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SYSTEMATIC REVISION OF THE PHORUSRHACIDAE (AVES: RALLIFORMES)

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ABSTRACT

Fossil remains of birds belonging to the family Phorusrhacidae were studied in several museums of South America, North America and Europe, the main objective being to characterize this family and solve the chaotic state of the nomenclature and classification of these birds. Reconstruction of some species has been done, with the purpose of having an idea about the size, body weight, posture and habit based in their skeletons. The European species, Ameghinornis minor *and* Aenigmavis sapea *are refuted as belonging to this family. Also several forms described from the Tertiary of Argentina are refuted, because they are based on inadequate segments of the skeleton for a good identification, as is the case of the genera* Cunampaia*,* Smiliornis*,* Pseudolarus*,* Lophiornis *and* Riacama*, frequently refered to as belonging to the Phorusrhacidae. The Phorusrhacidae family probably originated in South America, since the end of the Cretaceous, as a result of an endemism formed by the isolation of this landmass. During the end of the Pliocene, with the emersion of the Panama isthmus, the family spread to the North America where at least one species is known* Titanis walleri*, which perhaps represents the last known species of this family, probably becoming extinct in the beginning of the Pleistocene. A systematic revision has been conducted, dealing with the countless problems of nomenclature, and the Phorusrhacidae is now composed of five subfamilies, which are: Brontornithinae, Phorusrhacinae, Patagornithinae, Psilopterinae and Mesembriornithinae in which 13 genera and 17 species are considered. Characters of all taxa are described and a geochronological distribution of all species is presented.*

KEYWORDS: Phorusrhacidae, Ralliformes, Gruiformes, Tertiary, Giant birds.

INTRODUCTION

Historical background – At the end of the 19th century, Ameghino (1887) described a large, toothless jaw from the Miocene of the Province of Santa Cruz, naming it *Phorusrhacos longissimus* and assigning it to a new family of toothless mammals. In 1889, Moreno was the first to refer to the giant birds of the Mio-Pliocene from northern Argentina, proposing the term *Mesembriornis milneedwardsi* for a tibiotarsus, a fibula and a vertebra, associated and incomplete, and *Paleociconia australis* for an incomplete tarsometatarsus. Two years later, Moreno and Mercerat (1891) recognized for the first time that the mandible described by Ameghino was really that of a bird (they wrongly interpreted it as an upper jaw). In the same year Ameghino (1891a, 1891b)

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described other birds similar to *Phorusrhacos*, now recognizing all of them as birds belonging to the group of the Ratitae.

Moreno and Mercerat (1891) described a large amount of fossils of these giant birds from the La Plata Museum, most of which also coming from the Santa Cruz region, as was the case of those described by Ameghino. These authors, however, recognized certain peculiarities of these birds, thus placing them in a new order, the Stereornithes, having some affinities with "los Anseres, de los Herodines y de los Accipitres", dividing this order into four families, which are, the Brontornithidae, Stereornithidae (in which *Phorusrhacos* is included), Dryornithidae and Darwinornithidae.

The material studied and described by Moreno & Mercerat (1891), at least in part, is made up of segments from skeletons which are of significant diagnostic importance; the work being richly illustrated, thus constituting a landmark for Phorusrhacidae systematics.

A certain rivalry began as to the priority of the terms created by Ameghino (1891a and 1891b), and Moreno & Mercerat (1891). Mercerat himself (1897:227) declares that the "Catálogo de los Pájaros Fósiles de la República Argentina" of which he is co-author, and wherein the presentation done by Moreno is dated the 15th of April, 1891, was first published in mid-May, 1891 (several copies then being distributed in this form), the plates only being terminated on the fifth of August, 1891. Further on he also affirms that Ameghino's publication (1891a), dated as of June the 1st, 1891, was in fact published on the 11th of August, 1891, wherein Ameghino also describes *Tolmodus inflatus* as a mammal. The second publication of Ameghino (1891b) was printed in December, 1891.

In various subsequent works by various authors (*e.g.* Andrews, 1896 and 1899; Lambrecht, 1933; Sinclair & Farr, 1932), one observes a strong tendency to give precedence to the terms given by Ameghino over those by Moreno & Mercerat.

Brodkorb (1967), in his revision recognizes the priority of Moreno & Mercerat (1891) over the works of Ameghino of the same year.

In subsequent works, Ameghino (1895 and 1898) describes new fossils of the Phorusrhacidae, creating new terms, often complicating still further the nomenclature of these birds.

Andrews (1896 and 1899), in the detailed study of a certain species, recognizes the close relationship of the Stereornithes with the extant Cariamidae family, discerning a new position, to date still accepted, of the relationship with this family.

The proposed classifications – One of the first attempts at organizing the classification of these birds was done by Dolgopol de Saez (1927), only with those of the Santacrucian (Mid-Miocene), dividing them into two orders: (1) order Stereornithes with only one family, the Phororhacidae, with two genera, *Phororhacos* and *Psilopterus*, and (2) the order Brontornithes, also with one family, the Brontornithidae, with the genera *Brontornis*, *Rostrornis*, *Liornis* and *Paleociconia*. Dolgopol de Saez (*op. cit.*), in her classification, gave importance to the format of the ungual phalanges, these being flattened or raised (without specifying on which digit), to the branching or not of the distal foramen of the tarsometatarsus, and to the existence or not of the supratendinal bridge on the tibiotarsus (this without bothering about the frequent losses by fossilization and accidents in collecting).

Patterson & Kraglievich (1960), on studying the forms from the Pliocene, present an important contention on the synonymy, diversity and classification of these birds, placing them in the order Grues Bonaparte, 1857, suborder Cariamae. Moreover, the above mentioned authors propose dividing the Cariamae into two superfamilies, Cariamoidea Stejneger, 1887 and Phororhacoidea Patterson, 1941, and characterize the Phororhacoidea, setting them apart from the Cariamoidea by the following characteristics: (1) a completely desmognate cranium, (2) a relatively high and long rostrum (premaxillar region), (3) ribs without the uncinate processes, (4) very reduced wing bones and loss of the ability to fly, (5) a narrow pelvis with an incomplete pubis and shorter pre-acetabulum portion than the pos-acetabulum one. Further on, Patterson & Kraglievich (*op. cit.*) divide the Phororhacoidea into the families: Psilopteridae, with the subfamilies Psilopterinae (*Psilopterus*, *Smiliornis* and *Procariama*) and Hermosiornithinae (*Hermosiornis*), and the family Phororhacidae, with the subfamilies Phororhacinae (*Phororhacos*, *Devincenzia* and *Onactornis*) and Tolmodinae (*Tolmodus*, *Andrewsornis* and *Andalgalornis*). The cited authors (1960:11), moreover, considered the separation of the family Brontornithidae, criticizing, however, the separation of this as an order apart, as proposed by Dolgopol de Saez (1927).

Brodkorb (1967) in his recognized "Catalogue of Fossil Birds", considered the family Phorusrhacidae, giving priority to the spelling *Phorusrhacos* (Ameghino, 1887) over *Phororhacos*, this term having been emended by Ameghino (1889) himself, with the subfamilies Brontornithinae (*Physornis* and *Brontornis*), Paleociconiinae (*Andrewsornis*, *Palaeociconia* and

Andalgalornis) and Phorusrhacinae (*Phorusrhacos*, *Onactornis* and *Titanis*), as well as the family Cariamidae with the subfamilies Psilopterinae (*Riacama*, *Smiliornis*, *Pseudolarus*, *Psilopterus*, *Lophiornis* and *Procariama*), Prophororhacinae (*Prophororhacos*) and Cariaminae (with the extant *Cariama* and *Chunga*). The cited author ignored the characteristics by which Patterson & Kraglievich (1960) separated the Cariamoidea from the Phororhacoidea.

In 1981, Mourer-Chauviré described a few bones of birds from the Eocene-Oligocene of France, assigning them to the Ameghinornithinae, a new subfamily of the Phorusrhacidae, the first record of this family for Europe. On complementing her description, the cited author proposes a classification for the suborder Cariamae Fürbringer, 1888, wherein the Phorusrhacidae are divided into six subfamilies, namely, the Brontornithinae (*Physornis* and *Brontornis*), Palaeociconiidae (*Andrewsornis*, *Palaeociconia* and *Andalgalornis*), Phorusrhacinae (*Phorusrhacos*, *Onactornis* and *Titanis*), Psilopterinae (*Psilopterus*, *Lophiornis* and *Procariama*), Prophororhacinae (*Prophororhacos*) and Ameghinornithinae (*Ameghinornis*). Furthermore, Mourer-Chauviré considers the genera *Riacama*, *Smiliornis* and *Pseudolarus* as *insertae sedis*.

Geographical and chronological distribution – The greater part of the fossils of the Phorusrhacidae came from Argentina. This does not mean a more southern distribution in South America, but better conditions for the appearance of fossiliferous outcrops in this region, besides the greater technical development in the Paleontology of Argentina, from which one concludes a greater knowledge of fossils in general in that country within South America. Outside Argentina, the Phorusrhacidae birds are known in Uruguay (Kraglievich, 1932; Tambussi *et al.* 1999), Brazil (Alvarenga, 1982 and 1985a), the Antarctic (Case *et al.* 1987), and in North America (Brodborb, 1963). More recently, reference is made to these birds in Europe (Mourer-Chauviré, 1981; Peters, 1987), and, possibly still further in the Lower Tertiary, in North America (unpublished material, P. Houde and S. Olson, pers. inf.). These occurrences in the Lower Tertiary in North America and Europe make the biogeographical explanation of the origin and dispersion of the family very difficult.

The oldest fossil record of the Phororhacoidea birds is of Alvarenga (1985), represented by a relatively small-sized form, *Paleopsilopterus itaboraiensis* from the Mid-Paleocene (Itaboraian) from southeast Brazil, Rio de Janeiro, the Itaboraí Basin. The most recent occurrence is assigned to the limit between the Upper Pliocene and Lower Pleistocene (Late Blancan), from Florida, U.S.A., with a gigantic form, *Titanis wagleri*, described by Brodkorb (1963).

MATERIAL AND METHODS

The fossilized remains assigned to the Phorusrhacidae and deposited in the collections of the following museums were examined: Museo Argentino de Ciencias Naturales of Buenos Aires, Museo de La Plata, Museu Nacional do Rio de Janeiro, Departamento da Produção Mineral do Rio de Janeiro, Field Museum of Natural History of Chicago, American Museum of Natural History of New York, The Natural History Museum of London, Muséum National d'Histoire Naturelle de Paris, and Forschungsinstitut Senckenberg in Frankfurt.

The material refering to *Titanis walleri* Brodkorb, 1963, deposited in the Museum of the University of Florida, not only the type, but also several other parts assigned to the species, besides the tarsometatarsus of *Devincenzia gallinali* Kraglievich, 1932 (type) from the Museu National de Historia Natural of Montevideo, the skull and the bones of the hind-limbs type of *Hermosiornis rapax* Kraglievich, 1946, deposited in the museum of Mar del Plata, as well as the material whereon the original description of the genus *Ameghinornis* Mourer-Chauviré, 1981 (part deposited in the museum of Paris and part in the museum of Lyon) was based, were studied from casts kindly ceded by the authorities of these Institutions.

The collection of the Phorusrhacidae compiled by the Princeton University and described by Sinclair & Farr (1932), and recently transfered to the collections of the American Museum of Natural History and of the University of Yale, were studied and compared (those specimens transfered to the University of Yale), based only on the cited authors illustrations.

Amongst the fossils assigned to other groups of South American birds of a medium or large size, the fossils of *Argentavis magnificens* Campbell Jr. & Tonni, 1980 (Teratornithidae), *Opisthodactylus patagonicus* Ameghino, 1891, and other rheids, were examined, naturally looking for some mistake in identification. Moreover, the original fossils of *Neocathartes grallator* (Wetmore, 1944) of the family Bathornithidae (Olson, 1985), besides other original fossils and casts related to this family of the Tertiary from the Northern Hemisphere and very close to the Cariamidae (Cracraft, 1968 and 1971), were examined on a favourable occasion in the National Museum of Natural History, Washington, DC (seeing that the fossils of *Neocathartes gallator* are not deposited in this museum). Another family of the Lower Tertiary, especially in Europe, and related to the Cariamidae, are the Idiornithidae, which were studied using casts of *Elephrocnemus phasianus* offered by Cécile Mourer-Chauviré, of the University of Lyon, and from the available illustrations in the publication of this researcher (Mourer-Chauviré, 1983).

The evaluation of the body mass of certain phorusrhacids was done based on the hind-limbs, especially the measurements of the smallest circunference of the diaphysis of the femur and tibiotarsus, which present a direct relationship to the body mass of the bird (Campbell Jr. & Marcus, 1992). In the present work we compared the measurements of some phorusrhacids (diameter of the hind-limb bones) with the same measurements of homologous bones of the ratite birds, or other land birds, with a known mass/size. Several data on bone and body mass measurements of large present-day and fossil birds were obtained in the publications of Amadon (1947) and Wetmore (1967).

Several skeletons of present-day birds were examined as elements for comparison, all from the collection of Museu de Historia Natural of Taubaté (MHNT), amongst which: *Struthio camelus*, male (MHNT-01) and female (MHNT-1991); *Casuarius casuarius*, male (MHNT-03) and female (MHNT-1293); *Rhea americana*, male (MHNT-668); some original bones of the Dinornithidae (MHNT-wt/n.); the cast of a complete skeleton of *Aepyornis maximus* (MHNT-wt/n.); *Cariama cristata*, four specimens, two being males (MHNT-1214 and MHNT-1267), one female (MHNT-1136) and the other of undetermined sex (MHNT-78); *Opisthocomus hoazin* male (MHNT-665).

The anatomical nomenclature used was mainly according to Baumel & Witmer (1993), and in some cases, Howard (1929) and Gilbert *et al.* (1981).

Institutional Abbreviations – AMNH, American Museum of Natural History, New York; BMNH, The Natural History Museum, London; DGM, Divisão de Geologia e Mineralogia do Departamento Nacional da Produção Mineral, Rio de Janeiro; FMNH, Field Museum of Natural History, Chicago; MACN, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires; MGHN, Musée Guimet d'Histoire Naturelle, Lyon; MHNT, Museu de História Natural de Taubaté; MNHN, Muséum National d'Histoire Naturelle, Paris; MLP, Museo de La Plata; MMCN, Museo Municipal de Ciencias Naturales, Lorenzo Scaglia, Mar del Plata; MNHN-M, Museo Nacional de Historia Natural de Montevideo; MNRJ, Museu Nacional do Rio de Janeiro; PUM, Princeton University Museum, New Jersey; SMF, Forschungsinstitut Senckenberg, Frankfurt; TMM, Texas Memorial Museum, Austin; UF, University of Florida, Gainesville.

RESULTS AND DISCUSSION

Size and body mass calculated for the Phorusrhacidae – The Phorusrhacidae are amongst the largest birds that have ever existed on the planet, and *Brontornis burmeisteri* (Fig. 1A) is, without doubt, the largest phorusrhacid and the largest known bird of the American continent. Its size rivals that of the elephant birds (*Aeopyornis maximus*) of the Pleistocene-Holocene of Madagascar, classically considered the largest bird that has existed for all time.

The length of the femur, the tibiotarsus and the tarsometatarsus of *Brontornis burmeisteri* (MLP-88, 89 and 91), are very close to the measurements of the corresponding bones of *Aepyornis maximus*. However, especially the diameters and circuferences of these bones appear to be nearly 10 to 15% smaller in *Brontornis*.

Dinornis giganteus, the largest representative of the 13 species of moas (Dinornithidae), known from New Zeeland (Cracraft, 1976), had a body-mass estimated at weighing 230 to 240 kg (Amadon, 1947), or 278 kg (Campbell Jr. & Marcus, 1992), it most certainly hav-

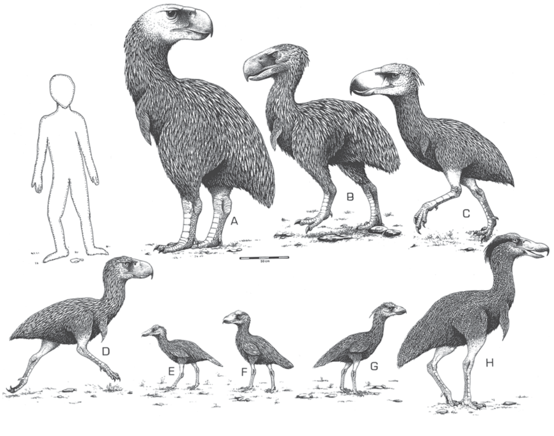

FIGURE 1. Reproduction (by E. Brettas) of some Phorusrhacidae keeping the due proportion as to size. The silhouette of a man 1.75 m high is used as a scale. A - *Brontornis burmeisteri;* B - *Paraphysornis brasiliensis;* C - *Phorusrhacos longissimus;* D - *Andalgalornis steuletti;* E - *Psilopterus bachmanni;* F - *Psilopterus lemoinei;* G - *Procariama simplex;* H - *Mesembriornis milneedwardsi.*

ing been the tallest bird that existed, apparent by the erect posture and long cervical column. According to the measurements presented by Cracraft (1976), the length of the bones of the hind-limbs of *Dinornis giganteus* is very near to the length of the same bones in *Aepyornis maximus*, in the latter, however, the diameter of these bones being much more larger. The body-mass of *Aepyornis maximus*, according to Amadon (1947), weighed 438 kg, and to Campbell Jr. & Marcus (1992), 542 kg.

