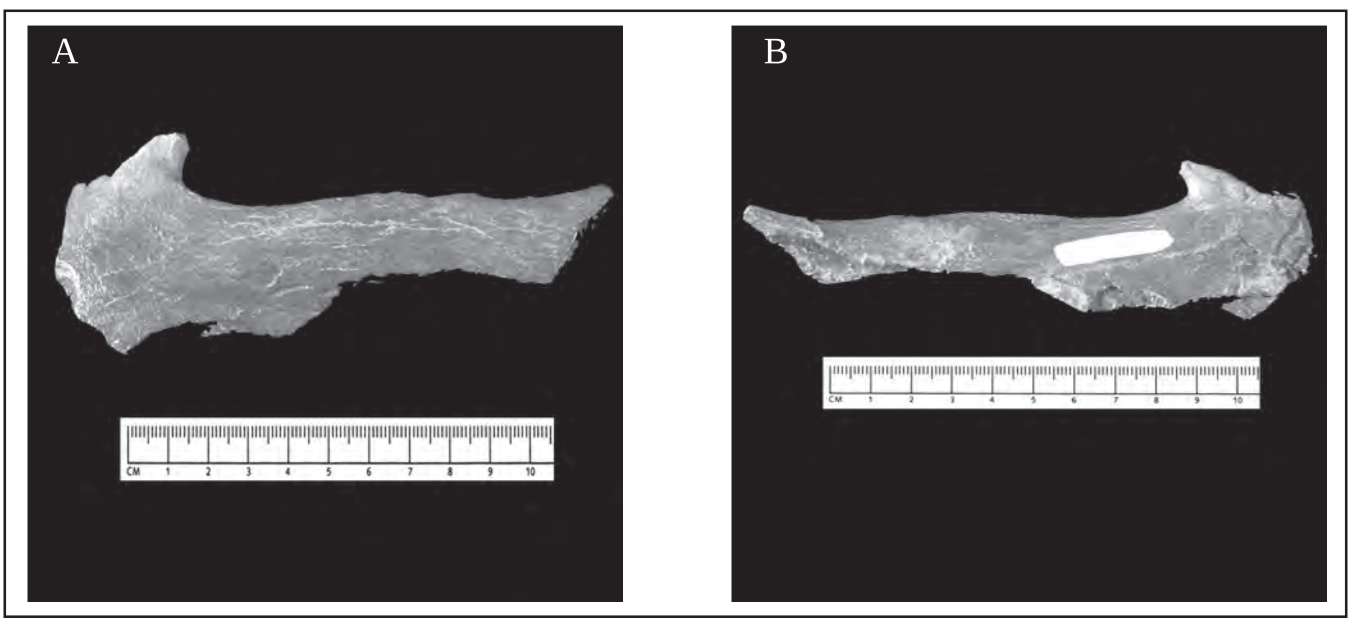

Figure 2. Narial opening, ventral bar (left), UF 137193: (a) lateral view; (b) medial view. The anterior most portion of the ventral bar is preserved. It is 135mm in length, its width (mediolateral) at terminal margin of narial opening is 7mm.

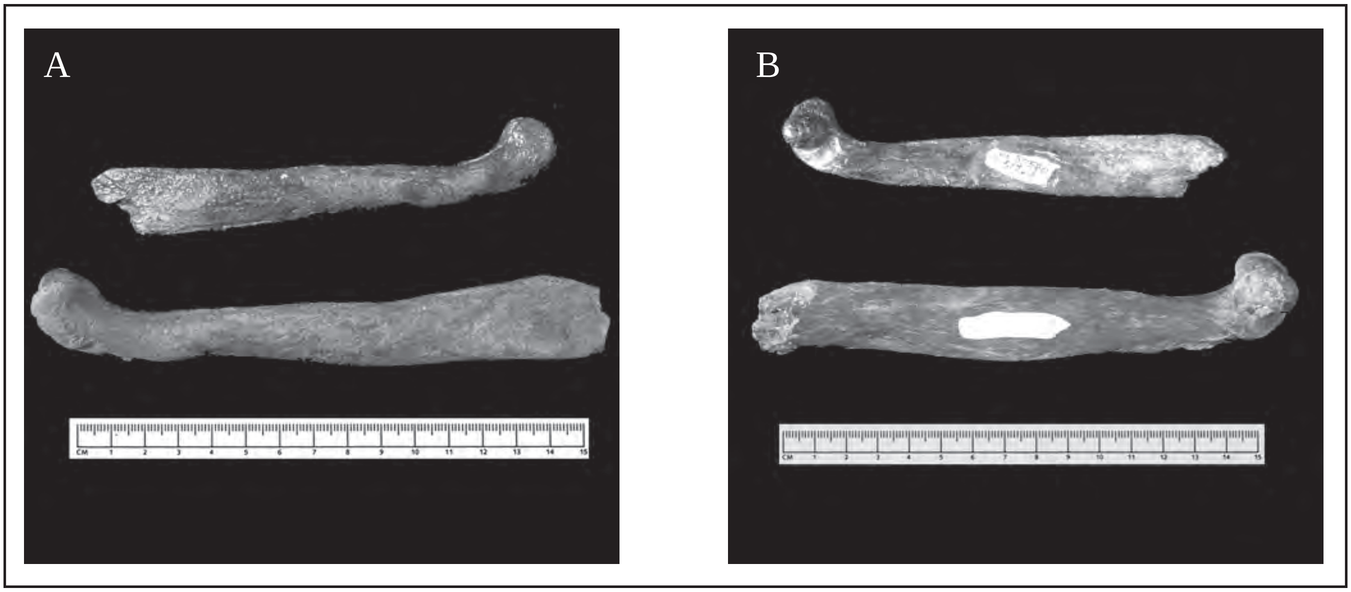

Figure 3. Quadratojugals: (Top) UF 57580 (left); (Bottom) UF 57585 (right): (a) lateral view; (b) medial view. Only the proximal ends of each are preserved, which includes the articulation tubercular for the quadrate. The larger specimen (Fig.3.2 UF 57585) has a more pronounced crest that is cranial to the articulation tubercular compared to the smaller specimen (Fig 3.1 UF 57580), which has a deep fossa anterocranial to the tubercular. As mentioned by Chandler (1994), there is a distinct difference is size of these bones, possibly indicating sexual dimorphism because there is no indication that the smaller one is a juvenile.