Brontornis burmeisteri (Fig. 1A) must have been about 175 cm high at the level of the back, and the head, when well-raised, could have reached around 280 cm high. Its body mass must have weighed approximately 15 to 20% less that of a large specimen of *Aepyornis maximus*, or in other words 350 to 400 kg. To be more precise in this calculation has the inconvenience of the small number of known specimens of *Brontornis burmeisteri*, in comparison to the much more numerous fossils of both *Aepyornis* and *Dinornis*.

Another bird which was also one of the biggest (in mass) that has ever existed was *Dromornis stirtoni*, member of an extinct family (Dromornithidae), of giant, cursorial carnivorous birds of the Middle and Upper Tertiary of Australia, which stood nearly as or even higher than *Aepyornis maximus* (Wroe, 1998). Together with *Brontornis burmeisteri*, these are the largest birds that have ever existed.

Paraphysornis brasiliensis, of which the skeleton of the only known specimen having been re-constructed, was calculated at having been around 140 cm high at the back. The head, when well-stretched, reaching 240 cm high. The femurs and tibiotarsi of this bird, when compared to the same bones of a large-sized male specimen of an ostrich (*Struthio camelus*) (MHNT-1), with a body-mass, when alive, of 130 kg, presented much larger diameters and circumferences, which lead to estimating the weight of *Paraphysornis brasiliensis* as having been around 180 kg.

In *Phorusrhacos longissimus* (Fig. 1C), the diameter of the hind-limb bones was similar to that of the same limbs of a large male ostrich, and so could have had an estimated mass of 130 kg. It was of the same height or maybe even a little higher than *Paraphysornis brasiliensis*, with a more slender build and possessed notably longer tarsometatarsi.

Patagornis marshi and *Andalgalornis steulleti* (Fig. 1D), were very near as to size and body-mass, the latter being slightly bigger. The diameter of the leg bones of both was around 15% larger than an adult male of the present-day rhea, *Rhea americana*, the height of the back being similar, about 90 to 100 cm, but weighing about 45 to 50 kg, seeing that an adult male rhea weighs around 35 kg. The difference in build between a rhea and these phorusrhacids lies in the head being much bigger and heavier in the latter.

The smallest phorusrhacids are to be found in the subfamily Psilopterinae. *Psilopterus bachmanni* (Fig. 1E), which, when compared with a present-day cariama (*Cariama cristata*), showed the length of the femur to having been around 40% longer and the tarsometatarsus 40% shorter, the tibiotarsi being approximately of the same length. The diameters and circumferences of these bones are, however, much bigger in *Psilopterus*.

Compared with *Cariama cristata*, *Psilopterus bachmani* was of approximately the same height, which was about 60 cm up to the back and 80 cm to the top of the head when well-raised, with a body-mass weighing nearly 5 kg. *Psilopterus lemoinei* (Fig. 1F), a little bigger, must have had a bulk weighing close to 7 kg. In the same subfamily Psilopterinae, *Procariama simplex* (Fig. 1G) could have reached nearly 70 cm at the height of the back and have a body-mass weighing near to 10 kg.

Amongst the Mesembriornithinae, *Mesembriornis incertus* was built very close to *Patagornis marshi* and *Andalgalornis steulleti*, whereas *Mesembriornis milneedwardsi* (Fig. 1H) was at least 20% bigger and heavier, its bulk reaching almost 70 kg, and the height at the back calculated at 110 or 120 cm, and at the top of the head when well-raised, near to 170 cm.

When attempting to calculate the size and bulk of the birds assigned to the Phorusrhacidae, from Europe, *Ameghinornis minor* Mourer-Chauviré, 1981, based only on the humerus and coracoid, must have had a build similar to that of *Psilopterus lemoinei* (a comparison that could be in error through a lack of knowledge regarding the skeleton of the hind-limbs). *Aenigmavis sapea* Peters, 1987, possessed hind-limb and humerus bones of a size comparable to those of a guan (*Penelope obscura*), with, however, a much shorter radius and ulna. In this case its body-mass would have been less than 1 kg.

Intra-specific variations – Cracraft (1976) when analizing the skeletons of a large number of kiwis (*Apteryx australis*) and several species of moas (Dinornithidae), concluded that there is a large degree of intra-specific variation as to the size of the different bones of these birds. Amongst present-day ratites, sexual dimorphism in size is frequent. In *Cariama cristata*, when observing four skeletons of adult specimens, a difference of 15% in the length of the tarsometatarsus, between the largest and smallest specimens, was noted, with an indication that the largest sizes were from males.

In the case of certain phorusrhacids, such as *Brontornis burmeinsteri*, a comparison of the tarsometatarsi of two specimens, FM-P13259 and MLP-91 (lectotype) (Figs. 2C and 2D), both coming from the same geographical region and geological formation, shows them as not to present any anatomical differences, apart from size, wherein the first is around 33% smaller than the second. The idea is that they are examples of intra-specific variation, possibly sexual dimorphism. There is the possibility that they represent two species and a better fossil documentation, however, is necessary to arrive at such a conclusion. It would not be easy to imagine two large predators, extremely similar, disputing the same ecological niche. In birds of prey, dimorphism of such an extent can be observed, as occurs with *Harpia harpyja* in which adults weigh from 4 kg (generally males) to 9 kg (generally females) (Thiollay, 1994).

Another interesting example occurs with the forms of the genus Psilopterus from the Mid-Miocene (Santa Cruz Formation) of Patagonia. Several species were described based on slight variations in size (Sinclair & Farr, 1932), besides differences as to the height of the upper maxilla and the nasal region. The existance of three species, as these authors believe, is possible, as it would also be possible to accept a single polimorphic species, where the differences represent differences of age and sex, as at present occurs with birds of several groups such as hornbills (Bucerotidae), curassows (Cracidae) and, in a similar way also, the cassowaries (Casuariidae). Another hypothesis is that these shapes might represent temporal differences (even at a specific level), or, in other words, be distributed at different stratigraphic levels.

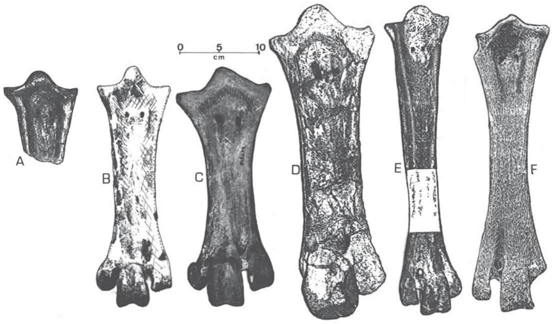

FIGURE 2. Dorsal view of the tarsometatarsi of the Brontornithinae (A-D) and Phorusrhacinae (E-F): A - *Physornis fortis* (MACN-A-52-185); B - *Paraphysornis brasiliensis* (DGM-1418-R); C - *Brontornis burmeisteri* (FM-P13259); D - *Brontornis burmeisteri* (lectotype MLP-91); E - *Phorusrhacos longissimus* (MLP-76.V.10.11, type of *Liornis minor* Dolgopol de Saez, 1927); F - *Devincenzia pozzi* (MNHN-M-189, type of *Devincenzia gallinali* Kraglievich, 1932). A-D left side; E-F right side.

Shape and proportions of the skeleton and their implications on habits – The Phorusrhacidae birds were unable to fly. This conclusion is easily arrived at by examining the proportional size of the wings (Fig. 3) and the body mass, compared with those of present-day forms.

The reduction in wing-size is more pronounced in the larger-sized species. In the diagram depicted in Fig. 3, it can be seen that *Paraphysornis*, when compared with certain smaller-sized forms, presents a greater reduction of the ulna (Table 1), this reduction appearing to be the main indicator of the loss of the ability to fly. Another example is the comparison of *Psilopterus* (the smallest Phorusrhacidae) with *Cariama cristata*, wherein *Psilopterus* possessed a much larger body-mass, besides an outstanding reduction of the ulna amongst the other wing bones. Moreover, a comparison of the hind-limb bones shows that the shortening of the femur and the relative lengthening of the tarsometatarsus of *Cariama* in relation to *Psilopterus*, associated to a smaller bulk appears to be a greater adaptation to running in *Cariama*. Thus *Psilopterus*, contrary to the conclusions of Tonni & Tambussi (1988), was unable to fly and was slower than *Cariama cristata* at running, the latter, on the other hand, achieving long gliding flights of up to some hundreds of meters.

The aptitude for speed in birds when running is proportional to the length of the tarsometatarsus in relation to the tibiotarsus. Thus, in the subfamily Brontornithinae, the largest and heaviest of the Phorusrhacidae, the length of the tarsometatarsus is between 50 to 60% of that of the tibiotarsus, indicating they were slow moving, walking birds, while in *Patagornis* this proportion is near to 70%, implying much greater agility and speed. Based on this fact, one can deduce that the representatives of the subfamily Brontornithinae must have had necrophagous habits, eating mainly dead or dying animals. This idea can be supported by the information that, in the Tremembé Formation (Taubaté Basin), a lacustrine formation, where the excellent specimen of *Paraphysornis brasiliensis* came from, periods of drought, with high fish motality, occurred. In the same place, the occurrence of a vulture (Vulturidae) fossil (Alvarenga, 1985b), was also recorded. It is possible that this Phorusrhacidae was hereabouts looking for fishes and other dead animals when, maybe, it sank into the marshy land and succumbed amongst a plentiful supply of fishes and other dead animals.

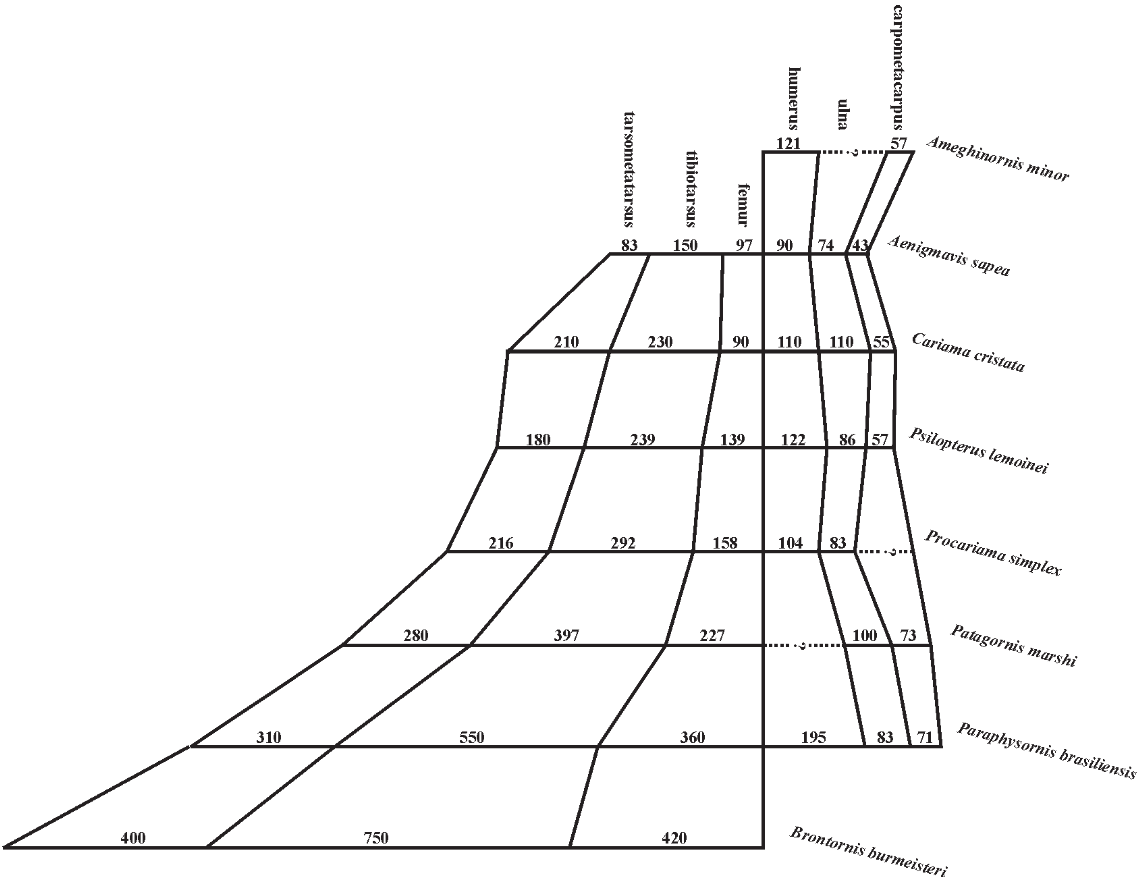

FIGURE 3. Comparative diagram of the length of the bones of the appendicular skeleton of *Ameghinornis minor*, *Aenigmavis sapea* and *Cariama cristata*, in a comparison with some Phorusrhacidae. Numbers represent approximate measurements in mm.

TABLE 1. Measurements (total lenght) of the scapular girdle and the forelimbs of some Phorusrhacidae (mm). Numbers in brackets are estimates on incomplete bones.

	Paraphysornis brasiliensis	*Titanis walleri*	*Patagornis Marshi*	*Psilopterus Bachmanni*	*Psilopterus lemoinei*			*Procariama simplex*	*Mesembriornis milneedwardsis*
Specimen	DGM-1418	UF-30003	BMNH-A524	PUM-15904	PUM-15402	AMNH-9157	BMNH-A559	FM-P14525	(measurements from Kraglievich, 1946)
Scapula	215.0	–	–	–	88.0	95.5	–	87.0	–
Coracoid	245.0	–	150.0	65.5	(74.0)	78.5	–	65.0	–
Humerus	195.0	–	–	–	103.0	–	122.5	104.0	180 a 200
Ulna	83.0	–	110.0	–	79.5	–	86.2	83.0	100 a 114
Radius	–	–	–	–	74.0	–	80.0	–	89 a 109
Carpometacarpus	71.5	9.7	76.0	–	47.5	–	56.8	–	–

Another aspect of the skeleton of the Phorusrhacidae is the expressive narrowing of the pelvis, upper maxilla and thorax. From these characteristics we can deduce that these birds often hunted in regions with high vegetation, permitting their greater agility between verticle obstacles. A very narrow upper maxilla would furthermore facilitate the apprehension of small animals hidden amongst trunks or stones.

Another inference derived from the skeleton is from the lacrimal bone (= prefrontal), this forming a large caudal expansion (the supra-orbital process), similar to that which nowadays occurs in hawks (Falconiformes), which certainly affords protection for the eyes against sunrays, thus favoring keeness of sight. From this one supposes that these birds inhabited more or less open sunlit regions and not shaded forests, and certainly hunted by sight.

Characterization of the Phorusrhacidae family – Within the order Ralliformes, the family Phorusrhacidae is characterized by: (1) a large or even gigantic build; (2) the shape of the body, especially the premaxila, the pelvis and the thorax being laterally flattened, giving the bird a slim appearance when viewed from the front; (3) a bulky premaxilla, especially high, with a pointed, strong apex, in the form of a hook; (4) a jaw with a very solid symphysis; (5) ample and pervious nostrils (there is no septum); (6) a desmognate palate; (7) the presence of well-developed basipterigoid processes; (8) pterigoids with an evident articulation for the basipterigoid process in the mid-portion; (9) the absence of uncinate processes on the ribs; (10) the pubis atrophied in the cranial half, the same as occurs in hawks (Accipitridae); (11) the reduction of the wings and loss of the ability to fly; (12) a coracoid with the extreme reduction of the procoracoidal and acrocoracoidal processes, possessing an ample scapular facet, in the form of a groove in the apex (Fig. 4B); (13) a humerus with the internal tuberosity bulging proximally, the proximal half of the diaphysis being strongly bent and the processus flexorius distally prominent (Fig. 5); (14) a tarsometatarsus with a triangular-shaped hypotarsus when viewed from below and without tendon grooves; (15) a strongly curved ungual phalanx.

The Cariamidae family, with two extant genera in South America (*Cariama* and *Chunga*), and two other very close extinct families that lived in the North American (Bathornithidae) and European (Idiornithidae) MiddleTertiary, are those that present a greater phylogenetic proximity with the Phorusrhacidae (Andrews, 1896; Brodkorb, 1967; Cracraft, 1968 and 1971; Mourer-Chauviré, 1983; Livezey, 1998). They differ, however, through their representatives being of smaller build, the premaxilla not being bulky, the presence of a schizognate palate, the frail mandibular symphysis, the absence of the basipterigoid processes, the relatively wide pelvis, the presence of the uncinate processes on the ribs, the internal tuberosity of the humerus, and a small or non-prominent *processus flexorius* (Fig. 5).

In the present work, the Ameghinornithinae Mourer-Chauviré, 1981, from Europe, of a size comparable to the smallest Phorusrhacidae, and known only through the coracoid, humerus and carpometacarpus, are excluded from the family Phorusrhacidae. In spite of the reduction of the acrocoracoidal process (Fig. 4A), the coracoid of *Ameghinornis* presents an excavated scapular facet, this being egg-shaped and extending towards the procoracoidal process, in a shape very typical of the Idiornithidae, thus reminding one especially

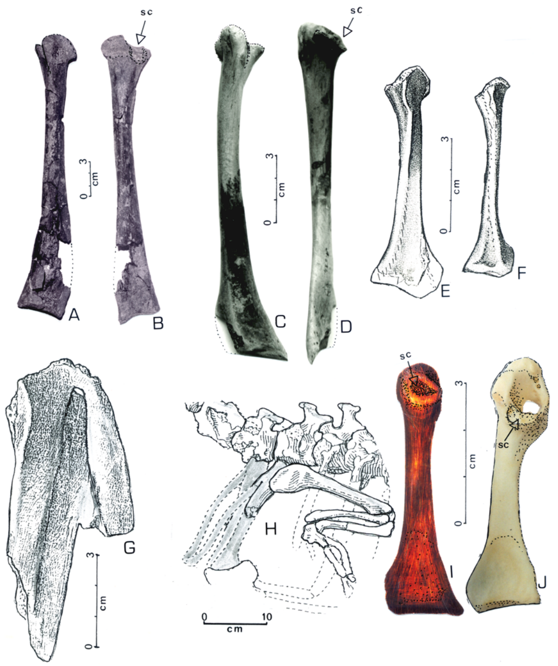

FIGURE 4. The coracoids of some Phorusrhacidae in comparison with *Ameghinornis minor* and *Cariama cristata.* The left coracoid of *Paraphysornis brasiliensis* (DGM-1418-R) viewed ventrally (A) and in lateral view (B); the right coracoid of *Patagornis marshi* (BMNH-A-524) in ventral view (C) and in lateral view (D); the left coracoid in ventral view of *Psilopterus lemoinei* (E) (PUM-15402, redrawn from Sinclair & Farr, 1932), and *P. bachmanni* (F) (PUM-15904, also redrawn from Sinclair & Farr, 1932); the omal extremity of the right coracoid of *Mesembriornis milneedwardsi*, fused with a part of the clavicle, viewed dorsally (G) (redrawn from Rovereto, 1914); a reproduction of the fused clavicle and coracoid in *Mesembriornis milneedwardsi* (H) (redrawn from Kraglievich, 1932); the left coracoid, viewed dorsally, of Ameghinornis minor (cast, MGHN-PQ1200) (I) and *Cariama cristata* (MHNT-1136) (J); sc = *scapular cotyle.*

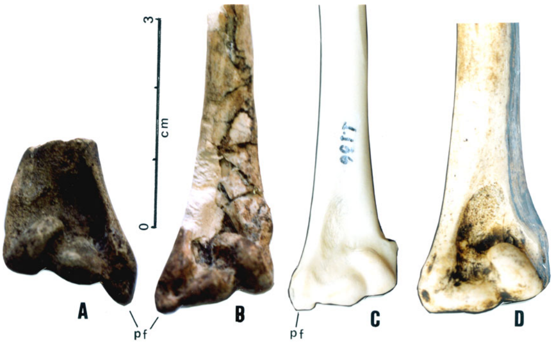

FIGURE 5. Distal end of the humerus in palmar view of: A - *Psilopterus lemoinei* (FM-cast PA-4), B - *Procariama simplex* (FM-P14525), C - *Cariama cristata* (MHNT-1136) and D - *Ameghinornis minor* (cast of holotype); pf = *processus flexorius.*

of *Idiornis minor* or *I. itardiensis* (cf. Mourer-Chauviré, 1983: pls. 3 and 4). The humerus of *Ameghinornis* is similar to that of the Phorusrhacidae as to the prominent ventral tubercle (but of a shape distinct from that of the Phorusrhacidae), and differing in other characteristics such as the distal part of the deltoid crest being much widened and outstanding and the *processus flexorius* not being prominent distally (Fig. 5D). The carpometacarpus assigned to *Ameghinornis* reminds one more of that of the Idiornithidae and Cariamidae than that of the Phorusrhacidae, which in turn present a very variable morphology (Fig. 6). Maybe its shape could be interpreted as being primitive for it further resembles that of the Opisthocomidae and Bathornithidae (Olson, 1985:144). The known bones of *Ameghinornis* compared with *Psilopterus* (the smallest Phorusrhacidae) and *Cariama*, are approximately of the same length. The ulna and radius themselves, much more reduced in *Psilopterus* than in *Cariama*, appear to be one more characteristic element of the Phorusrhacidae family, by the greater reduction than that of the other wing bones. Unfortunately, the radius and ulna of *Ameghinornis* are unknown for comparison.

Aenigmavis sapea Peters, 1987, another European form described as "Phorusrhacidae" subfamily *incertae sedis*, and of a much smaller build, is also excluded from the Phorusrhacidae family. Amongst the few osteological characteristics shown by *Aenigmavis*, the hypotarsus formed by two long and parallel crests differs substancially from that of the Phorusrhacidae. The proportions of the *Aenigmavis* skeleton are different from those observed in the Phorusrhacidae (Fig. 3): the femur is much longer than the tarsometatarsus, which is only observed in the Phorusrhacidae of the subfamily Brontornithinae (certainly the most derived phorusrhacids). Such a proportion is also observed as common in birds with arboreal habits (*e.g.* Columbiformes, Psittaciformes, Coraciiformes), as well as in the Galliformes of the Cracidae family, with arboreal habits, such as *Pipile* and *Penelope*, thus excluding running habits for *Aenigmavis*, which must, therefore, remain in *insertae sedis*. The genera *Cunampaia* Rusconi, 1946; *Smilornis* Ameghino, 1891; *Pseudolarus* Ameghino, 1891; *Lophiornis* Ameghino, 1891; and *Riacama* Ameghino, 1899, are also excluded, based on there being few bone segments of very debatable diagnostic value.

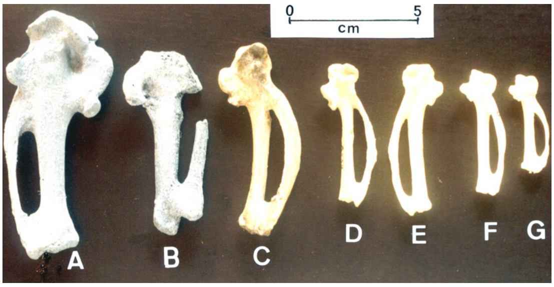

FIGURE 6. Lateral view of the carpometacarpus (A and E right side; B, C, D, F and G left side). A - *Titanis walleri* (cast, UF-30003); B - *Paraphysornis brasiliensis* (DGM-1418-R); C - *Patagornis marshi* (cast, BMNH-A-516); D - *Psilopterus australis* (cast, BMNH-A-559); E - *Ameghinornis minor* (cast, MHNP-QU15750); F - *Cariama cristata* (MHNT-1136); G - *Opisthocomus hoazin* (MHNT-665).

Some fossils, still undescribed, coming from the North American Eocene (the Green River Formation), possibly belonging to the Phorusrhacidae (P. Houde, pers. inf.) are also exluded from this family. The examined fossils only consist of wing bones and part of the scapular girdle, of a relatively small-built bird, wherein only the humerus shows some characteristics of the Phorusrhacidae, such as an extremely accentuated bend of the diaphysis, an extremely protruding ventral tubercle, besides a distally prominent *processus flexorius*. In this humerus, the ventral tubercle is much more developed than in any of the known Phorusrhacidae and is projected more in the anconal than proximal direction. The examined carpometacarpus presents some characteristics common to the Psilopterinae, Cariamidae, Bathornithidae and Opisthocomidae, or, in other words, presents several plesiomorph characteristics, which are of no assistance in an attempt at classification. The observed similarities appear to be more an adaptive convergence due to the loss of the ability to fly, it being extremely premature to classify such birds amongst the Phorusrhacidae.

The Phorusrhacidae thus consists of five subfamilies: the Brontornithinae (Moreno & Mercerat, 1891), Phorusrhacinae (Ameghino, 1889), Patagornithinae (Mercerat, 1897), Psilopterinae (Dolgopol de Saez, 1927) and Mesembriornithinae (Kraglievich, 1932). All the known forms are from South America, except for *Titanis walleri*, a Phorusrhacinae from North America, which testifies to these birds having emigrated to North America after the elevation of the isthmus of Panama from the Pliocene on.

SYSTEMATICS

The classification herein presented is especially based on the morphology and proportions of the mandibular symphysis and of the tarsometatarsus, for two main reasons: first because one is dealing with resistant bony segments and most often conserved in almost all the species of this family, and also due to the fact that such structures should reflect specialization in food habits as well as differences in the strength and ability of the diverse species.

Order Ralliformes Reichenbach, 1852
Suborder Cariamae Fürbringer, 1888
Family Phorusrhacidae Ameghino, 1889

Phororhacosidae Ameghino, 1889; 1891.
Phororhacidae Lydekker, 1893; Ameghino, 1895.
Phorusrhacidae Brodkorb, 1963,1967; Mourer-Chauviré, 1981.
Brontornithidae Moreno & Mercerat, 1891.
Devincenziidae Kraglievich, 1932.
Stereornithidae Moreno & Mercerat, 1891.
Darwinornithidae Moreno & Mercerat, 1891.
Patagornithidae Mercerat, 1897.
Mesembriorniidae Kraglievich, 1932.

Remarks – Ameghino (1887) described *Phorusrhacos longissimus* based on an incomplete mandible, afterwards (1889) emending the original generic term to *Phororhacos*, which was widely accepted (Chiappe & Soria, 1990), proposing for this the criation of the family Phororhacosidae. As Brodkorb (1963) warned, the original spelling (*Phorusrhacos*) has a guaranteed priority. Moreover, Brodkorb emended the name of the family, already previously altered by Lydekker (1893), to the Phorusrhacidae, to which almost all the authors since 1963 have acted in accordance. The terms *Phorusrhacos* and Phorusrhacidae were definitely made official by the International Commission on Zoological Nomenclature, Opinion 1687: Bulletin of Zoological Nomenclature, 49(2), June, 1992.

Subfamily Brontornithinae Moreno & Mercerat, 1891

Brontornithidae Moreno & Mercerat, 1891.
Brontornithinae; Brodkorb, 1967; Mourer-Chauviré, 1981.

Diagnosis Revised – Phorusrhacidae of a gigantic build, reaching over two meters high, heavy and robust. The mandibular symphysis is proportionally shorter, wider and higher than in the other Phorusrhacidae (Fig. 7). The tarsometatarsus is proportionally short, widened and flattened dorso-plantarwise (Fig. 2 and Fig. 8), its length reaching only 50% to 60% of that of the tibiotarsus (Fig. 3). In *Brontornis*, the dorsomedial extremity of the articular surface of the mesotrochlea of the tarsometatarsus is proximally projected, when viewed in profile (Fig. 8C), whilst in *Paraphysornis* this portion is more medially expanded. Even though the trochlae of *Physornis* are as yet unknown, one can assume that the dorsomedial portion of the mesotrochlea in the Brontornithinae may be always expanded and could constitute one more characteristic of the subfamily.

Included Genera – *Brontornis* Moreno & Mercerat, 1891, *Physornis* Ameghino, 1895, and *Paraphysornis* Alvarenga, 1993.

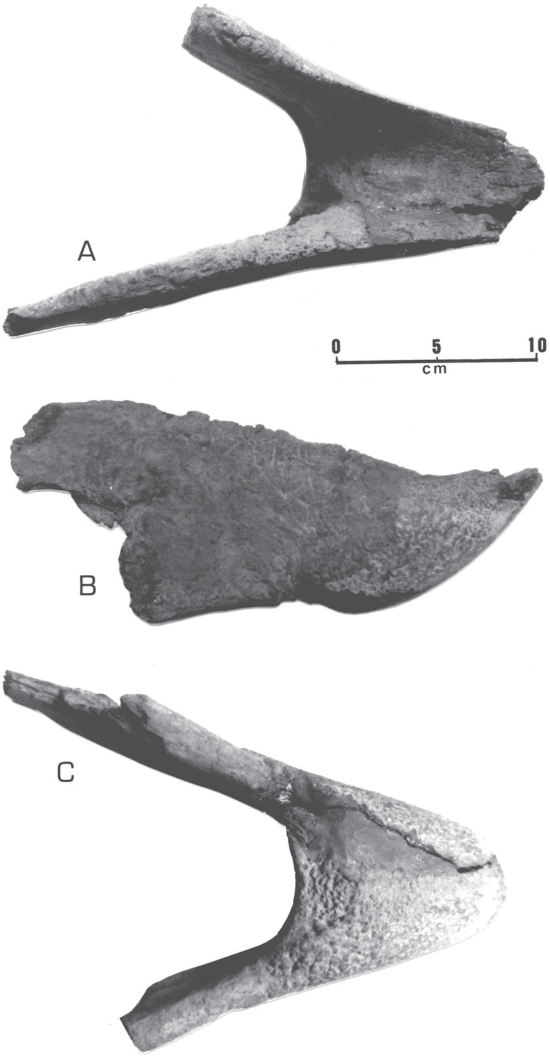

FIGURE 7. An incomplete jaw of *Brontornis burmeisteri* (MNHN-1902-6) in: A - dorsal view, B - lateral view and C - ventral view.

FIGURE 8. *Brontornis burmeisteri* (FM-P13259), left complete tarsometatarsus (l) and distal end of the right one (r), in dorsal view (A), plantar view (B), and lateral view (C). This specimen, around 25% smaller than the lectotype (MLP-91), represents an important variation in size in these birds. The arrow in "C" indicates the dorsoproximal spreading of the edge of the articular surface of the middle trochlea, a characteristic of the Brontornithinae.

Remarks – Case *et al.* (1987) described the fragment of a beak coming from the La Meseta Formation (Upper Eocene ?) from Seymour Island (Antarctic) as a possible portion of the premaxilar region of a Phorusrhacidae. Just by examining the published illustrations, the appearance of the pieces surmises the mandibular symphysis of a Brontornithinae, close to *Brontornis*. More material and information are required in order to arrive at a precise definition of this possible, as yet unknown, Brontornithinae.

Genus *Brontornis* Moreno & Mercerat, 1891

Brontornis Moreno & Mercerat, 1891:20,37; Brodkorb, 1967.
Rostrornis Moreno & Mercerat, 1891:20,40; Brodkorb, 1967 (syn. of *Brontornis*).

Type Species – *Brontornis burmeisteri* Moreno & Mercerat, 1891.

Included Species – Only the type species.

Distribution – Lower to Mid-Miocene in Argentina.

Diagnosis Revised – Certainly the biggest of the Phorusrhacidae, it is the largest bird known from the Americas and one of the largest that has ever existed. The mandibule possesses a proportionally shorter, wider and higher symphysis than *Physornis* and *Paraphysornis* (*e.g.* Alvarenga, 1993: Fig. 1) The internal condyle of the tibiotarsus is medially diverted. The cotyls of the tarsometatarsus are rounded off and the hypotarsus forming a prominent medial crest, having a slightly pronounced lateral edge (*e.g.* Alvarenga, 1993: Fig. 2). As regards the remaining Brontornithinae, the hypotarsus of *Brontornis* is placed on a more distal level in relation to the articular cotyles (Fig. 9).

Remarks – *Liornis* Ameghino,1895, with the species *L. floweri* Ameghino, 1895, and *L. minor* Dolgopol de Saez, 1927, are evident synonyms of *Phorusrhacos* Ameghino, 1887; *Devincenzia* Kraglievich 1932, is surely a robust form of Phorusrhacinae. These two genera were dealt with as synonyms of *Brontornis* by Brodkorb (1967).

Brontornis burmeisteri Moreno & Mercerat, 1891

Brontornis burmeisteri Moreno & Mercerat, 1891:37; Brodkorb, 1967.
Rostrornis floweri Moreno & Mercerat, 1891:40; Brodkorb 1967 (syn. of *B. burmeisteri*).
Brontornis platyonyx Ameghino, 1895; Brodkorb 1967 (syn. of *B. burmeisteri*).

Lectotypes – The left femur, tibiotarsus, fibula and tarsometatarsus (MLP-88-91), certainly belonging to the same individual, designated by Brodkorb (1967).

Hypodigm – lectotypes; portion of the mandible including the symphysis and part of the right branch (MHNP-1902-6, Fig. 7); two large fragments of the

FIGURE 9. The hypotarsal region of *Brontornis burmeisteri* (specimen FM-P13259) is situated on a more distal level than the articular cotylae, whereas in *Physornis* and *Paraphysornis* the proximal portion of the hypotarsus is on approximately the same level.

mandibular symphysis (MLP-94-95), mistakenly attributed to the premaxillas by Moreno & Mercerat (1891); quadrate, several complete and incomplete thoracic and caudal vertebras, phalanges and fragments of the hindlimbs (MLP-92-93 and 96-117, Fig. 10B); the complete left and the distal end of the right tarsometatarsus (FM-P13259, Fig. 10A); a distal extremity of the right tarsometatarsus (BMNH-A578); distal extremity of the left tarsometatarsus (BMNH-A580); 10 podal and ungual phalanges, the majority belonging to the left foot, apparently from the same specimen (BMNH-A549, Fig. 11); distal end of the left femur (FM-P15309).

Horizon and Locality – Lower and Middle Miocene (Santacrucian) of Argentina, Province of Santa Cruz: Lago Argentina, Monte Leon, Monte Observación, Kariaken, La Cueva, Rio Gallegos.

Measurements – Table 2.

Illustrations – Moreno & Mercerat (1891).