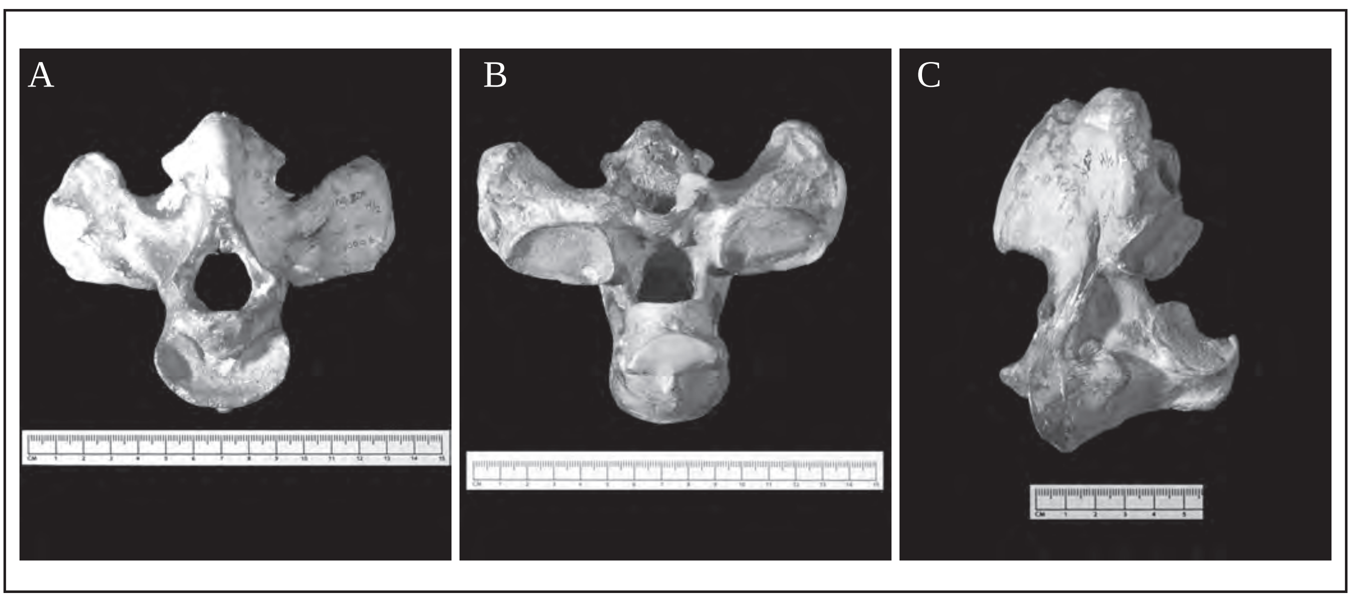

Figure 4. Vertebra, 2nd cervical (axis), UF 30006: (a) anterior view; (b) posterior view; (c) lateral view. The specimen is complete. The anterior projection of the process dorsalis is ventrally projected, the dorsal most crest is narrow and rounded at its dorsal terminus. The facies articularis is directed antero-ventrally at a 30° angle. The processus tranversus has enlarged postero-dorsally directed projections, extending just past the articulation surface.

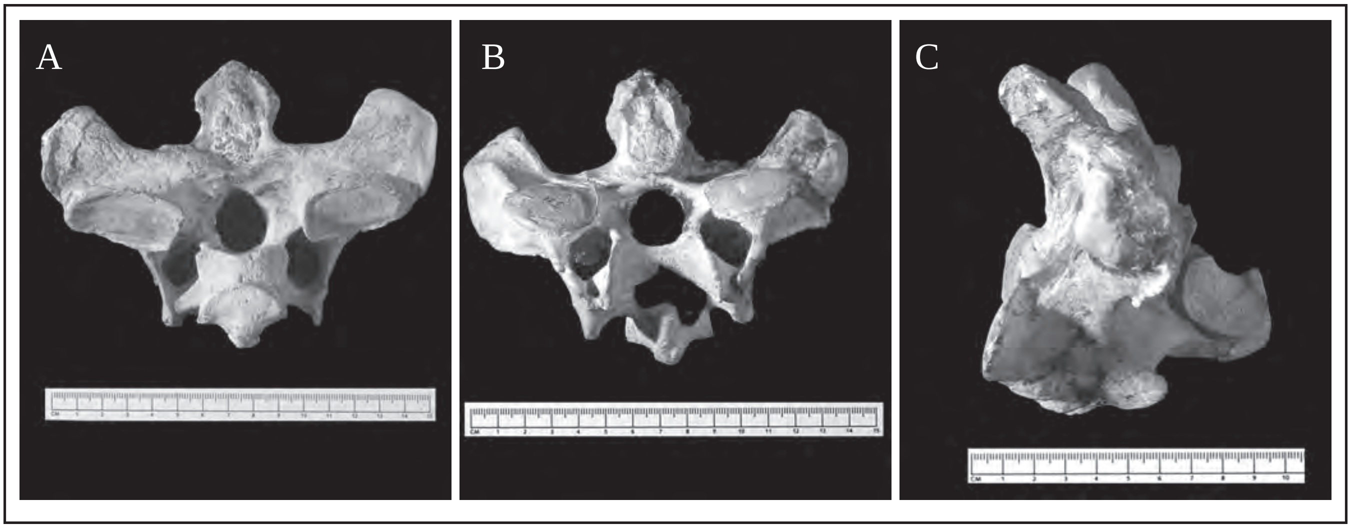

Figure 5. Vertebra, 3rd cervical, UF 30005: (a) anterior view; (b) posterior view; (c) lateral view. Complete. As in C2, the dorsal terminus of the process dorsalis is rounded at its terminus, however it is positioned more dorsally then in C2 (Carr 1981). The facies articularis is directed antero-dorsally at almost a 90° angle. The processus tranversus have enlarged posteriorly directed projections, the maximum extension is even with the facies articularis. The articulation surfaces of the processus transversus face anteriorly. The orientation of the vertebral arterial canal is directed anteroventrally-posterodorsally.

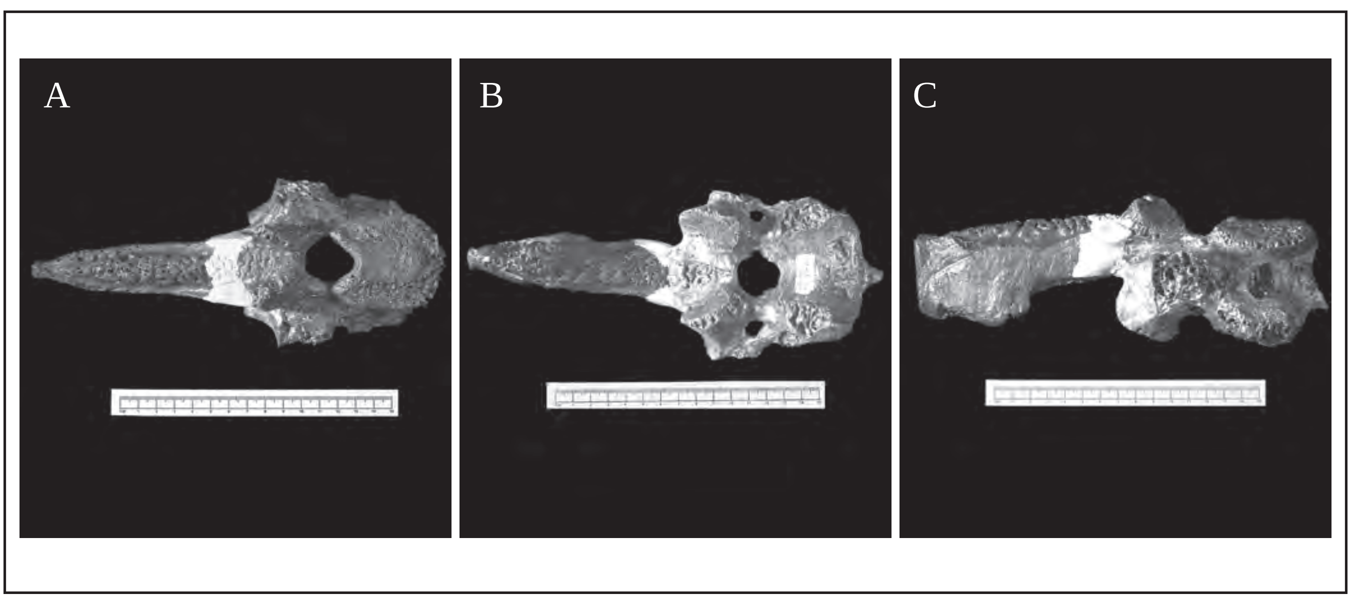

Figure 6. Vertebra, thoracic, UF 10415: (a) anterior view; (b) posterior view; (c) lateral view. This specimen is incomplete, it is missing the processus transversus. The processus dorsalis is extremely pronounced. The facies articularis is directed dorso-medially with a slight upward orientation. The bone is very spongy, suggesting a young individual.

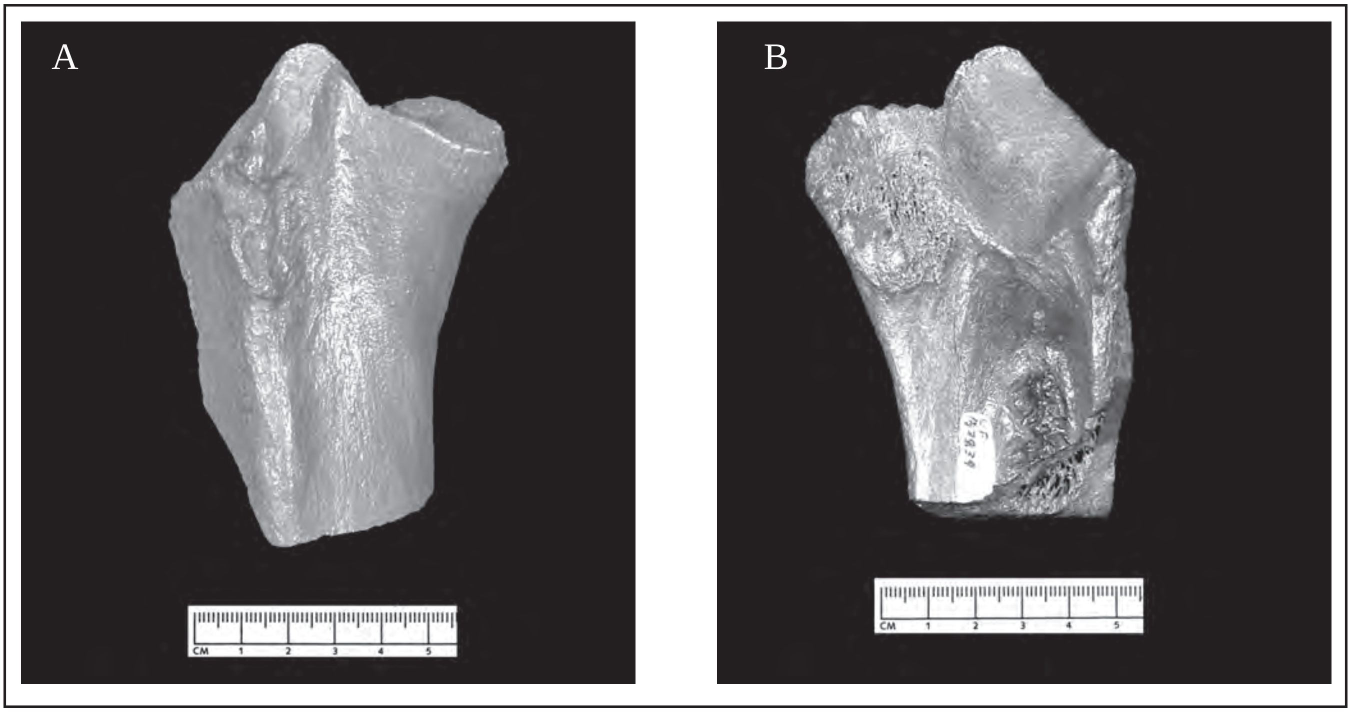

Figure 7. Humerus (left), proximal end, UF 137839: (a) anterior view; (b) posterior view. The bone is broken just distal to the sulcus for the ligament transverses. See Chandler (1994) for a complete description.

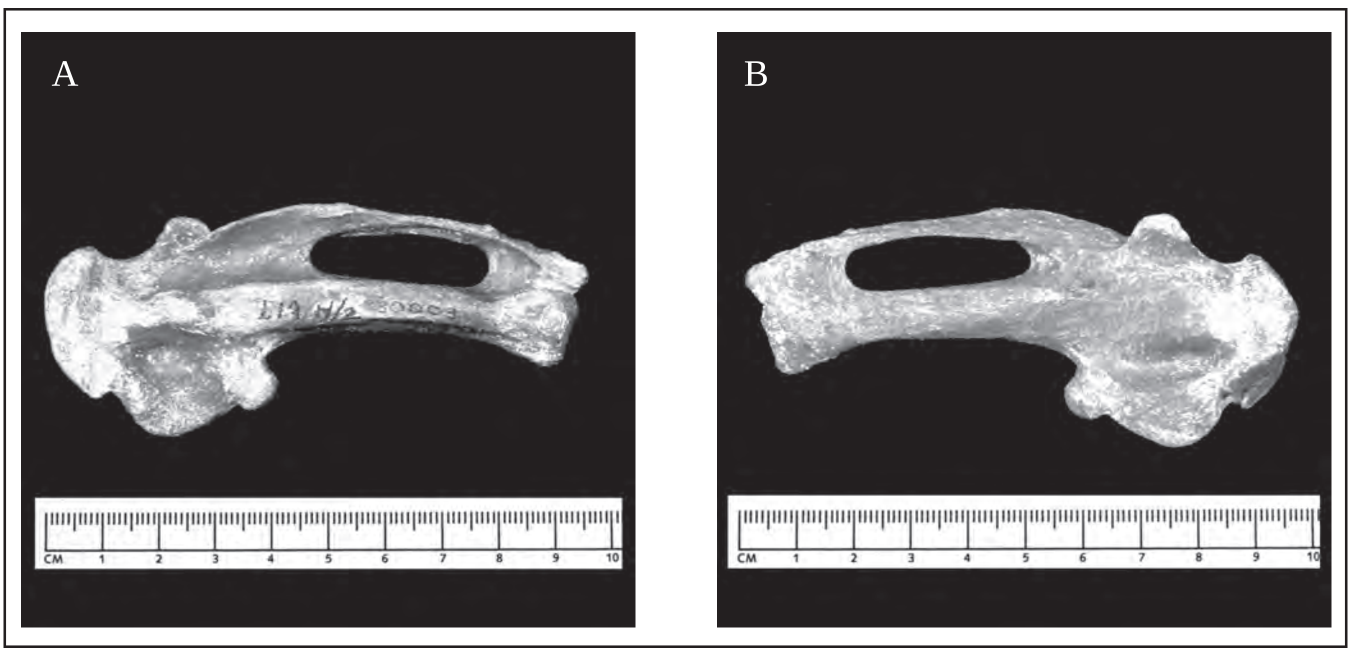

Figure 8. Carpometacarpus (left), UF 30003: (a) anterior view; (b) posterior view. This specimen has a broad trochlea carpalis, without a sulcus, and the absence of the process pisiformis. The process intermatacarpus is distinct and located on the proximal edge of the metacarpus minimus. The process alularis is prominent and distinctly rounded in shape. The articular surface for the digit major is flat and without a distinct sulcus. See also Chandler (1994).

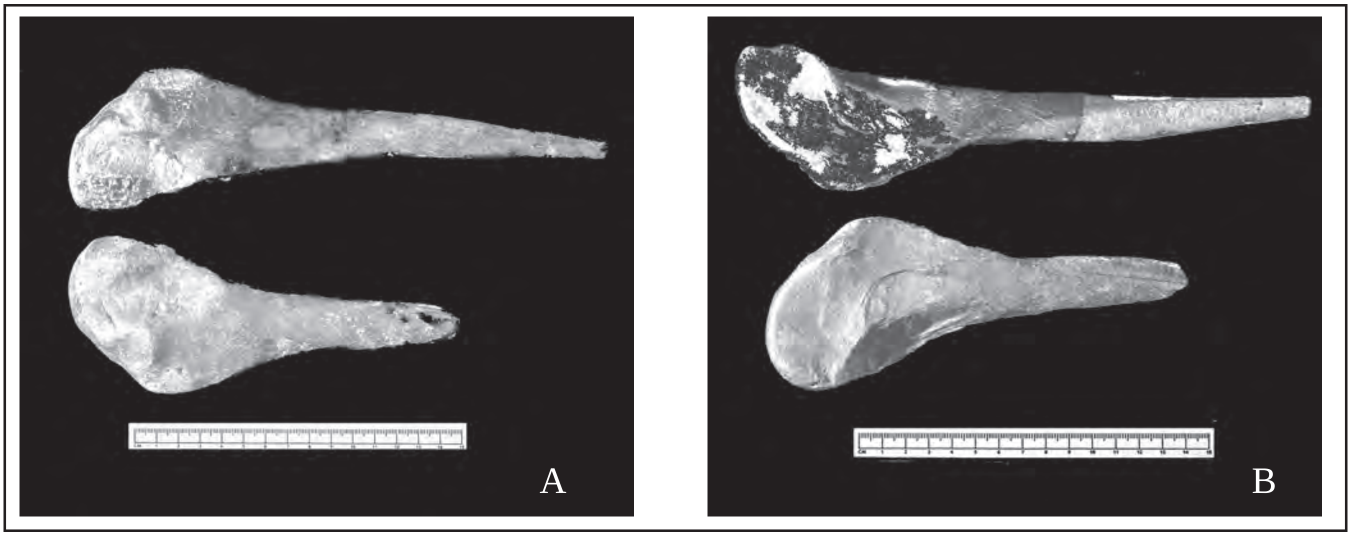

Figure 9. Fibula (left), proximal end, UF 9051 and Fibula (right), proximal end, UF 7421: (a) lateral view; (b) medial view. Both specimens are incomplete. The lateral side of the head of the fibulas exhibit a protuberance located anteriorly and just caudal to the crest. Just anterior to this crest is a pronounced facet that runs cranio-caudally.