Remarks – The trochleae of the right tarsometatarsus of specimen MLP-112 (Fig. 10B), which Moreno & Mercerat (1891) conceived and assigned to *Rostrornis floweri*, is a mistaken assemblage, wherein the internal trochlea is, in fact, an external left trochlea. Such an error in assemblage also served Dolgopol de Saez (1927) to characterize the genus *Rostrornis*. An appreciable difference in the size of the tarsometatarsus of specimens FM-P13259 and MLP-91 (lectotype) (Fig. 2C and 2D), shows the second to be around 33% larger than the first, which possibly testifies to a sexual dimorphism, seeing that by the characteristics, both are adults. Two distal fragments of tarsometatarsus from the museum in London (BMNH-A578 and A580) are in accordance with this difference in size (Table 2).

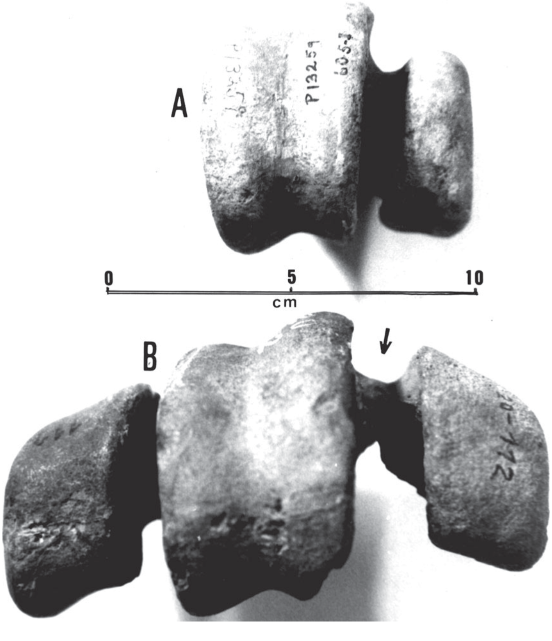

FIGURE 10. *Brontornis burmeisteri:* distal view of the right tarsometatarsus. A - cast of specimen FM-P13259, lacking the external trochlea; B - specimen MLP-112. Note the error in assembling (B) the "internal" trochlea (arrow), which, in fact, is the left external trochlea. This mistake, which was initially made by Moreno & Mercerat (1891), was also passed on by Dolgopol de Saez (1927), serving as a notable difference for the characterization of the genus *Rostrornis*.

FIGURE 11. Podal phalanges (BMNH-A549), type of *Brontornis platyonyx* Ameghino, 1895. The measurements and morphology are concordant with those of *B. burmeisteri.*

Ameghino (1895) described *Brontornis platyonyx*, basing it on the much smaller build than *B. burmeisteri*. His measurements are, however, compatible with the abovementioned variation for the species (Fig. 11).

Genus *Physornis* Ameghino, 1895

Physornis Ameghino, 1895:576; Brodkorb, 1967.
Aucornis Ameghino, 1898:9; Brodkorb, 1967 (syn. of *Physornis*).

Type Species – *Physornis fortis* Ameghino, 1895.

Included Species – Only the type species.

Distribution – Middle and Upper Oligocene of Argentina.

Diagnosis Revised – Of a gigantic size, rivaling with *Brontornis*. A very short and wide mandibular symphy-

TABLE 2. Measurements of *Brontornis burmeisteri* (cm). Numbers in brackets are estimates on incomplete bones.

Mandible	MLP-94	MHNP-1902-6		
Length of the symphysis on the dorsal surface	(14.4)	(14.7)		
Maximum width at the base of the symphysis	(9.4)	10.1		
Height at the base of the symphysis	(7.5)	8.4		
Femur	MLP-88	FM-P15309		
Total length	(42.0)	–		
Width in the middle of the diaphysis	7.5	–		
Dorsoventral diameter in the middle of the diaphysis	5.8	–		
Maximum distal width	(15.5)	(15.5)		
Dorsoventral diameter of the internal condyle	–	11.0		
Dorsoventral diameter of the lateral condyle	–	11.7		
Tibiotarsus	MLP-89			
Total length	75.0			
Width in the middle of the diaphysis	6.3			
Tarsometatarsus	MLP-91	FM-P13259	BMNH-A578	BMNH-A580
Total length	40.0	30.2	–	–
Maximum proximal width	13.2	11.5	–	–
Width in the middle of the diaphysis	7.4	5.8	–	–
Width at the distal foramen level	9.7	8.0	9.9	8.1
Width of the trochlea at the distal end:				
internal	–	2,5	–	–
middle	5.5	4.4	5.5	4.8
lateral	3.7	3.3	3.7	–

sis, characteristically with an almost flat ventral surface in the mid-portion (Fig. 12 and *e.g.* Alvarenga, 1993: Fig. 1). The lateral cotyl of the tarsometatarsus is almost quadrangular, when viewed proximally (Fig. 13A). The lateral edge of the hipotarsus, when viewed from the rear, forms a prominent crest which distiguishes it well from *Brontornis* and *Paraphysornis* (Fig. 13 and *e.g.* Alvarenga, 1993: Fig. 2).

Remarks – The genus *Physornis* and its type species *P. fortis*, were described by Ameghino in 1895, based on a fragment of the mandible comprehending part of the symphysis and the right branch, this description, unfortunately, not being accompanied by an illustration.

Patterson (1941:52) examined the type of *Physornis fortis*, nowadays deposited in the museum of London (BMNH-A583), arriving at the conclusion that this is a bony fragment without any morphological characteristic, possibly being the iliac crest of a mammal, thus proposing the rejection of the terms, both for the genus as well as the species, as being indeterminate. We had also the opportunity of examining the aforementioned type material (Fig. 14), arriving at the

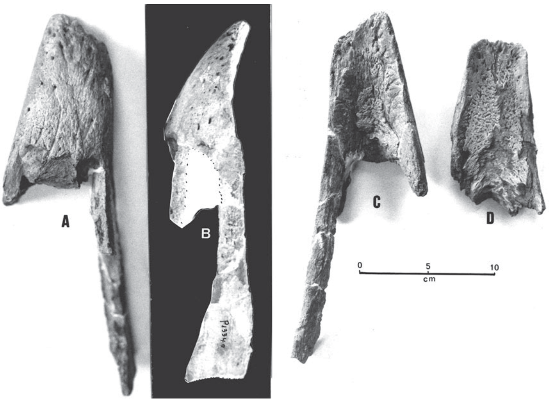

FIGURE 12. *Physornis fortis;* symphysis with a part of the left mandibular branch (FM-P13340) in views: A - ventral, B - left lateral, C - dorsal, D - mandibular symphysis (FM-P13619) in dorsal view.

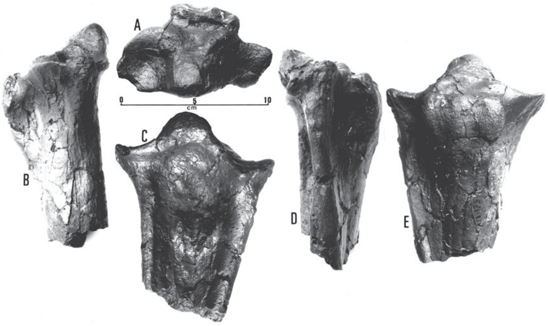

FIGURE 13. Proximal end of the left tarsometatarsus of *Physornis fortis* (MACN-A-52-185) in views: A - proximal, B - medial, C - dorsal, D - lateral and E - plantar. This specimen appears to be associated to the fragment of mandibular symphysis (MACN-A-52-186) and served as type for *Aucornis euryrhynchus* Ameghino, 1899.

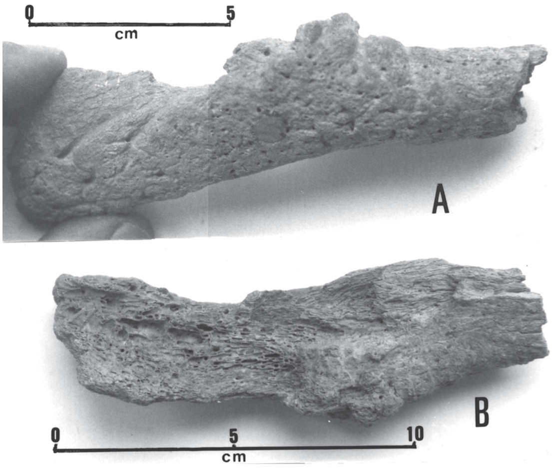

FIGURE 14. Fragment of the symphysis and right mandibular branch of *Physornis fortis* (type: BMNH-A583) ventral (A) and dorsomedial (B) views. Compare with Fig. 12A.

conclusion that this is undoubtedly a fragment of the symphysis and part of the right branch of a large Phorusrhacidae. The experience acquired in the restoration of the mandible of *Paraphysornis* (Alvarenga, 1982), contributed to us for the immediate recognition of the texture of a real mandibular symphysis of a Phorusrhacidae. Further, it is evident that Ameghino had prior experience, having examined and described several other mandibular symphysis of Phorusrhacidae, such as, *Phorusrhacos longissimus* Ameghino, 1887; *Phororhacos sehuensis* Ameghino, 1891; *Phororhacos platygnathus* Ameghino, 1891; *Tolmodus inflatus* Ameghino, 1891, and others, this showing his intimacy with this anatomical portion, which, apparantly, is often conserved in the Phorusrhacidae fossils.

Although it is an almost shapeless fragment and, thus, very inadequate for typifying a species, the type demonstrates, besides the size and the geographical and stratigraphical source, also the flat portion of the ventral surface of the mandibular symphysis, which is characteristic of this genus (Figs. 12A and 14).

Physornis fortis Ameghino, 1895

Physornis fortis Ameghino, 1895:576; Brodkorb, 1967.
Aucornis euryrhyncus Ameghino, 1898:9; Brodkorb, 1967 (syn. of *Physornis fortis*).

Type – A fragment around 137 cm in length, constituting the ventral portion of the mandibular symphysis and the adjacent part of the right mandibular branch (BMNH-A583: Fig. 14).

Hypodigm – Type; a mandibular symphysis, including a part of the left branch (Figs. 12A-C), associated to the caudal portion of the left quadratojugal (Fig. 15A), and to the atlas (Fig. 16A), besides fragments of vertebras, phalanges etc. (FM-P13340). A well conserved madibular symphysis (Fig. 12D), associated to the caudal extremity of the right quadratojugal (FM-P13619).

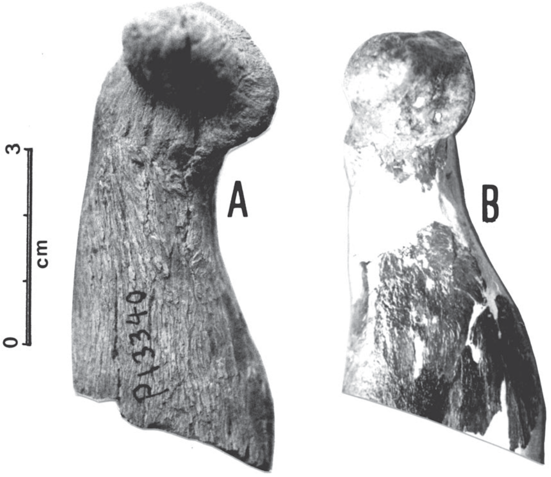

FIGURE 15. Caudal portion of the left quadratojugal, in medial view of: A - *Physornis fortis* (FM-P13340); B - *Paraphysornis brasiliensis* (DGM-1418-R).

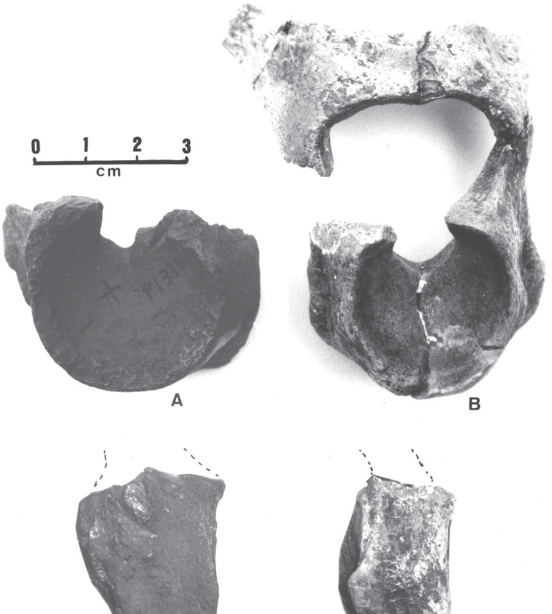

FIGURE 16. Atlas of A - *Physornis fortis* (FM-P13340); B - *Paraphysornis brasiliensis* (DGM-1418-R). Cranial (above) and right lateral (below) views. *Physornis* possesses more volume and articular surface for the occipital condyle.

A proximal portion of the left tarsometatarsus (MACN-A-52-185, Figs. 2A and 13). A rostral extremity of the mandibular symphysis (MACN-A-52-186). A phalanx 1 of the toe II from the left foot (MACN-A-52-187); these last three bones were associated and served as type for *Ancornis euryrhyncus* Ameghino, 1898. A phalanx 1 of the toe IV from the left foot (MACN-A-52-188). In the Museum of Amherst College, Massachussetts, U.S.A., there is also a right femur, incomplete on the proximal extremity, without number (?), refered to and figured by Loomis (1914:226).

Horizon and Locality – Middle to Upper Oligocene of Argentina (Deseadan). Province of Santa Cruz, Argentina: Puerto Deseado, Punta Nova, La Flexa, in the levels of occurrence of *Pyrotherium*. For a better indication of the geological age, see Mac Fadden (1985) and Marshall *et al.* (1986).

Measurements – Table 3.

Illustrations – Loomis, 1914: Fig. 149.

Remarks – The size of the mandibular symphysis (type: BMNH-A583), originally described by Ameghino (1895), is in perfect agreement with the two measured specimens in the Field Museum of Chicago (Table 3). A flat (not convex) region in the mid-ventral portion of the symphysis is noted in all the specimens.

The branches of the mandible of *Physornis*, in comparison with those of *Phorusrhacos*, are really more further apart from the median line, as in the original description by Ameghino (op. cit.), which implies a skull with a wider base. Ameghino perfectly described the only large built Phorusrhacidae of the stratigraphic layers characterized by the presence of *Pyrotherium* (Deseadan). Thus, there is no reason for the rejection of the genus *Physornis* and the species *P. fortis*, as being indeterminate, as suggested by Patterson (1941).

Although the complete shape of the tarsometatarsus of *Physornis* is unknown, the proximal portion of this is shown to be quite flattened in the dorsoventral extent. Associating this to the short and wide mandibular symphysis, besides the quite large build, it fits in perfectly amongst the Brontornithinae.

Aucornis solidus Ameghino, 1898, considered by Brodkorb (1967) as synonymous of *Physornis fortis*, was created only based on a proximal extremity of a phalanx (MACN-A-52-110), of a much smaller-sized bird than *Physornis fortis*, possibly synonymous of *Andrewsornis abbotti* Patterson, 1941, which should be left as a *species inquirenda*, seeing that one is dealing with an absolutely insufficient segment to diagnose a species.

The two symphysis examined in the Field Museum of Chicago, showed an interesting difference on the dorsal surface, which, almost flat in FM-P13340, forms a longitudinal channel in FM-P13340 (Figs. 12C and 12D). These differences were interpreted as being individual variation.

Genus *Paraphysornis* Alvarenga, 1993

Type Species – *Physornis brasiliensis* Alvarenga, 1982.

TABLE 3. Measurements of *Physornis fortis* (cm). Numbers in brackets are estimates on incomplete bones.

Mandible	FM-P13340	FM-P13619
Length of the mandible on the dorsal surface	(11.0)	11.3
Width of the base of the symphysis	7.0	(7.5)
Height at the base of the symphysis	(5.9)	–
Atlas	FM-P13340	
Condyloid fossa (maximum width)	3.82	
Femur*		
Smallest transverse diameter of the diaphysis	5.8	
Maximum distal width	14.8	
Tarsometatarsus	MACN-A52-185	
Maximum proximal width	10.5	
Proximal dorsoventral diameter	6.7	
Width of the diaphysis on the level of the fracture (Fig. 13)	5.4	
Falanx 1, digit IV, left foot	MACN-A52-188	
Length of the axis	6.3	
Maximum proximal width	4.5	
Maximum distal width	(3.2)	

* Measurements from Loomis (1914) of the specimen (w/n.) in Amherst College, Massachusetts.

Included Species – Only the type species.

Distribution – Upper Oligocene or the Lower Miocene of Southeast Brazil.

Diagnosis – Maybe the smallest of the Brontornithinae, the size being comparable to that of a smaller-sized *Brontornis burmeisteri* (Figs. 1B and 2B). The mandibular symphysis is longer and narrower than in the remaining Brontornithinae (*e.g.* Alvarenga, 1993: Fig. 1), being, however, proportionally wider and shorter than in the Phorusrhacinae. The cotyles of the tarsometatarsus are slightly quadrangular, especially the inner one (*e.g.* Alvarenga, 1993: Fig. 2).The lateral edge of the hypotarsus expands until very near to the lateral part of the lateral cotyle, not forming the lateral crest characteristic of *Physornis*.

Paraphysornis brasiliensis (Alvarenga, 1982)

Physornis brasiliensis Alvarenga, 1982.

Holotype – The almost complete skeleton of one specimen (Fig. 17), most of the upper maxilla, braincase, pelvis and sternum being missing (DGM-1418-R).

Hypodigm – Only the type material.

Horizon and Locality – The Tremembé Formation, Taubaté Basin, State of São Paulo, Brazil. Age near to the Upper Deseadean, certainly the Upper Oligocene or the Lower Miocene (Soria & Alvarenga, 1989, and Alvarenga, 1990).