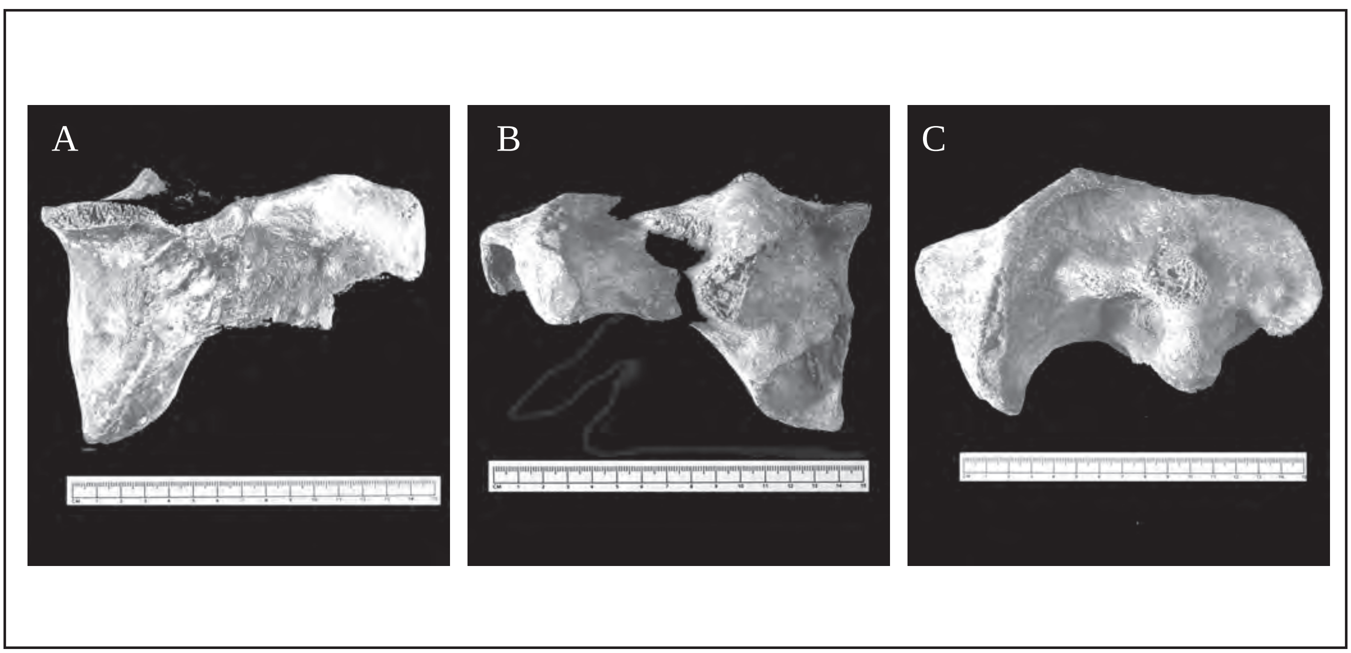

Figure 10. Tibiotarasus (right), proximal end, UF 7333: (a) anterior view; (b) dorsal view; (c) proximal articular surface. The crista cnemialis lateralis is very pronounced, extending far beyond the shaft of the tibiotarsus. The foramen interosseum proximale is absent. The crista cnemialis cranialis is abbreviated, and does not extend down the shaft. The fossa flexoria is well pronounced. The facies articularis lateralis is directed dorsally, with a caudal terminus that extends laterally.

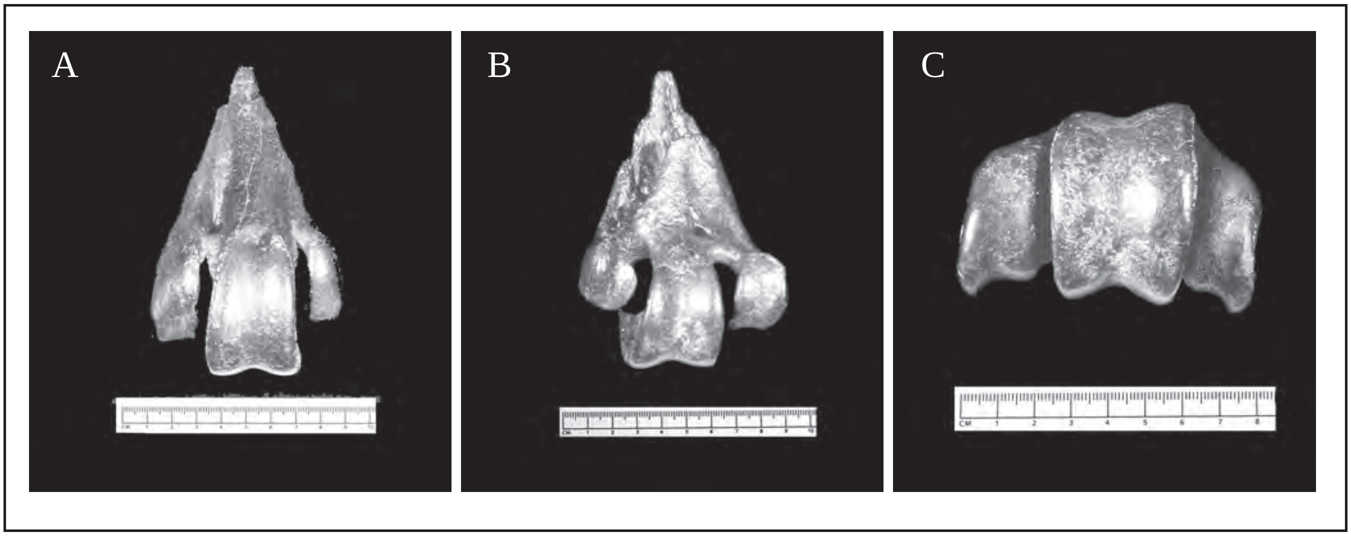

Figure 11. Tarsometatarsus (right), distal end, UF 4108 (type): (a) anterior view; (b) posterior view; (c) plantar view. As described by Brodkorb (1963).