Measurements – Tables 1 and 4; Alvarenga (1982).

Illustrations – Alvarenga (1982, 1993).

Remarks – A comparison as to the size of the Brontornithinae, becomes difficult due to the lack of a larger number of individuals and better knowledge of species size variations. The dimension of the tarsometatarsus of *Paraphysornis* (the only known specimen) is equivalent to that of a small *Brontornis* (FM-P13259), even though a little less bulky (Figs. 2B and 2C). On the other hand, a comparison of the basal portion of the quadratojugal (Fig. 15), of the atlas (Fig. 16), of the third cervical vertebra and of the proximal portion of the tarsometatarsus of *Physornis* and *Paraphysornis*, shows a slight superiority in the size of these in *Physornis*. However, other specimens, as they come to light, may alter this difference, for the time being established.

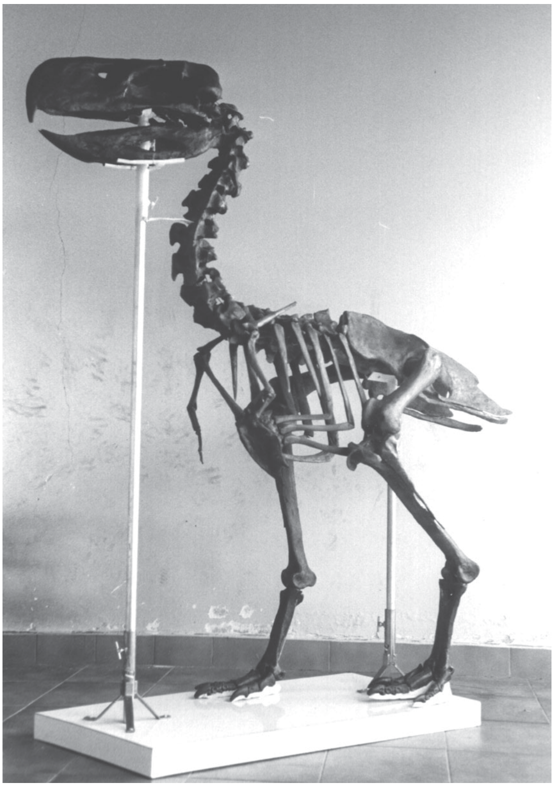

FIGURE 17. Reproduction of the skeleton of *Paraphysornis brasiliensis*, based on the holotype (DGM-1418-R) of which about 75% of the skeleton is known. The shapes of the upper maxilla, the skull, the pelvis and the sternum, were reproduced based on other species of other genera of Phorusrhacidae.

Subfamily Phorusrhacinae Ameghino, 1889

Phororhacosidae Ameghino, 1889.
Phororhacidae Ameghino, 1895.
Phororhacinae Kraglievich, 1932.
Phorusrhacinae Brodkorb, 1963; 1967.

Diagnosis Revised – Phorusrhacidae, of a gigantic build, having, however, a more slender and lighter constitution, certainly being more nimble, agile and faster (Fig. 1C), than the Brontornithinae. The mandibular symphysis, relatively longer, narrower and not so high (Figs. 18 and 19), is more than twice as long as the width of the base. The tarsometatarsus (Figs. 2E and 2F), relatively long and slender, is always longer than 60% of the length of the tibiotarsus (Figs. 20 and 21).

TABLE 4. Measurements of *Paraphysornis brasiliensis* (cm), specimen DGM-1418-R. Numbers in brackets are estimates based on incomplete bones.

Mandible	
Total length	51.1
Length of the symphysis, dorsal surface	8.7
Height at the base of the symphysis	7.7
Atlas	
Condyloid fossa (maximum width)	2.9
Femur	
Total length	(35.0)
Width in the middle of the diaphysis	4.7
Dorsoventral diameter in the middle of diaphysis	5.5
Maximum distal width	12.6
Dorsoventral diameter of the internal condyle	11.3
Dorsoventral diameter of the external condyle	10.4
Tibiotarsus	
Total length (excluding cnemial crest)	55.0
Width in the middle of diaphysis	5.4
Tarsometatarsus	
Total length	31.5
Maximum proximal width	10.0
Proximal dorsoventral diameter	7.1
Maximum distal width	10.5
Falanx 1, digit IV, left foot	
Length on the axis	(5.9)
Maximum proximal width	(4.0)
Maximum distal width	2.7

Included Genera – *Phorushacos* Ameghino, 1887, *Devincenzia* Kraglievich, 1932 and *Titanis* Brodkorb, 1963.

Genus *Phorusrhacos* Ameghino, 1887

Phorusrhacos Ameghino, 1887:24; Bordkorb, 1967.
Phororhacos Ameghino, 1889:659.
Stereornis Moreno & Mercerat, 1891:21, 45; Brodkorb, 1967 (syn. of *Phorusrhacos*).
Darwinornis Moreno & Mercerat, 1891:26, 60; Brodkorb, 1967 (syn. of *Phorusrhacos).*
Owenornis Moreno & Mercerat, 1891:25, 64; Brodkorb, 1967 (syn. of *Phorusrhacos*).
Mesembriornis Moreno, 1889:29; Brodkrob, 1967 (syn. of *Phorusrhacos*).
Titanornis Mercerat, 1893:5; Brodkorb, 1967 (syn. of *Phorusrhacos*).
Callornis Ameghino, 1895:574; Brodkorb, 1967 (syn. of *Phorusrhacos*).
Eucallornis Ameghino, 1901:78; Brodkorb, 1967 (syn. of *Phorusrhacos*).
Liornis Ameghino, 1895:570; syn. nov.

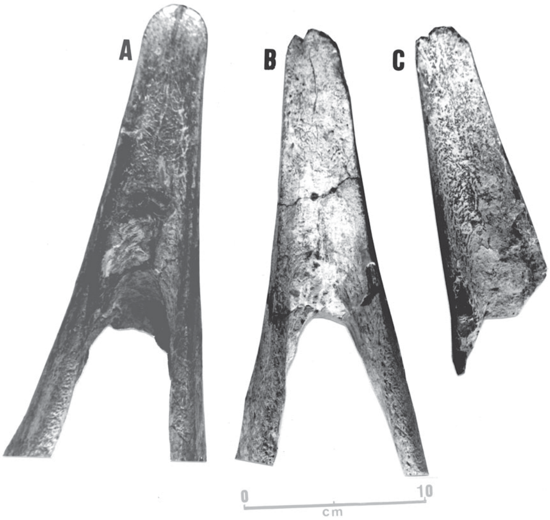

FIGURE 18. Mandibular symphysis of *Phorusrhacos longissimus* in dorsal view: A - BMNH-A 529; B - BMNH-A 530; C - BMNH-A 684.

FIGURE 19. Incomplete mandible of *Phorusrhacos longissimus* (BMNH-A530) in left lateral view.

FIGURE 20. *Phorusrhacos longissimus* (AMNH-9146). Left tarsometatarsus from Cañon de Las Vacas, Province of Santa Cruz, Argentina. Dorsal view. Maximum length 362 mm, calculated at 370 mm if it were complete.

Type Species – *Phorusrhacos longissimus* Ameghino, 1887.

Included Species – Only the type species.

Distribution – Lower and Middle Miocene of Argentina.

Diagnosis – Of a very big build, being, however, smaller than *Devincenzia*. The length of the tarsometatarsus is about 70% of that of the tibiotarsus (Figs. 20 and 21),

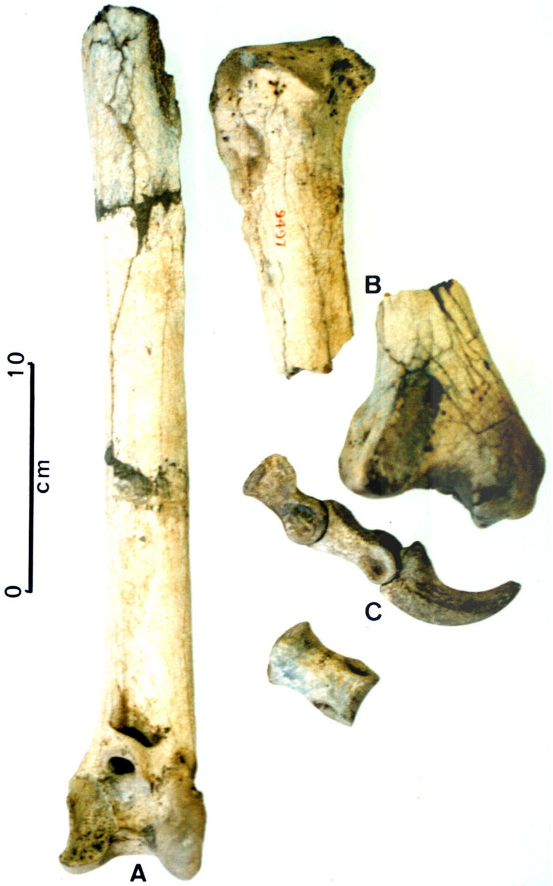

FIGURE 21. *Phorusrhacos longissimus* (AMNH-9497). Associated bones of the left leg, coming from Monte Leon, Province of Santa Cruz, Argentina. A - Ventral view of the tibiotarsus, lacking the proximal end. B - Dorsal view of the femur, lacking a segment of the diaphysis. C - Phalanges (also assigned to the left foot). It was based on these bones that an estimate of the total length of the femur (around 31 cm) and of the tibiotarsus (nearly 50 cm), were made.

the distal portion of the mid-trochlea not being laterally expanded as is the case of *Titanis* (Fig. 22).

Remarks – Within the subfamily, *Phorusrhacos* is that which possesses the largest amount of fossils, these coming from the Santacruzian sediments in Argentina. To elaborate a more detailed anatomical diagnosis which would separate *Phorusrhacos* from both *Devincenzia* and *Titanis* becomes, however, difficult through the deficiency in material, seeing that the latter two genera are very badly represented. It is worthwhile pointing out that *Devincenzia*, with a size which appears to exceed that of *Phorusrhacos*, comes from more recent levels of Argentina and Uruguay, whereas *Titanis*, with the same size, is only known from a still more recent terrain of North America.

Phorusrhacos longissimus Ameghino, 1887

Phorusrhacos longissimus Ameghino, 1887:24; Brodkorb, 1967.
Phororhacos longissimus Ameghino, 1889:659.
Stereornis rollieri Moreno & Mercerat, 1891:21, 45; Brodkorb, 1967 (syn. of *P. longissimus*).
Stereornis gaundryi Moreno & Mercerat, 1891:21,47; Brodkorb, 1967 (syn. of *P. longissimus*).
Mesembriornis studeri Moreno & Mercerat, 1891:21, 48; Brodkorb 1967 (syn. of *P. longissimus*).
Mesembriornis quatrefragesi Moreno & Mercerat, 1891:22, 50; Brodkorb, 1967 (syn. of *P. longissimus*).
Darwinornis copei Moreno & Mercerat, 1891:24, 60; Brodkorb, 1967 (syn. of *P. longissimus*).
Darwinornis zittelli Moreno & Mercerat, 1891:25, 63; Brodkorb, 1967 (syn. of *P. longissimus*).
Darwinornis socialis Moreno & Mercerat, 1891:25, 63; Brodkorb, 1967 (syn. of *P. longissimus*).
Owenornis affinis Moreno & Mercerat, 1891:25, 64; Brodkorb, 1967 (syn. of *P. longissimus*).

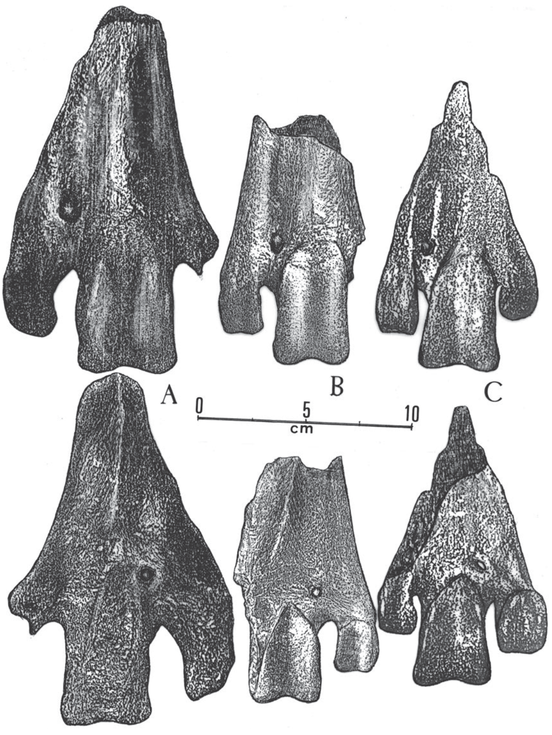

FIGURE 22. Right tarsometatarsus (distal end) of the Phorusrhacinae: A - *Devincenzia pozzi* (type: MACN-6554); B - *Phorusrhacos longissimus* (MLP-132) and C - *Titanis walleri* (type: UF-4108). Dorsal (above) and plantar (below) views. Note in *Titanis* a widening of the transverse diameter on the distal end of the mid-trochlea.

Owenornis lydekkeri Moreno & Mercerat, 1891:25, 64; Brodkorb, 1967 (syn. of *P. longissimus*).
Phororhacos sehuensis Ameghino, 1891:258; Brodkorb, 1967 (syn. of *P. longissimus*).
Phororhacos platygnathus Ameghino, 1891:452; Brodkorb, 1967 (syn. of *P. longissimus*).
Titanornis mirabilis Mercerat, 1893:5; Brodkorb, 1967 (syn. of *P. longissimus*).
Callornis giganteus Ameghino, 1895:78; Brodkorb, 1967 (syn. of *P. longissimus*).
Eucallornis giganteus Ameghino, 1901:78; Brodkorb, 1967 (sin. of *P. longissimus*).
Liornis floweri Ameghino, 1895; syn. n.
Liornis minor Dolgopol de Saez, 1927; syn. n.

Type – A mandibular symphysis, including part of the right mandibular branch, but lacking the rostral extremity, MLP-118 (originally described as the mandible of a toothless mammal).

Hypodigm – Type; several segments of skeletons which served as the type for the various synonyms of the species (MLP-119 to 139, 171 to 182). The species is known from segments of almost all the skeleton, there lacking, however, a better representation of the skull. Ameghino (1895) tells of the observation and measurements of the skull of a specimen in nature, in fragments and encrusted in crumbling rock. The mandible, the rostral extremity of the upper maxilla and a fragment apparently from the caudal portion of the supra-orbital process (BMNH-A529, Figs. 18A, 23B, 23C, 24A and 24C), coming from this specimen, were collected. Several other segments of the mandible represent the species (Figs. 18 and 19). For *P. longissimus* there is still lacking an appropriate number of associated bones for a whole reconstruction of the bird. The specimen AMNH-9146 (Fig. 20) represents an almost complete left tarsometatarsus, and the AMNH-9497 (Fig. 21) is represented by some associated bones of a leg.

Horizon and Locality – Lower and Middle Miocene (Santacrucian) of Argentina; Santa Cruz Formation, the Province of Santa Cruz: La Cueva, Tagua Quemada, Monte Observación, Rio Shehuen.

Measurements – Table 5; Moreno & Mercerat, 1891; Ameghino, 1895.

Illustrations – Moreno & Mercerat, 1891 and Ameghino, 1895.

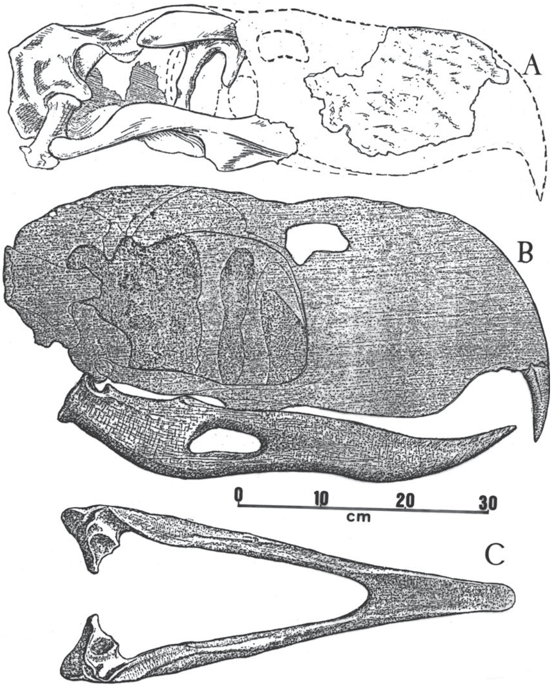

FIGURE 23. A - Restoration of the skull of *Devincenzia pozzi*, modified by Patterson & Kraglievich (1960), based on specimen MLP-37-11-7-8 (type of *Onactornis pozzi* Cabrera, 1939). B and C - *Phorusrhacos longissimus*, drawing by Ameghino (1895), based on a "complete skull, but in such a bad state of conservation that it is almost reduced to dust" (BMNH-A529); C - dorsal view of the mandible. The skulls of both Phorusrhacinae are of approximately the same size, and differences in height can, at least partially, be attributed to deformation in fossilization and defects in the reassembling of the skull of *Devincenzia pozzi*.