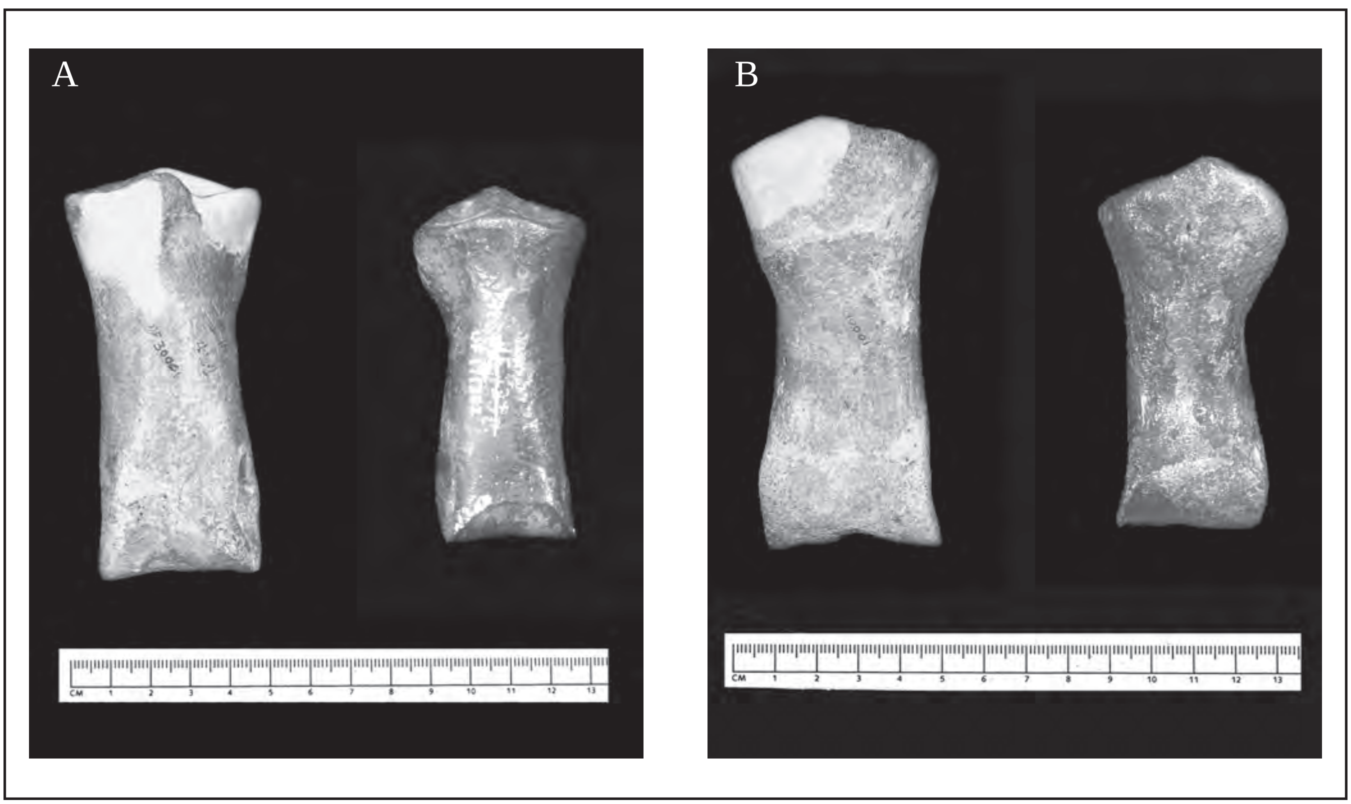

Figure 12. Digit III (left), phalanx 1, UF 30001 and Digit III (right), phalanx 1, UF 171382: (a) anterior view; (b) posterior view.

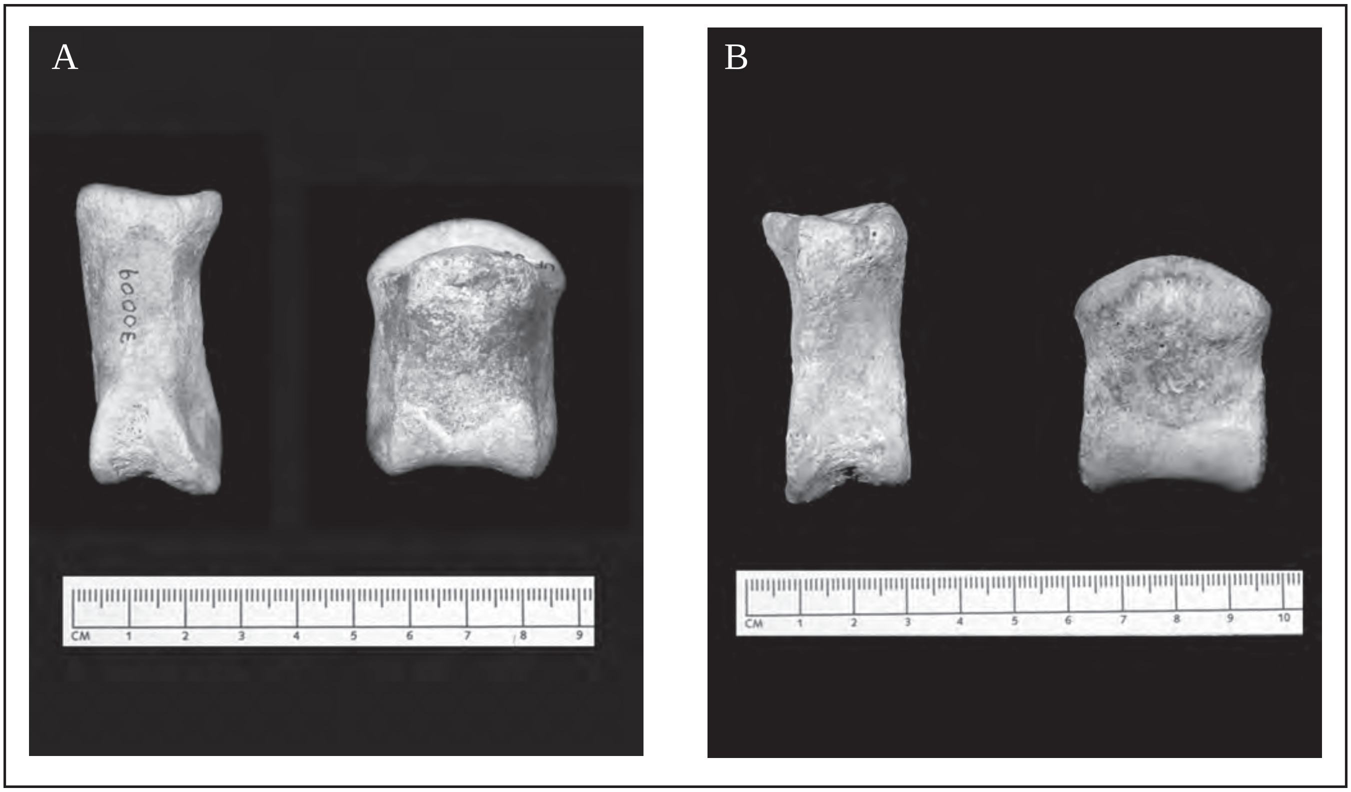

Figure13. Digit IV (left), phalanx 1, UF 30009 and Digit III (right), phalanx 2, UF 30010: (a) anterior view; (b) posterior view.