FIGURE 24. *Phorusrhacos longissimus*. A - Caudal portion of the supraorbital processes of the lacrimal (?) (BMNH-A529). B and C - Fragments corresponding to the apex of the upper maxilla, respectively: BMNH-A529 and BMNH-A535. A and B belong to the same specimen mentioned in figures 23B and 23C.

Genus *Devincenzia* Kraglievich, 1932

Devincenzia Kraglievich, 1932:323, 338.
Onactornis Cabrera, 1939:15; syn. n.

TABLE 5. Measurements of *Phorusrhacos longissimus* (cm). Numbers in brackets are estimates based on incomplete bones.

	MLP-118		BMNH-A529		BMNH-A530		BMNH-A684
Skull*							
Total length	–		(65)		–		–
Width at base	–		(30)		–		–
Height of maxilla	–		(25)		–		–
Mandible							
Total length	–		55		–		–
Length of symphysis	(16)		17.9		–		–
Height- base of the symphysis	5.3		6.2		5.7		5.4
Width- base of symphysis	7.0		6.7		6.6		6.0
	BMNH-A581	BMNH-A531	BMNH-A545	MLP-131	MLP-76V.1011	AMNH-9497	AMNH-9146
Femur							
Total length	–	–	–	–	–	–	(31.0)
Width middle of diaphysis	–	–	–	–	–	–	3.62
Maximum distal width	–	–	–	–	–	–	9.2
Tibiotarsus							
Total length	–	–	–	–	–	–	(50.0)
Smallest width of diaphysis	–	–	–	–	–	–	3.9
Maximum distal width	–	–	–	–	–	–	6.2
Tarsometatarsus							
Total length	–	–	–	38.5	(40.0)	37.0	–
Proximal width	–	–	–	8.0	(8.4)	–	–
Width- middle of diaphysis	–	–	–	3.7	3.7	3.6	–
Width at distal foramen level	6.0	7.1	6.5	6.4	6.5	6.3	–
Width of the middle trochea	2.9	–	3.5	3.3	3.6	3.4	–

* Measurements from Ameghino (1895)

Type Species – *Devincenzia gallinali* Kraglievich, 1932, junior synonym of *Devincenzia pozzi* (Kraglievich, 1931).

Included Species – Only the type species.

Distribution – Upper Miocene to the Lower Pliocene of Argentina and Uruguay.

Diagnosis – They are the biggest of the known Phorusrhacinae, with a height comparable to that of the largest Brontornithinae, being, however, lighter. The skull is about 65 cm long, equivalent to that of *Phorusrhacos*, this being possibly flattened dorso-ventrally (Fig. 32A). The tarsometatarsus is substantially sturdier than that of *Phorusrhacos* (Figs. 2F and 22A).

Remarks – The general appearance of the tarsometatarsus of *Devincenzia* (MNHN-189, Fig. 2F), appears to indicate an intermediate position between the Phorusrhacinae and Brontornithinae, as observed by Kraglievich (1932) himself. However, the appearance of the bony cortex makes it clear that one is dealing with a not yet completely adult individual. As happens with several present-day Ralliformes, especially the Rallidae and Cariamidae, besides other groups of birds, it is normal that the proximal metaphysary portion of the tarsometatarsus reaches, in youngsters, a larger width than that in the adults, associated to a shorter length of the bone. Consequently, one supposes that the tarsometatarsus of *Devincenzia*, in the adult phase, might be a little longer and with the proximal region slightly narrower than appears in the refered specimen. The origin of this tarsometatarsus (MNHN-189), type of *Devincenzia gallinali* Kraglievich, 1932, and, consequently, its geological age, are unknown. From the appearance of the bone (and certainly the remains of the encrusted substract), Kraglievich supposed it to have originated from the Arroyo Roman, Rio Negro, Uruguay, and points out the difference of color, especially when compared with the bones coming from Patagonia, without, however, comparing it with specimens from the Huayquerian of north Argentina, studied years before by he himself (1931).

Devincenzia pozzi (Kraglievich, 1931). comb. n.

Phororhacos pozzi Kraglievich, 1931:306.

Phororhacos longissimus mendocinus Kragkievich, 1931:314; syn. n.

Devincenzia gallinali Kraglievich, 1932:323, 338; syn. n.
Onactornis depressus Cabrera, 1939:15; Brodkorb, 1967
(syn. of *O. pozzi*).
Onactornis pozzi; Brodkorb,1967:165; syn. n.
Onactornis mendocinus; Brodkorb, 1967:166; syn. n.

Type – Distal portion of the right tarsometatarsus (Fig. 22A), associated to the ungual phalanx of digit II (MACN-6554 and 6681).

Hypodigm – Type; a skull much deformed by dorsoventral flattening, most of the upper maxilla being incomplete (Fig. 23A), together with the proximal phalanges of digits II and III (MLP-37-III-7-8), type of *Onactornis depressus* Cabrera, 1939; right tarsometatarsus, without the inner trochlea and a large part of the hypotarsus (MNHN-M-189, Fig. 2F), type of *Devincenzia gallinali* (Kraglievich, 1932); fragment of the madibular symphysis (MACN-6933), described by Kraglievich (1931) as *Phororhacos* ? *aff. platygnathus*; proximal portion of a right femur, with the head missing (MACN-6930); distal portion of the left tibiotarsus (MACN-13243).

Horizon and Locality – Upper Miocene to the Lower Pliocene of Argentina, Provinces of Buenos Aires and Entre Rios (Huayquerian and "Mesopotamian") and Uruguay (Arroyo Roman ?).

Measurements – Table 6; Kraglievich, 1931; Patterson & Kraglievich, 1960.

Ilustrations – Kraglievich (1931 and 1932) and Cabrera (1939).

Remarks – Tambussi *et al.* (1999) described an almost complete right tibiotarsus (MNHN-M-1563) about 720 mm long, coming from the Raigon Formation (Pliocene) of south Uruguay. In this specimen the cnemial crests are extremely large and cranially projected, in a similar way to what occurrs in *Titanis walleri* (UF-7333), and different from what occurs with Brontornithinae. This tibiotarsus should be assigned to the genus *Devincenzia* and very probably to *D. pozzi* by the characters of a Phorusrhacinae, the size, age and geographic distribution. Unfortunatelly there is no sufficient material for a definite comparison. Another question would be a better definition of the difference in age between the sediments of the Raigon Formation of Uruguay with the Huayquerian and "Mesopotamian" of Argentina, as well as a new study on the possibility that the tarsometatarsus type of *D. gallinali* (Kraglievich, 1932), may have also been collected in the Raigon Formation and not in the Arroyo Román as supposed by Kraglievich (1932).

Genus *Titanis* Brodkorb, 1963

Type Species – *Titanis walleri* Brodkorb, 1963.

Included Species – Only the type species.

Distribution – Upper Pliocene to Lower Pleistocene of Florida and Texas (U.S.A.).

Diagnosis – Size similar to that of *Phorusrhacos*, with a less sturdy tarsometatarsus than that of *Devincenzia*. The mid-trochlea, in the more distal portion, is spread out

TABLE 6. Measuments of *Devincenzia pozzi* and *Titanis walleri* (cm). Numbers in brackets are estimates on incomplete bones.

	Devincenzia pozzi			*Titanis walleri*	
	MACN-6554[1]	MHNM-189[2]	MLP-37.III.7.8[3]	UF-4108	UF-4109
Skull					
Total length	–	–	(65.0)	–	–
Width at base	–	–	(33.0)	–	–
Height of maxilla	–	–	(17.0)	–	–
Tarsometatarsus					
Total length	–	(40.0)	–	–	–
Proximal width	–	(11.0)	–	–	–
Width at the distal foramen level	8.5	8.6	–	6.0	–
Width of the middle trochea	4.8	4.3	–	3.6	–
Falanx 1, digit III					
Length (ventral surface)	–	–	(12.5)	–	10.4
Proximal height	–	–	5.0	–	5.8
Proximal width	–	–	5.1	–	5.4

[1] Type of *Phororhacos pozzi* Kraglievich, 1931.
[2] Type of *Devincenzia gallinali* Kraglievich 1932.
[3] Type of *Onactornis depressus* Cabrera, 1939.

onto the sides, differentiating it from the two aforementioned species (Fig. 22C), this aspect reminding one of the Mesembriornithinae.

Titanis walleri Brodkorb, 1963

Holotype – Distal portion of the right tarsometatarsus (UF-4108).

Hypodigm – Holotype; phalanx I of digit III (UF-4109) associated (?) to the holotype; phalanx 1 of digit III (TMM-43060-115); proximal extremity of the left tibiotarsus (UF-7333); complete left carpometacarpus (UF-30003, Fig. 6A); two complete cervical vertebras (C2 and C3); the proximal portion of the right fibula, phalanges 1, 2 and 3 of the left digit III and two phalanges 1 of digit IV (left and right) (UF wt/n.).

Horizon and Locality – Upper Pliocene to Lower Pleistocene (end of the Blancanian to the beginning of the Irvingtonian) of Florida, (Inglis, on the border between Gilchrist and Columbia County), and the Pleistocene of Texas (Baskin, 1995).

Measurements – Tables 1 and 6, Carr (1981), Chandler (1994) and Baskin (1995).

Illustrations – Brodkorb, (1963), Carr (1981), Chandler (1994) and Baskin (1995).

Remarks – This is the only Phorusrhacidae known outside South America, one of the most recent species, attesting to these birds crossing over to North America on the forming of the land-bridge connecting North and South America, in the Panama region, at the end of the Pliocene. When compared with other Phorusrhacidae, the examined material indicates a large variation in the size of *Titanis*, maybe leading one to presume sexual dimorphism.

Subfamily Patagornithinae Mercerat, 1897, revalid. name

Patagornithidae Mercerat, 1897.
Tolmodinae Kraglievich, 1932.
Paleociconiinae Brodkorb, 1967; Mourer-Chauviré, 1981.

Diagnosis Revised – A relatively medium-sized Phorusrhacidae, smaller and slimmer than the Phorusrhacinae (Fig. 1D). A long and narrow mandibular symphysis (Figs. 25 and 26). Long and slender tarsometatarsi, more than 70% of the length of the tibiotarsus. The tibiotarsi and tarsometatarsi are proportionally more slender than those of the Phorusrhacinae.

Included Genera – *Patagornis* Moreno & Mercerat, 1891, *Andrewsornis* Patterson, 1941, and *Andalgalornis* Patterson & Kraglievich, 1960.

Remarks – Brodkorb (1967) considered the term *Paleociconia* revalidated by Moreno & Mercerat (1891), and based on this created the subfamily Paleociconiinae. The genus *Paleociconia* Moreno, 1889, having as type-species *Paleociconia australis* assigned by Richmond (1901), is based on a distal half of a left tarsometatarsus, once again described and also pictured by Moreno & Mercerat (1891). Patterson & Kraglievich (1960:6-8), comment on the extremely superficial diagnosis, without any illustration, by Moreno (1889), and consider *Paleociconia australis* as *nomen nudum*. Kraglievich (1931:305) and Brodkorb (1967), consider the genus *Paleociconia* revalidated by Moreno & Mercerat (1891), having as type-species *Paleociconia cristata* Moreno & Mercerat, designated by Rovereto (1914:163). It so happens that *Paleociconia cristata* Moreno & Mercerat, 1891, is based on the very resumed description of two broken cervical vertebras, of a much smaller species, possibly a Psilopterinae, without the characteristics to permit a precise identification and so should be considered as *species inquirenda*. One ungual phalanx ilustrated by

FIGURE 25. *Andrewsornis abbotti*. Mandibular symphysis (FM-P13383), from Pico Truncado, Rio Deseado, Province of Santa Cruz, Argentina: A - left lateral, B - dorsal and C - ventral, views. Left femur (FM-P14678): D - dorsal, E - lateral and F - ventral, views.

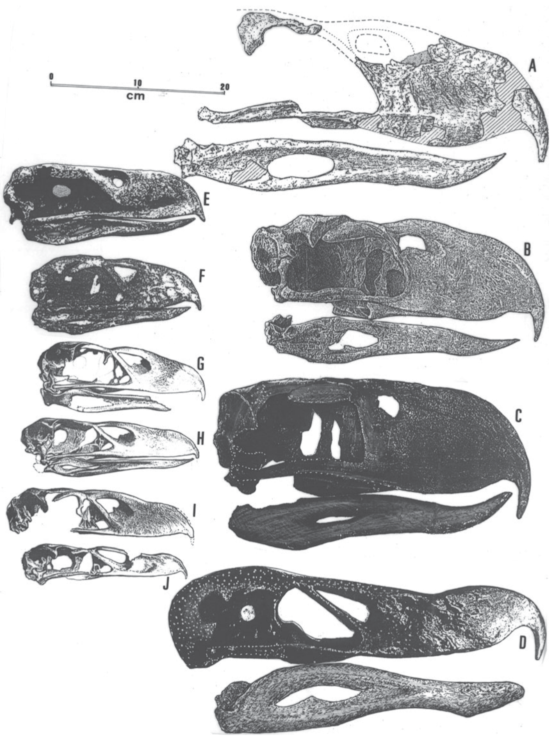

FIGURE 26. Skulls of the Patagornithinae (A-C), Mesembriornithinae (D) and Psiloterinae (E-J). A - *Andrewsornis abbotti* (FM-P13417; from Patterson, 1941), B - *Patagornis marshi* (BMNH-A-516; from Andrews, 1899), C - *Andalgalornis steulleti* (FM-P14357); D - *Mesembriornis milneedwardsi* (MMP-S155); E - *Procariama simplex* (FM-P14525); F - *Psilopterus lemoinei* (FM-P13257); G - *Psilopterus lemoinei* (PUM-15402); H - *Psilopterus lemoinei* (AMNH-9157); I - *Psilopterus lemoinei* (PUM-15109); J - *Psilopterus bachmanni* (PUM-15904). G-J inverted figures from Sinclair & Farr (1910).

Moreno & Mercerat (PL. XIX-12) is only assigned to *Paleociconia cristata*, without any description, thus being also insufficient to validate the taxon. The term *Paleociconia* becomes even more confused when Lydekker (1891) committed a grave mistake while describing and picturing the distal extremity of a tarsometatarsus of a true *Ciconiidae* of the Pleistocene of Lagoa Santa, Brazil, on assigning it to *Paleociconia australis* Moreno, 1889. In spite of the commentaries emitted by the abovementioned authors, Moreno (1889) had created the genera *Mesembriornis* and *Paleociconia*, and nowadays, knowing the respective material on which these genera were based, it is known that they are synonyms and that *Paleociconia* (Moreno, 1889:29) is a junior synonym of *Mesembriornis* (Moreno, 1889:30), which in turn is an available name, with type material also available for new studies, and so cannot be rejected as *nomen nudum*.

Genus *Patagornis* Moreno & Mercerat, 1891 revalid. name

Patagornis Moreno & Mercerat, 1891 (May).
Tolmodus Ameghino, 1891 (June); Brodkorb, 1967 (syn. of *Paleociconia*).
Morenomerceraria Lambrecht, 1933; Brodkorb, 1967 (syn. of *Paleociconia*).
Paleociconia Brodkorb, 1967; Mourer-Chauviré, 1981.

Type Species – *Patagornis marshi*, Moreno & Mercerat, 1891. Designated by Richmond, 1902.

Included Species – Only the type species.

Distribution – The Lower and Middle Miocene of Argentina.

Diagnosis – The antorbital fenestra with the rostral edge moderately inclined (much inclined in *Andrewsornis* and little inclined in *Andalgalornis*) (Figs. 26A, 26B and 26C). The dorsal portion of the nostrils is very outstanding. Slightly curved mandibular symphysis (the apex is not raised) (Fig. 26B).

Remarks – *Patagornis* Moreno & Mercerat, 1891 (May-August) has priority over *Tolmodus* Ameghino, 1891 (June), as held by Mercerat (1897:227) on the question.

Patagornis marshi Moreno & Mercerat, 1891 revalid. name

Patagornis marshi Moreno & Mercerat, 1891 (May).
Tolmodus inflatus Ameghino, 1891 (June); Brodkorb, 1967 (syn. of *Paleociconia cristata*).
Phororhacos inflatus; Ameghino, 1891 (August); Andrews, 1899; Brodkorb, 1967 (syn. of *Paleociconia cristata*).
Paleociconia cristata; Brodkorb, 1967.

Lectotype – (by present designation): A mandibular symphysis lacking the rostral extremity (MLP-143), described and portrayed by Moreno & Mercerat as a premaxilla.

Hypodigm – One of the best represented Phorusrhacidae by the amount of fossils. Together with the lectotype, several segments of the skeleton, amongst which various bone segments from the hind-limbs, are described and well portrayed by Moreno & Mercerat (1891), of which at least the majority could belong to the same individual. (MLP-144 to 158). An almost complete and well-preserved skeleton (BMNH-A516), is described in details by Andrews (1899). Another almost complete, although badly deformed skeleton is at the Museo de La Plata (MLP-84-III-9-21), and includes the skull (Fig. 27). A parcial skeleton (AMNH-9264) was well-portrayed by Sinclair & Farr (1910: PL. XXXII), although the authors did not identify it. A complete and isolated tarsometatarsus (FM-P13213) was the only long bone of a young Phorusrhacidae examined in the present work, the proximal epiphysis being completely unfused to the diaphysis, and the total length (243 mm) almost 90% of that of an adult. A fragmment of the rostral portion of the mandibular symphysis of a Phorusrhacidae (BMNH-586) is described and portrayed by Ameghino (1891b) as belonging to the extremity of the premaxilla of *Opisthodactilus patagonicus*, when in fact it should be assigned to a mandibular symphysis of *Patagornis marshi*.