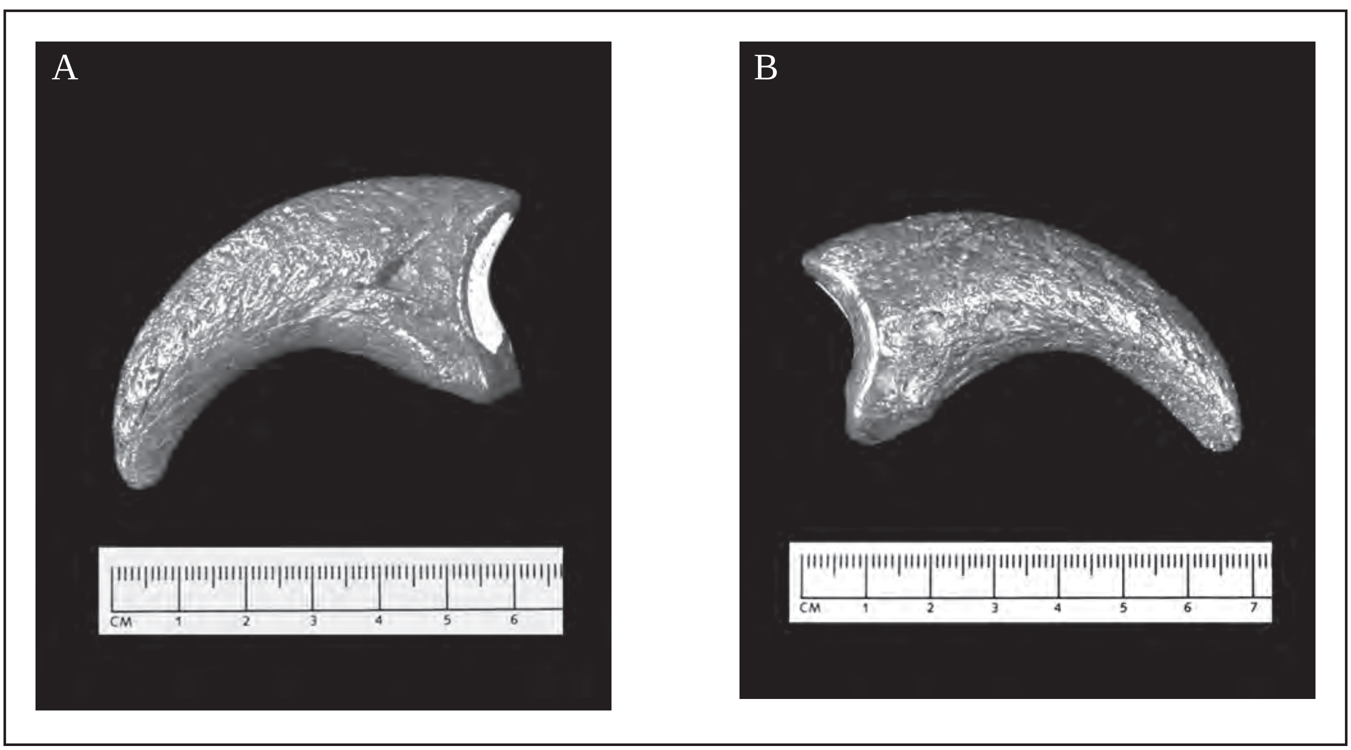

Figure 14. Phalanx, distal end (claw), UF 10417.

Appendix 2. Selected measurements of the more complete elements preserved among the phorusrhacids. These are the data used in our allometry analyses (see Methods). All measurements are in millimeters (mm), weights are in kg. An asterix (*) that accompanies a specimen number indicates they are composites, additional specimen numbers are footnoted. Abbreviations are as follows: Institutions: AMNH; American Museum of Natural History; BMNH = British Museum of Natural History; DGM = Divisao de Geologia e Mineralogia do Departamento Nacional da Producao Mineral; FLMNH = Florida Museum of Natural History; FM = Field Museum of Natural History; MLP = Museo de La Plata; MACN = Museo Argentino de Ciencias Naturales; MMP= Museo de Mar del Plata; PUM = Princeton University Museums; TMM = Texas Memorial Museum; and USNM = Smithsonian Museum of Natural History. H= height; L = length; W = width; D = diameter; C = cervical vertebrae; CMC = carpometacarpus; CMCProx = proximal portion of carpometacarpal; Dig3.1 = digit III, phalanx I; Dig3.1 = proximal portion of digit III, phalanx I; Fem = femur; FemProx = proximal portion of femur; FemDis = distal portion of femor; Fib = fibula; FibDis = distal portion of fibula; Hum = humerus; HumProx = proximal portion of humerus; HumDist = distal most portion of humerus; Mass = weight; MSH = maximum standing height; T-7 = thorasic vertebra #7; T neck = total length of neck; TMT = tarsometatarsus; TMTProx = proximal portion of tarsometatarsus; TMTDMid = midshaft diameter of tarsometatarsus; TMTTroch = tarsometatarsus trochlea; TT = tibiotarsus; TTDis = distal portion of tibiotarsus; Sac = sacrum; SHB = standing height to the back.

Measurements taken and corresponding columns: (1) skull length: beak tip to paraoccipital process; (2) skull width: cranium at temporal fossae; (3) foramen magnum diameter; (4) length of beak; (5) length of quadratojugal; (6) width of quadratojugal, center of bone: (7) coracoid length. (8) atlas, maximum length; (9) atlas, maximum height; (10) atlas, maximum width, (11) axis, maximum length; (12) axis, maximum height; (13) axis, maximum width; (14) cervical 3, maximum length; (15) cervical 3, maximum height; (16) cervical 3, maximum width: (17) total neck length; T7: (18) thorasic vertebrae number 7 (T-7), maximum length; (19) T-7, maximum height; (20) T-7, maximum width; (21) humerus, maximum length; (22) humerus, maximum width at proximal end; (23) humerus, maximum width at distal end; (24) ulna, maximum length; (25) carpometacarpus (CMC), maximum length; (26) CMC, maximum width at proximal end; (27) femur, maximum length; (28) femur, maximum width at proximal end; (29) femur, maximum width at distal end; (30) tibiotarsus (TT), maximum length, including cnemial crest; (31) TT, maximum width at distal end; (32) fibula, maximum length; (33) fibula, maximum width at distal end; (34) tarsometatarsus (TMT), maximum length; (35) TMT diameter at its proximal end; (36) TMT diameter from mid-shaft; (37) TMT, width through the trochlea; (38) digit III, phalanx I (Dig3.1), maximum length at distal end; (39) Dig3.1, maximum height at the proximal end; (40) sacrum, maximum length; (41) sacrum, maxiumum height from haemal ridge of sacrum to top of iliac crest; (42) standing height of bird from the bottom of the feet to the top of its back (SHB); (43) maximum standing height of bird to the top of its head (MSH); (44) mass. All measurements are recorded in millimeters, weight is recorded in kilograms.

Taxon	Specimen	Citation	Skull (TL)
<u>SubfamilyPhorusrhacinae</u>			
Titanis walleri	*composite	see Table 1	
Devencenzia pozzi			
(Onactornis depressus)	*composite	Cabera, 1939	650.0
Phorusrachos inflatus	*BMNH A517	Andrews, 1899	337.0
P. inflatus	*BMNH A516 'type'	Andrews, 1899	337.0
P. longissimus	*composite	Alvarenga, 1999; Alvarenga & Höfling, 2003	
<u>Subfamily Psilopternae</u>			
Procariama simplex	FM P14525	Alvarenga, 1999; Alvarenga & Höfling, 2003	243.0
Psilopterus bachmanni			
(Pelecyornis puerredonensis)	PUM 15904	Sinclair and Farr, 1932	185.0
P. lemoinei (P. tenuirostris)	AMNH 9157	Sinclair and Farr, 1932	200.0
P. lemoinei (P. australis)	AMNH 9257	Sinclair and Farr, 1932; Alvarenga, 1999; Alvarenga & Höfling, 2003	198.0
P. lemoinei (P. australis)	PUM 15109	Sinclair and Farr, 1932	203.0
P. lemoinei (P. australis)	PUM 15402	Sinclair and Farr, 1932; Alvarenga, 1999; Alvarenga & Höfling, 2003	185.5
<u>Subfamily Mesembriornithinae</u>			
Mesembriornis sp.	AMNH 7012 (cast)		376.0
M. milneedwardsi	MMP S155	Alvarenga, 1999; Alvarenga & Höfling, 2003	440.0
M. milneedwardsi	MACN 5944	Kraglievich,1940	340.0
<u>Subfamily Brontornithinae</u>			
Brontornis burmeisteri	*composite	Alvarenga, 1999; Alvarenga & Höfling, 2003	
Physiornis fortis	*composite	Alvarenga, 1999; Alvarenga & Höfling, 2003	
Paraphysiornis brasiliensis	DGM 1418	Alvarenga, 1999; Alvarenga & Höfling, 2003	
<u>Subfamily Patagornithinae</u>			
Patagornis marshi	BMNH A516	Alvarenga, 1999; Alvarenga & Höfling, 2003	337.0
Andalgalornis steulleti	FM P14357	Alvarenga, 1999; Alvarenga & Höfling, 2003	385.0
<u>Family Cariamidae</u>			
Cariama cristata	AMNH 8904		104.0
Cariama cristata	AMNH 1722		120.0
Cariama cristata	AMNH 1392		101.6
Cariama cristata	FMNH 106728		100.0
Cariama cristata	USNM 612030		106.0
Cariama cristata	USNM 555731		105.0
Chunga burmeisteri	AMNH 4250		104.8

Devencenzia = MHMN 1892,MLP 37-III-7-8; **P. longissimus*= AMNH 9146, MLP 131*; *B. burmeisteri* = MLP 89, 91, TMTTroch W is estimated; **P. fortis*= FM P1-3340; MACN A52-185, A52-188