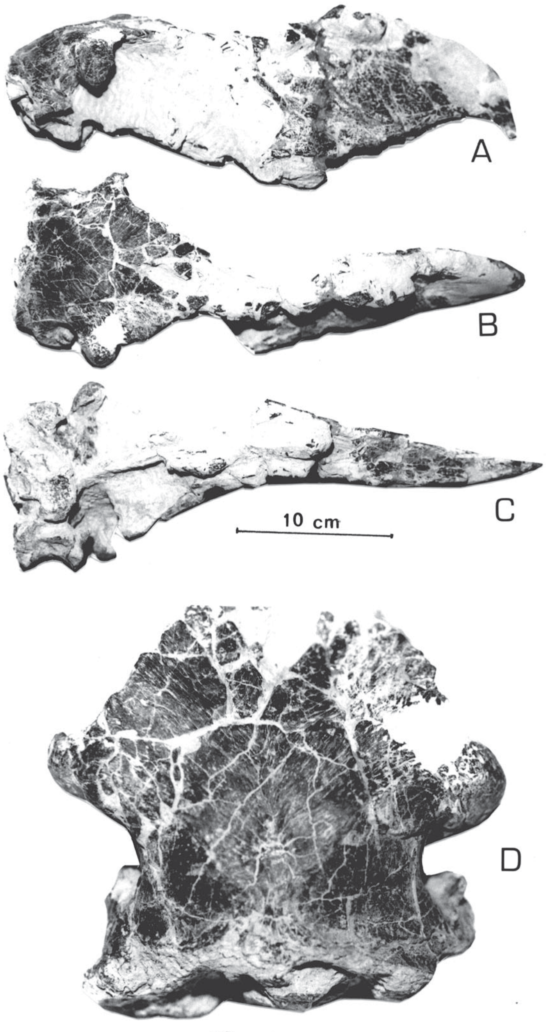

FIGURE 27. Skull of *Patagornis marshi* (MLP-84-III-9-21) from the Province of Santa Cruz, Argentina, which was associated to a large part of the skeleton, still in the preparation phase. A - right lateral view; B - dorsal view; C - ventral view, and D - dorsocaudal view; approximate length of the skull, 35 cm.

Horizon and Locality – Lower to Middle Miocene (Santacrucian) of Argentina, Province of Santa Cruz, the Santa Cruz Formation: Monte Observación, Tagua Quemada, La Cueva.

Measurements – Tables 1 and 7; Andrews (1899).

Illustrations – Moreno & Mercerat (1891: PL. XIV and XV), Andrews (1899), Ameghino (1899), and Sinclair & Farr (1932: PL. XXXII).

Genus *Andrewsornis* Patterson, 1941

Type Species – *Andrewsornis abbotti* Patterson, 1941.

Included Species – Only the type species.

Distribution – Middle to Upper Oligocene of Argentina.

Diagnosis Revised – The largest of the known Patagornithinae. On the skull, the rostral edge of the antorbital fenestra is very inclined. When compared with *Patagornis* and *Andalgalornis*, the mandibular symphysis is proportionally smaller and the mandibular fenestra bigger and oval-shaped (Fig. 26A).

Andrewsornis abbotti Patterson, 1941

Type – Incomplete skull, mandible (Fig. 26A), omal extremity of a coracoid, the second and ungual phalanges of digit II (FM-P13417).

Hypodigm – Type; a mandibular symphysis (FM-P13383) (Figs. 25A, 25B and 25C); a left femur with only the internal condyle missing (FM-P14678) (Figs. 25D, 25E and 25F).

Horizon and Locality – Middle and Upper Oligocene of Argentina, (Deseadan); Cabeca Blanca (Chubut), Pico Truncado (Santa Cruz).

Measurements – Table 7; Patterson, (1941).

TABLE 7. Measurements of the Patagornithinae (cm). Numbers in brackets are estimates based on incomplete bones.

	Patagornis marshi		*Andrewsornis abbotti*			*Andalgalornis steulleti*	
	BMNH-A516	MLP-84.III.9.21	FM-P13417	FM-P13383	FM-P14678	FM-P14357	MACN-69321
Skull							
Total length	33.7	34.5	(44.0)	–	–	38.5	–
Height of maxilla	11.5	(10.5)	–	–	–	13.0	–
Width at the base	12.0	(12.0)	–	–	–	14.0	–
Mandible							
Total length	30.5	–	39.4	–	–	34.0	–
Length of symphysis	9.0	–	10.0	8.5	–	11.5	–
Height at the base of symphysis	2.9	–	3.8	3.3	–	3.8	–
Width at the base of symphysis	3.2	–	–	–	–	4.7	–
Femur							
Total length	22.7	–	–	–	22.0	–	–
Proximal width	5.9	–	–	–	4.9	–	–
Width at the middle of the diaphysis	2.5	–	–	–	2.3	–	(2.6)
Distal width	6.2	–	–	–	–	–	5.2
Tibiotarsus							
Total length	39.5	38.0	–	–	–	–	–
Width at the middle of diaphysis	4.3	–	–	–	–	–	–
Distal width	2.7	–	–	–	–	–	–
Tarsometatarsus							
Total length	–	27.3	–	–	–	–	–
Proximal width	4.7	–	–	–	–	–	–
Width of the middle trochlea	1.9	–	–	–	–	–	–

[1] Type of *Phororhacos deautieri* Kraglievich, 1931.

Illustrations – Patterson (1941).

Remarks – The mandibular symphysis of specimen FM-P13383 (Figs. 25A, 25B and 25C), is smaller than that of the type specimen and the femur (FM-P14678) (Figs. 25D, 25E and 25F) is still smaller than the corresponding bone of *Patagornis marshi*. However, the measurements of the type specimen lead one to believe it to have been a larger bird. This is certainly one more example of intraspecific variation in these birds, and possibly even sexual dimorphism. A phalanx of digit II (MACN-A-52-110), whereon Ameghino (1898) described *Aucornis solidus*, is very probably attributed to this species and the name of which naturally could have priority. However, the diagnostic value of this phalanx is very debatable, as also one can question the correct geographical and stratigraphical origin of the specimen as well. It is thus preferable in this case to consider *Aucornis solidus* Ameghino, 1898 as a *species inquirenda*.

Genus *Andalgalornis* Patterson & Kraglievich

Type Species – *Andalgalornis ferox* Patterson & Kraglievich 1960 (junior synonym of *A. steulleti* Kraglievich 1931).

Included Species – Only the type species.

Distribution – Upper Miocene and Lower Pliocene of Argentina.

Diagnosis Revised – Upper maxilla proportionally higher than in the rest of the Patagornithinae, with the dorsal portion of the nostrils not raised. The rostral edge of the antorbital fenestra is almost straight and verticalized. The mandibular symphysis is longer, with the apex curved dorsally (Fig. 26C). The cervical vertebrae and especially the cervicodorsal ones, are sturdier than in *Patagornis*, and comparing herewith to the pelvis, the iliac crests are dorsally joined, forming a dorsal projection which is more prominent in the region above the acetabulum (Fig. 28B).

Andalgalornis steulleti (Kraglievich, 1931)

Phororhacos steulleti Kraglievich, 1931:312.
Phororhacos deautieri Kraglievich, 1931:312; Brodkorb, 1967 (syn. of *Andalgalornis steulleti*).
Andalgalornis ferox Patterson & Kraglievich, 1960; syn. n.
Andalgalornis steulleti; Brodkorb, 1967:162.

FIGURE 28. Comparison of the pelvis of: A - *Patagornis marshi* (BMNH-A516) and B - *Andalgalornis steulleti* (FM-P14357). The joined dorsal iliac crests form a dorsal projection on the most cranial part in *Patagornis* (A), whilst in *Andalgalornis* (B) this projection does not exist and the crest is higher in half of the pelvis.

Type – phalanx 1 of digit IV, left side (MACN-4244).

Hypodigm – Type; distal portion of the right femur (MACN-6932), type of *Phororhacos deautieri* Kraglievich, 1931. Partial skeleton consisting of the skull, mandible, pre-synsacral vertebrae (except the atlas), the pelvis and some broken ribs (FM-P 14357), type of *Andalgalornis ferox* Patterson & Kraglievich, 1960.

Horizon and sites – Upper Miocene to Lower Pliocene of Argentina: Andalgala Formation, "Mesopotamian" (= Huayquerian ?), the Entre Rios and Catamarca (Chiquimil) Provinces.

Measurements – Table 7, Patterson & Kraglievich (1960).

Illustrations – Kraglievich (1931), Patterson & Kraglievich (1960).

Remarks – The fossils of *Phororhacos steulleti* and *P. deautieri* come from the "Mesopotamian", whilst those of *Andalgalornis ferox* from Huayquerian (the Andalgala Formation), possibly different ages of the Upper Miocene and (or) Lower Pliocene (Tonni, 1980); Noriega (1995) believes that the "Mesopotamian" is within the Huayquerian. It is possible that the synonymous species herein became distinct (in time), but there is not enough material to corroborate such a hypothesis.

Subfamily Psilopterinae Dolgopol de Saez, 1927

Pelecyornidae Ameghino, 1891.
Psilopteridae Dolgopol de Saez, 1927.
Psilopteriidae Kraglievich, 1932.
Psilopterinae Patterson & Kraglievich, 1960; Brodkorb, 1967; Mourer-Chauviré, 1981.

Diagnosis Revised – A relatively small-built Phorusrhacidae, with thinner legs, and a relatively light and graceful body. Relatively big nostril openings; the rostral edge of the antorbital fenestra is well slanted. The mandible possesses a much lengthened fenestra, sometimes divided forming two fenestras. The mandibular symphysis is relatively small when compared to the total length of the mandible. The cervical vertebras are proportionally longer and narrower than in the remaining subfamilies. The length of the tarsometatarsus is about 70 to 75% of that of the tibiotarsus. The leg bones are proportionally slimmer than in the Patagornithinae and the other Phorusrhacidae.

Included Genera – *Psilopterus* Moreno & Mercerat, 1891, *Procariama* Rovereto, 1914 and *Paleopsilopterus* Alvarenga, 1985.

Genus *Psilopterus* Moreno & Mercerat, 1891

Psilopterus Moreno & Mercerat, 1891 (May-August).
Pelecyornis Ameghino, 1891 (December); Brodkorb, 1967 (syn. of *Psilopterus*).
Staphylornis Mercerat, 1897; Brodkorb, 1967 (syn. of *Psilopterus*).

Type Species – *Psilopterus comunis* Moreno & Mercerat, 1891, designated by Richmond, 1902 (a junior synonym of *Psilopterus bachmani* Moreno & Mercerat, 1891).

Included Species – *P. bachmani* (Moreno & Mercerat, 1891), *P. lemoinei* (Moreno & Mercerat, 1891), *P. affinis* (Ameghino, 1899) and *P. colzecus* (Tonni & Tambussi, 1988).

Diagnosis Revised – The smallest Psilopterinae. A rather high intercotylar tubercle on the tarsometatarsus, and the lateral edges of the hypotarsus are little or not spread (Fig. 29B).

Distribution – Mid-Oligocene to Upper Miocene of Argentina.

Psilopterus bachmanni (Moreno & Mercerat, 1891) comb. n.

Patagornis bachmanni Moreno & Mercerat, 1891 (pp. 24 and 58).

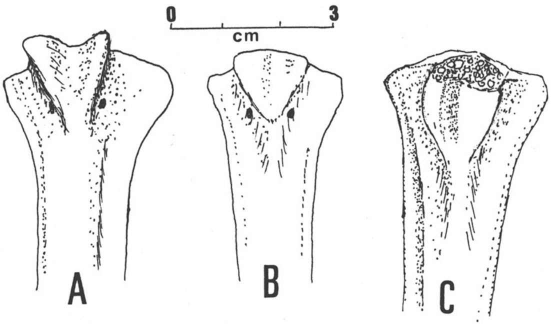

FIGURE 29. Proximal end of the right tarsometatarsus, plantar view, showing the variation of the hipotarsus in the three genera of the Psilopterinae: A - *Procariama simplex*; B - *Psilopterus lemoinei* and C - *Paleopsilopterus itaboraiensis*.

Psilopterus communis Moreno & Mercerat, 1891 (pp. 26 and 68); Brodkorb, 1967.
Psilopterus intermedius Moreno & Mercerat, 1891 (pp. 26 and 68); Brodkorb, 1967 (syn. of *P. communis*).
Phororhacos delicatus Amegino, 1891; Brodkorb, 1967, (syn. of *P. communis*).
Pelecyornis pueyrredonensis Sinclair & Farr, 1932; Brodkorb 1967 (syn. of *P. communis*).

Lectotype – (by present designation): proximal portion of the left tarsometatarsus (MLP-168).

Hypodigm – lectotype. A proximal and a distal portion of a femur (MLP-165-166) and a distal portion of the tibiotarsus, all of the left side (MLP-167), which appear to be associated to the lectotype. An almost complete skeleton (PUM-15.904), described and pictured by Sinclair & Farr (1932).

Horizon and Locality – Middle Miocene (Santacrucian) of Argentina, Santa Cruz Province: Santa Cruz, Lake Pueyrredon, Monte Observación, La Cueva.

Diagnosis Revised – Perhaps the smallest of all the known Phorusrhacidae (Fig. 1E), estimated at being between 70 to 80 centimeters high, rivalling only *Psilopterus affinis* in size. Relatively low skull and upper maxilla, in height (Fig. 26I), presenting a certain similarity with the Mesembriornithinae. Differences with *P. lemoinei* as to the different segments of the skeleton are well described by Sinclair & Farr (1932). A peculiarity of *P. bachmanni* is to be found in the extremely slanted rostral edge of the antorbital fenestra, very different from *P. lemoinei* (Figs. 26G and 26I).

Measurements – Table 8 and Sinclair & Farr (1932).

Ilustrations – Sinclair & Farr (1932) and Moreno & Mercerat (1891).

Remarks – *Patagornis bachmanni* has priority over *Psilopterus communis* (both of Moreno & Mercerat, 1891). *Psilopterus minutus* Ameghino, 1981, dealt with as a separate species by Brodkorb (11967), is represented only by an incomplete tarsometatarsus, inseparable from *P. bachmanni* (v. Sinclair & Farr, 1932:188).

Psilopterus lemoinei (Moreno & Mercerat, 1891) comb. n.

Patagornis lemoinei Moreno & Mercerat, 1891 (pp. 23 and 58).
Psilopterus australis Moreno & Mercerat, 1891 (pp. 26 and 68); Brodkorb, 1967.
Pelecyornis tubulatus Ameghino, 1895; Brodkorb, 1967 (syn. of *Psilopterus australis*).
Phororhacos modicus Ameghino, 1895; syn.n.
Staphylornis gallardoi Mercerat, 1897; Brodkorb, 1967 (syn.? of *Psilopterus australis*).
Staphylornis erythacus Mercerat, 1897; Brodkorb, 1967 (syn.? of *Psilopterus australis*).
Pelecyornis tenuirostris Sinclair & Farr, 1932; Brodkorb, 1967 (syn. of *Psilopterus australis*).

Lectotype – (by present designation): Distal end of a right tibiotarsus (MLP-162).

Hypodigm – Besides the lectotype and the material that served as type for the diverse synonyms, a plentiful and splendid material is discribed and pictured by Sinclair & Farr (1932). An ungual phalanx (MLP-164), described and pictured by Moreno & Mercerat (1891) as belonging to this species, certainly belongs to *Patagornis marshi*.

Horizon and Locality – Middle Miocene (Santacrucian) of Argentina, Santa Cruz Province: Santa Cruz, Killik Aike, Monte Observación, Take Harvey, La Cueva, Corriguen Kaik, Tagua Quemada.

Diagnosis Revised – Larger-sized than *P. bachmanni* (Fig. 1F), with the skull and upper maxilla notably higher (Figs. 26F, 26H and 26I), and a less slanted rostral edge of the antorbital fenestra. Other differences in the diverse segments of the skeleton are described and pictured by Sinclair & Farr (1932).

Measurements – Table 8 and Sinclair & Farr (1932).

TABLE 8. Measurements of the Psilopterinae (mm). Numbers in brackets are estimates based on incomplete bones.

	Psilopterus bachmanni	*Psilopterus lemoinei*				*Psilopterus affinis*	*Psilopterus colzecus*	*Procariama simplex*	*Paleopsilopterus itaboaiensis*
	PUM-159041	PUM-154022	PUM-151093	AMNH-92574	AMNH-91575	MACN-type	MLP-type	FM-P14525	MNRJ-type
Skull									
Total length	185.0	(185.5)	203.0	(198.0)	200.0	–	–	243.0	–
Width base	43.0	58.0	–	54.0	43.0	–	–	68.0	–
Height base	33.0	51.5	53.0	49.0	42.0	–	–	57.0	–
Mandible									
Total length	–	–	–	–	–	–	–	198.0	–
Length of symphysis	–	–	–	–	39.0	–	3.6 42.5	–	
Height at coronoid process	–	25.5	–	–	24.0	–	–	30.0	–
Femur									
Total length	118.0	135.0	–	149.5	138.5	–	–	158.0	–
Maximum proximal width	22.5	31.4	–	32.0	29.5	–	–	35.0	–
Width middle of diaphysis	9.0	14.0	–	14.0	–	–	–	17.0	–
Maximum distal width	23.5	30.0	–	33.0	26.0	–	–	36.0	–
Tibiotarsus									
Total length	199.0	216.0	–	240.0	238.5	–	–	292.0	–
Maximum distal width	18.5	23.0	–	22.5	21.0	–	–	28.0	28.0
Tarsometatarsus									
Total length	145.0	164.0	–	178.5	179.5	–	–	216.0	–
Maximum proximal width	20.0	–	–	26.0	24.5	2.1	–	30.0	28.0
Width middle of diaphysis	9.0	10.5	–	12.0	–	–	–	14.0	15.0
Maximum distal width	20.0	23.7	–	26.5	–	2.2	26.0	29.1	–

[1] Type of *P. pueyrredonensis* Sinclair & Farr, 1932. Measurements from the original work.
[2] Measurements from Sinclair & Farr (1932).
[3] Measurements from Sinclair & Farr (1932).
[4] Measurements from Sinclair & Farr (1932).
[5] Type of *P. tenuirostris* Sinclair & Farr, 1932. Measurements from the original work.