Taxon	Specimen	Skull (W)	Skull FMH	Beak (L)	Q-Jugal (L)	Q-Jugal (W)	Coracoid (L)	Atlas (L)
SubfamilyPhorusrhacinae								
Titanis walleri	*composite				170.0	23.0		
Devencenzia pozzi								
(Onactornis depressus)	*composite	191.0						
Phorusrachos inflatus	*BMNH A517	70.0	17.0					
P. inflatus	*BMNH A516 'type'	114.0	17.0				157.0	
P. longissimus	*composite							
Subfamily Psilopternae								
Procariama simplex	FM P14525	68.0						
Psilopterus bachmanni								
(Pelecyornis puerredonensis)	PUM 15904	26.5	12.0	114.0	65.0	4.5	65.0	7.0
P. lemoinei (P. tenuirostris)	AMNH 9157	43.0	10.5				78.5	
P. lemoinei (P. australis)	AMNH 9257	54.0	12.0	104.5	46.4			
P. lemoinei (P. australis)	PUM 15109			133.0	96.0			
P. lemoinei (P. australis)	PUM 15402	58.0	9.5	127.0	70.0	7.0	74.0	
Subfamily Mesembriornithinae								
Mesembriornis sp.	AMNH 7012 (cast)	117.0		247.0	101.6	20.3		
M. milneedwardsi	MMP S155	143.0						
M. milneedwardsi	MACN 5944							
Subfamily Brontornithinae								
Brontornis burmeisteri	*composite							
Physiornis fortis	*composite							
Paraphysiornis brasiliensis	DGM 1418						245.0	
Subfamily Patagornithinae								
Patagornis marshi	BMNH A516	120.0						
Andalgalornis steulleti	FM P14357	140.0						
Family Cariamidae								
Cariama cristata	AMNH 8904	37.5	6.0	65.0	47.0	1.5	51.5	4.0
Cariama cristata	AMNH 1722	27.8	7.9	70.4	51.4	1.0	57.1	3.9
Cariama cristata	AMNH 1392	23.2	7.9	63.4	45.4	1.0	49.7	2.3
Cariama cristata	FMNH 106728	37.0	7.5	56.5	45.0	1.5	46.5	4.0
Cariama cristata	USNM 612030	26.0	6.8	70.7	52.5	1.7	54.0	4.6
Cariama cristata	USNM 555731	27.0		61.3	42.0	1.8	52.7	3.5
Chunga burmeisteri	AMNH 4250	23.2	9.5	61.5	51.2	1.0	52.5	

Devencenzia = MHMN 1892,MLP 37-III-7-8; **P. longissimus*= AMNH 9146, MLP 131*; *B. burmeisteri* = MLP 89, 91, TMTTroch W is estimated; **P. fortis*= FM P1-3340; MACN A52-185, A52-188

Taxon	**Specimen**	**Atlas (H)**	**Atlas (W)**	**Axis (L)**	**Axis (H)**	**Axis (W)**	**C3 (L)**	**C3 (H)**	**C3 (W)**	**T Neck**
Subfamily Phorusrhacinae										
Titanis walleri	*composite			127.0	107.0	65.0	141.0	109.0	74.0	
Devencenzia pozzi										
(Onactornis depressus)	*composite									
Phorusrachos inflatus	*BMNH A517									
P. inflatus	*BMNH A516 'type'									
P. longissimus	*composite									
Subfamily Psilopternae										
Procariama simplex	FM P14525									
Psilopterus bachmanni										
(Pelecyornis puerredonensis)	PUM 15904	13.5	14.0	19.0			28.0	24.0	23.0	
P. lemoinei (P. tenuirostris)	AMNH 9157			19.9	46.6	38.7				
P. lemoinei (P. australis)	AMNH 9257			29.9	51.3	42.1				
P. lemoinei (P. australis)	PUM 15109									
P. lemoinei (P. australis)	PUM 15402									
Subfamily Mesembriornithinae										
Mesembriornis sp.	AMNH 7012 (cast)			83.8	63.5		63.5	50.8		
M. milneedwardsi	MMP S155									
M. milneedwardsi	MACN 5944	29.0	23.0	49.0	20.0		46.0	62.0		
Subfamily Brontornithinae										
Brontornis burmeisteri	*composite									
Physiornis fortis	*composite									
Paraphysiornis brasiliensis	DGM 1418									
Subfamily Patagornithinae										
Patagornis marshi	BMNH A516									
Andalgalornis steulleti	FM P14357									
Family Cariamidae										
Cariama cristata	AMNH 8904	15.0	9.0	19.0	19.0	14.0	17.0	12.5	15.0	
Cariama cristata	AMNH 1722	9.9	9.0	10.1	13.5	7.8	13.7	13.7	10.4	210.0
Cariama cristata	AMNH 1392	9.2	7.2	8.8	13.9	5.3	14.1	11.3	12.9	194.0
Cariama cristata	FMNH 106728	9.0	8.0	9.0	13.0	12.5	13.5	11.0	14.0	
Cariama cristata	USNM 612030	9.2	8.9	14.7	13.5	14.2	17.5	13.0	13.6	216
Cariama cristata	USNM 555731	8.7	8.5	10.2	11.0	12.1	16.8	12.8	13.9	180
Chunga burmeisteri	AMNH 4250			12.6	9.7	13.7	16.3	10.6	13.6	170

Devencenzia = MHMN 1892,MLP 37-III-7-8; **P. longissimus*= AMNH 9146, MLP 131*; *B. burmeisteri* = MLP 89, 91, TMTTroch W is estimated; **P. fortis*= FM P1-3340; MACN A52-185, A52-188

Taxon	Specimen	T-7 (L)	T-7 (H)	T-7 (W)	Hum (L)	HumProx (W)	HumDis (W)	Ulna (L)	CMC (L)
<u>SubfamilyPhorusrhacinae</u>									
Titanis walleri	*composite	91.0	215.9	76.0					94.0
Devencenzia pozzi									
(Onactornis depressus)	*composite								
Phorusrachos inflatus	*BMNH A517								
P. inflatus	*BMNH A516 'type'								
P. longissimus	*composite								76.0
<u>Subfamily Psilopternae</u>									
Procariama simplex	FM P14525				104.0				
Psilopterus bachmanni									
(Pelecyornis puerredonensis)	PUM 15904								
P. lemoinei (P. tenuirostris)	AMNH 9157	25.1	38.7	15.3					
P. lemoinei (P. australis)	AMNH 9257	25.2	44.9		111.0	26.0	23.0		
P. lemoinei (P. australis)	PUM 15109								
P. lemoinei (P. australis)	PUM 15402				103.0	24.4	19.5	79.5	47.5
<u>Subfamily Mesembriornithinae</u>									
Mesembriornis sp.	AMNH 7012 (cast)	49.3	138.0	47.4					
M. milneedwardsi	MMP S155								
M. milneedwardsi	MACN 5944				18.0	17.0	9.0		80.0
<u>Subfamily Brontornithinae</u>									
Brontornis burmeisteri	*composite								
Physiornis fortis	*composite								
Paraphysiornis brasiliensis	DGM 1418				195.0			83.0	71.5
<u>Subfamily Patagornithinae</u>									
Patagornis marshi	BMNH A516				76.0				76.0
Andalgalornis steulleti	FM P14357								
<u>Family Cariamidae</u>									
Cariama cristata	AMNH 8904				118.0				
Cariama cristata	AMNH 1722	10.6	21.2	8.7	106.6	24.8	9.4		54.5
Cariama cristata	AMNH 1392	17.5	19.7	11.8	99.0	22.9	11.6		41.3
Cariama cristata	FMNH 106728				84.0				
Cariama cristata	USNM 612030	17.9	26.2	16.5	110.2	24.4	9.0		
Cariama cristata	USNM 555731	10.5	24.9	21.2	103.0	27.1	7.9		
Chunga burmeisteri	AMNH 4250	16.9	19.7	20.5	92.7	22.1	6.7		41.5

Devencenzia = MHMN 1892,MLP 37-III-7-8; **P. longissimus*= AMNH 9146, MLP 131*;* **B. burmeisteri* = MLP 89, 91, TMTTroch W is estimated; **P. fortis*= FM P1-3340; MACN A52-185, A52-188

Taxon	Specimen	CMCProx (W)	Fem (L)	FemProx (W)	FemDis (W)	TT(L)	TTDis (W)
Subfamily Phorusrhacinae							
Titanis walleri	*composite	18.0					88.9
Devencenzia pozzi							
(Onactornis depressus)	*composite						
Phorusrachos inflatus	*BMNH A517		227.0		43.0	375.0	43.0
P. inflatus	*BMNH A516 'type'		227.0	59.0	62.0	395.0	43.0
P. longissimus	*composite		310.0	36.2	92.0	500.0	62.0
Subfamily Psilopternae							
Procariama simplex	FM P14525		158.0	35.0	36.0	292.0	28.0
Psilopterus bachmanni							
(Pelecyornis puerredonensis)	PUM 15904		118.0	22.5	23.5	199.0	18.5
P. lemoinei (P. tenuirostris)	AMNH 9157		138.5	29.5	26.0	238.5	21.0
P. lemoinei (P. australis)	AMNH 9257		149.5	32.0	33.0	240.0	22.5
P. lemoinei (P. australis)	PUM 15109						
P. lemoinei (P. australis)	PUM 15402		135.0	31.4	30.0	216.0	23.0
Subfamily Mesembriornithinae							
Mesembriornis sp.	AMNH 7012 (cast)						
M. milneedwardsi	MMP S155		277.0	85.0	87.0	458.0	57.0
M. milneedwardsi	MACN 5944	13.0	252.0	76.0	78.0	421.0	52.0
Subfamily Brontornithinae							
Brontornis burmeisteri	*composite		420.0		155.0	750.0	63.0
Physiornis fortis	*composite			58.0	148.0		
Paraphysiornis brasiliensis	DGM 1418		350.0	47.0	126.0	550.0	54.0
Subfamily Patagornithinae							
Patagornis marshi	BMNH A516		227.0	59.0	62.0	395.0	27.0
Andalgalornis steulleti	FM P14357						
Family Cariamidae							
Cariama cristata	AMNH 8904		91.0	21.0	21.0	222.0	21.0
Cariama cristata	AMNH 1722	18.0	88.4	20.4	12.2	230.0	15.6
Cariama cristata	AMNH 1392	13.2	79.2	16.3	8.7	193.0	14.3
Cariama cristata	FMNH 106728		73.0	18.0	17.5	154.5	14.0
Cariama cristata	USNM 612030		91.4	21.5	20.5	235.0	15.3
Cariama cristata	USNM 555731		85.5	20.7	19.6	216.0	15.9
Chunga burmeisteri	AMNH 4250	93.3	70.9	17.9	17.4	179.0	24.7

Devencenzia = MHMN 1892,MLP 37-III-7-8; **P. longissimus*= AMNH 9146, MLP 131*; *B. burmeisteri* = MLP 89, 91, TMTTroch W is estimated; **P. fortis*= FM P1-3340; MACN A52-185, A52-188

Taxon	Specimen	Fib (L)	FibDis (W)	TMT(L)	TMTProx (D)	TMTDMid	TMTTroch (W)
Subfamily Phorusrhacinae							
Titanis walleri	*composite	91.4					76.0
Devencenzia pozzi							
(Onactornis depressus)	*composite			400.0	110.0		
Phorusrachos inflatus	*BMNH A517						
P. inflatus	*BMNH A516 'type'						
P. longissimus	*composite			385.0	80.0	37.0	
Subfamily Psilopternae							
Procariama simplex	FM P14525			216.0	30.0	14.0	29.1
Psilopterus bachmanni							
(Pelecyornis puerredonensis)	PUM 15904		16.0	145.0	20.0	9.0	20.0
P. lemoinei (P. tenuirostris)	AMNH 9157			179.5	24.5		
P. lemoinei (P. australis)	AMNH 9257			178.5	26.0	12.0	26.5
P. lemoinei (P. australis)	PUM 15109						
P. lemoinei (P. australis)	PUM 15402		20.0	164.0		10.5	23.7
Subfamily Mesembriornithinae							
Mesembriornis sp.	AMNH 7012 (cast)						
M. milneedwardsi	MMP S155			375.0	61.0		25.0
M. milneedwardsi	MACN 5944			360.0		45.0	55.0
Subfamily Brontornithinae							
Brontornis burmeisteri	*composite			400.0	132.0	74.0	*105.0
Physiornis fortis	*composite				105.0	67.0	
Paraphysiornis brasiliensis	DGM 1418			315.0	71.0		
Subfamily Patagornithinae							
Patagornis marshi	BMNH A516			280.0	47.0		
Andalgalornis steulleti	FM P14357						
Family Cariamidae							
Cariama cristata	AMNH 8904	200.0	17.0	201.5		18.5	8.0
Cariama cristata	AMNH 1722	77.9	11.5	195.0	3.1	4.7	15.3
Cariama cristata	AMNH 1392	83.4	10.6	170.0	1.8	3.6	14.0
Cariama cristata	FMNH 106728	134.0	10.0			6.5	13.0
Cariama cristata	USNM 612030	90.0	13.4	207.0		7.7	14.8
Cariama cristata	USNM 555731	83.5	11.7	186.0		9.7	15.4
Chunga burmeisteri	AMNH 4250	na	na	151.0	2.0	4.7	14.2

Devencenzia = MHMN 1892, MLP 37-III-7-8; **P. longissimus*= AMNH 9146, MLP 131; **B. burmeisteri* = MLP 89, 91, TMTTroch W is estimated; **P. fortis*= FM P1-3340; MACN A52-185, A52-188

Taxon	Specimen	Dig3.1 (L)	Dig3.1Prox (H)	Sac (L)	Sac (H)	*SHB	*MSH	*Mass
<u>SubfamilyPhorusrhacinae</u>								
Titanis walleri	*composite	104.0	48.7					
Devencenzia pozzi								
(Onactornis depressus)	*composite	125.0	57.0					
Phorusrachos inflatus	*BMNH A517							
P. inflatus	*BMNH A516 'type'			415.0	103.0			
P. longissimus	*composite					1,300	2,400	130
<u>Subfamily Psilopternae</u>								
Procariama simplex	FM P14525					700		10
Psilopterus bachmanni								
(Pelecyornis puerredonensis)	PUM 15904	28.5	30.0	147.0	38.0	600	700	5
P. lemoinei (P. tenuirostris)	AMNH 9157	36.0			39.8			
P. lemoinei (P. australis)	AMNH 9257			193.0	47.3			
P. lemoinei (P. australis)	PUM 15109							
P. lemoinei (P. australis)	PUM 15402	33.0		152.0		600	800	5
<u>Subfamily Mesembriornithinae</u>								
Mesembriornis sp.	AMNH 7012 (cast)			175.0	70.0			
M. milneedwardsi	MMP S155					1,100	1,700	70
M. milneedwardsi	MACN 5944							
<u>Subfamily Brontornithinae</u>								
Brontornis burmeisteri	*composite					1,750	2,800	350
Physiornis fortis	*composite							
Paraphysiornis brasiliensis	DGM 1418					1,400	2,400	130
<u>Subfamily Patagornithinae</u>								
Patagornis marshi	BMNH A516					900		45
Andalgalornis steulleti	FM P14357					1,000		50
<u>Family Cariamidae</u>								
Cariama cristata	AMNH 8904			96.0				
Cariama cristata	AMNH 1722	50.3	6.8	121.0	23.1			
Cariama cristata	AMNH 1392			115.0	17.7			
Cariama cristata	FMNH 106728			79.0				
Cariama cristata	USNM 612030	23.4	8.3	126.0	26.8			
Cariama cristata	USNM 555731	24.3	7.7	114.5	26.8			
Chunga burmeisteri	AMNH 4250	47.0	7.3	116.0	20.4			

Devencenzia = MHMN 1892,MLP 37-III-7-8; **P. longissimus*= AMNH 9146, MLP 131*; *B. burmeisteri* = MLP 89, 91, TMTTroch W is estimated; **P. fortis*= FM P1-3340; MACN A52-185, A52-188