Illustrations – Sinclair & Farr (1932).

Remarks – One of the best represented Phorusrhacidae by the relative abundance of fossils. Some observed discrepancies, especially in the skulls (Figs. 26F, 26G, 26H and 26I), should be attributed to differences in age or sex. *Psilopterus lemoinei* and *P. bachmanni* are herein dealt with as being two very similar species that appear to have lived together, disputing very similar niches. The most important difference between the two is in the size and proportions of the upper maxilla, and the differences in slant of the rostral edge of the antorbital fenestra. A deeper study might lead to different conclusions, as to the number of species of the genus *Psilopterus* from the Santacruzian of Argentina, as was discussed before under the sub-title: "intra-specific variations".

Psilopterus affinis (Ameghino, 1899) comb. n.

Phororhacos affinis Ameghino, 1899.

Type – The right tarsometatarsus lacking a segment of diaphysis (MACN-A-52-184).

Hypodigm – Only the type material.

Horizon and Locality – Guaranitica Formation of Patagonia (= Deseado Formation). The Middle to Upper Oligocene of Argentina (Deseadan), Chubut Province: Cabeca Branca.

Measurements – Table 8.

Diagnosis – Small size, rivalling *Psilopterus bachmanni*. It differs from all the others of the same kind as regards the upper part of the hipotarsus, where a transversal groove separates this from the cotylar surface.

Remarks – Treated as synonymous of *Andrewsornis abbotti* by Brodkorb (1967), just because it came from the same stratigraphic levels, it differs from this latter by being of a much smaller build. Brodkorb (*op. cit.*), furthermore, cites the epithet *affinis* as being pre-occupied by *Owenornis affinis* Moreno & Mercerat, 1891, a junior synonymon of *Phorusrhacos longissimus*, an unfounded concept, seeing that they are perfectly distinct genera. Without doubt, this is the least known species amongst the Phorusrhacidae. It is possible that, with new material and better study, the meagre and insufficient material based whereon Ameghino (1899) decribed other species coming from the "Guaranítica" (Deseadan) Formation of Patagonia, could be clarified: *Riacama caliginea*, *Smiliornis penetrans* and *Pseudolarus guaraniticus*. Some of these could possibly be synonymous with *Psilopterus affinis*, whereupon to the latter may be added more peculiarites which would justify separating it into a genus apart.

Psilopterus colzecus Tonni & Tambussi, 1988

Holotype – The incomplete skeleton of an individual (MLP-76-VI-12-2) consisting of the right incomplete mandibular symphysis, humerus, radius and ulnar, the right femur, the diaphysal portion of the tibiotarsus and tarsometatarsus, and the distal portion of the left tarsometatarsus together with the repective phalanges.

Hypodigm – Only the type material.

Horizon and Site – The Upper Miocene (Chasicoan) of Argentina: Arroyo Chasicó Formation, Province of Buenos Aires; Partido de Villarino.

Diagnosis – A size similar to that of *P. lemoinei*, representing the most recently known form of the genus. The most outstanding differences are in details of the trochlea of the tarsometatarsus with the other congenerous forms, are pointed out by Tonni & Tambussi (1988).

Measurements – Table 8 and Tonni & Tambussi (1988).

Illustrations – Tonni & Tambussi (1988).

Genus *Procariama* Rovereto, 1914

Type Species – *Procariama simplex* Rovereto, 1914.

Included Species – Only the type species.

Distribution – Upper Miocene to Lower Pliocene of Argentina. (Catamarca Province).

Diagnosis Revised – It is very similar to *Psilopterus*, being distiguished from this by the larger size and sturdier build (Fig. 1G), and by a slight difference in the proportion of the bones of the hind-limbs, where the femur is proportionally shorter (Patterson & Kraglievich, 1960:16). The wing bones of *Procariama* are also proportionally smaller (Fig. 3). In the tarsometatarsus, the hipotarsus forms two expansions (one lateral the other medial) in the most proximal part, this thus looking like two crests (Fig. 29A), different from both *Psilopterus* and *Paleopsilopterus*.

Procariama simplex Rovereto, 1914

Lectotype – Incomplete skeleton constituted by an incomplete skull, pelvis, proximal and distal portions of the left femur, distal portion of the right tibiotarsus, proximal and distal portions of the right tarsometatarsus, foot and ungual phalanges of the left foot (almost complete) and fragments of the phalanges of the right foot (MACN-8225), designated by Patterson & Kraglievich (1960).

Hypodigm – Lectotypes; right femur distally incomplete, distal portion of the left tarsometatarsus and some associated phalanges (MACN-6939); an almost complete skeleton in an excellent state of conservation (FM-P 14525) (Figs. 30, 31 and 32).

Horizon and Locality – Upper Miocene and Lower Pliocene (Huayquerian) of Argentina: Catamarca Province: Andalgala, Corral Quemado (Belem), Chiquimil, Rio Santa Maria (Estratos Araucanos).

Measurements – Table 8 and Patterson & Kraglievich (1960).

Illustrations – Rovereto (1914).

Remarks – The similar size to that of *Mesembriornis incertus* (Figs. 33F and 33G), plus the same stratigraphic occurrence, could lead to confusion amongst the fossils of these species, which, in fact, occurred with Rovereto (1914) in his original description. See the remarks related to *Mesembriornis incertus*.

Genus *Paleopsilopterus* Alvarenga, 1985

Type Species – *Paleopsilopterus itaboraiensis* Alvarenga, 1985.

Included Species – Only the type species.

Distribution – Middle Paleocene of Brazil (Rio de Janeiro).

Diagnosis – Heavier built than *Psilopterus*, similar to *Procariama*. The intercotylar tubercle of the tarsometatarsus is wide and rounded, and lower than in the abovementioned genera. The hypotarsus is laterally and distally expanded, covering the proximal foramina when viewed from below (Fig. 29C).

Paleopsilopterus itaboraiensis Alvarenga, 1985

Type – Proximal portion of the right tarsometatarsus (MNRJ-4040-V).

Hypodigm – Type; left and right tibiotarsus, proximally deformed and incomplete (Paratypes, DGM-1431-R).

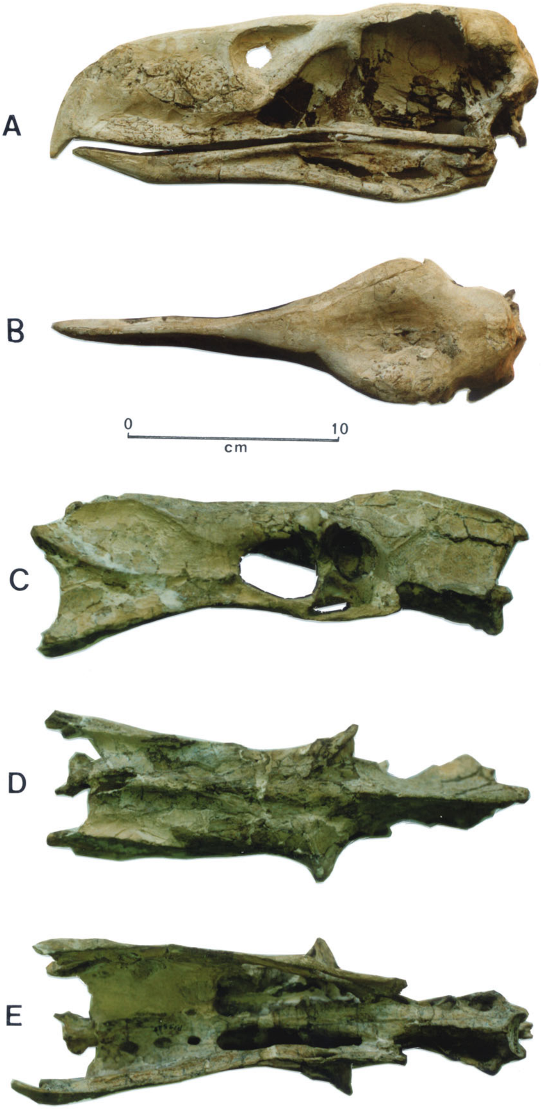

FIGURE 30. *Procariama simplex* (FM-P14525), from Corral Quemado, Argentina. Skull, A - left lateral and B - dorsal, views. Pelvis, C - right lateral, D - dorsal, and E - ventral, views.

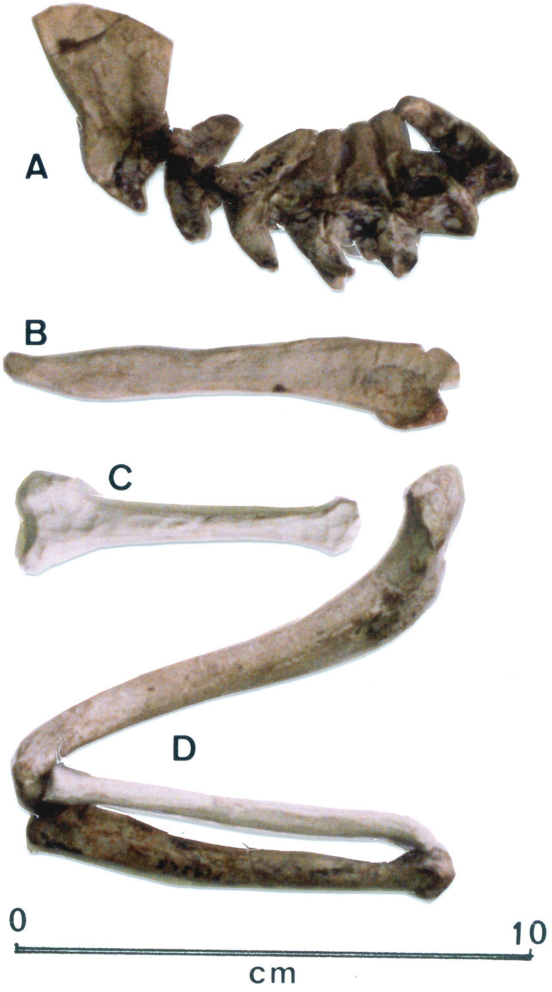

FIGURE 31. *Procariama simplex* (FM-P14525), from Corral Quemado, Catamarca, Argentina. A - caudal vertebrae and pygostyle, right lateral view; B - right scapula, lateral view; C - left coracoid, dorsal view; D - right humerus, radius and ulna, lateral view.

Horizon and Locality – Middle Paleocene (Itaboraian) of southeastern Brazil: Rio de Janeiro, Itaboraí.

Measurements – Table 8 and Alvarenga (1985 a).

Illustrations – Alvarenga (1985 a).

Remarks – It is the oldest Phorusrhacidae known.

Subfamily Mesembriornithinae Kraglievich, 1932 stat. n.

Mesembriorniidae Kraglievich, 1932.
Hermosiornidae Rovereto, 1914; Brodkorb, 1967 (syn. of Prophorhacinae).

FIGURE 32. *Procariama simplex* (FM-P14525), from Corral Quemado, Catamarca, Argentina. A - femurs, dorsal view; B - tibiotarsus, ventral view; C - tarsometatarsus, dorsal view. r = right; l = left

Hermosiorniidae Kraglievich, 1932
Hermosiornithidae Wetmore, 1934.
Hermosiornithinae Patterson & Kraglievich, 1960.
Prophororhacinae, Brodkorb, 1967; Mourer-Chauviré, 1981.

Diagnosis Revised – This is a relatively middle-sized Phorusrhacidae. The upper maxilla is relatively low, especially in the middle part, being rostrally lengthened (Fig. 1H and Fig. 26D). There is a short and relatively low mandibular symphysis. The coracoid is anchylosed to the clavicle (Figs. 4G and 4H). On the tibiotarsus, the apex of the internal condyle is more prominent and proximally bent, thus forming a more acute angle (when seen in internal view), with the diaphysis. They are the slimmest of the Phorusrhacidae, in which the tarsometatarsus reaches around 80 to 85% of the length of the tibiotarsus (Fig. 33), and wherein the middle trochlea is distally spread, with a width equal or more than the smallest transverse diameter of the diaphysis. The Mesembriornithinae are amongst the most recent of the Phorusrhacidae (Fig. 34).

Included Genera – *Mesembriornis* Moreno, 1889 (unique).

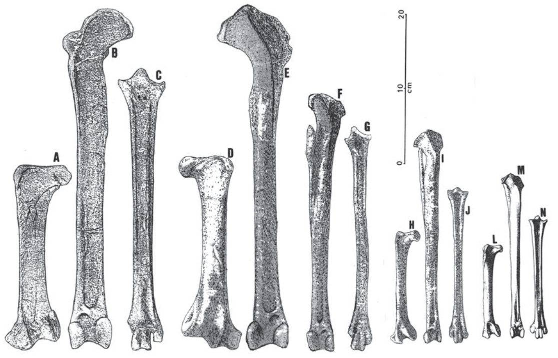

FIGURE 33. Bones of the hind limbs, of the Mesembriornithinae (A-G) and Psilopterinae (H-N). *Mesembriornis milneedwardsi* (MACN-5944; from Rovereto, 1914): A - right femur, dorsal view, B - left tibiotarsus, ventral view, and C - left tarsometatarsus, dorsal view. *Mesembriornis milneedwardsi* (MMP-S155): D - left femur, dorsal view, E - right tibiotarsus, ventral view. *Mesembriornis incertus* (FM-P14422): F - right tibiotarsus, ventral view, and G - right tarsometatarsus, dorsal view. *Procariama simplex* (FM-P14525): H - right femur, dorsal view, I - tibiotarsus, ventral view, and J - right tarsometatarsus, dorsal view. *Psilopterus lemoinei* (AMNH-9157 and 9257 from Sinclair & Farr, 1910): L - right femur, dorsal view, M - right tarsometatarsus, ventral view, and N - right tarsometatarsus, dorsal view.

Genus *Mesembriornis* Moreno, 1889; revalid. name.

Mesembriornis Moreno, 1889:29
Paleociconia Moreno, 1889:30.
Prophororhacus Rovereto, 1914:114.
Hermosiornis Rovereto, 1914:163.

Type Species – *Mesembriornis milneedwardsi* Moreno, 1889, designated by Richmond, 1902.

Included Species – The type species and *M. incertus* Rovereto, 1914.

Distribution – Upper Miocene to Upper Pliocene of Argentina.

Diagnosis – The same as for the subfamily.

Mesembriornis milneedwardsi Moreno, 1889 revalid.name

Mesembriornis milneedwardsi Moreno, 1889:29; Moreno & Mercerat, 1891; Brodkorb, 1967 (syn. of *Prophororhacos australis*).
Paleociconia australis Moreno, 1889:30; Moreno & Mercerat, 1891.
Driornis pampeanus Moreno & Mercerat, 1891 (part: only femur).
Hermosiornis milneedwardsi Rovereto, 1914.
Hermosiornis rapax Kraglievich, 1946; syn. n.
Prophororhacos australis Brodkorb, 1967:172.

Type – The centrum of a cervical vertebra associated to the proximal part of both the right tibiotarsus and fibula (MLP-140-142).

Hypodigm – Type; distal half of the left tarsometatarsus, lacking the external trochlea (MLP-87- type of *Paleociconia australis* Moreno, 1889); an almost complete skeleton, lacking especially the skull (MACN-5944); almost complete skeleton, including the skull and mandible, besides the left and incomplete humerus, radius and ulna, the femurs, and the right tibiotarsus and tarsometatarsus (MMP-S155); distal fragment of the right femur (MLP-170).

Horizon and Locality – The Middle and Upper Pliocene of Argentina (Montehermosan), Province of Buenos Aires; the Monte Hermoso and Chapadmalal Formations; Monte Hermoso, Rio Loberia.

Measurements – Table 9, Rovereto (1914), Kraglievich (1946) and Patterson & Kraglievich (1960).

Illustrations – Rovereto (1914) and Kraglievich (1932: PL. LVIII and 1946).

Remarks – Only a slighter larger size of specimen MMP-S155 does not justify the Kraglievich's (1946) specific separation of *Hermosiornis rapax*. Patterson & Kraglievich (1960:19) commented that specimens MACN-5944 and MLP-140-142 may belong to the same individual, which seems to be very probable. The skull of specimen MMP-S155 (Fig. 26D) is the only known one of Mesembriornithinae and even though pictured in Kraglievich's (1946), without comments, it is on some parts reconstructed; the rostral extremity, as well as the nostril region, are reconstructions; the height of the upper maxilla, in the middle part, is well defined but the length seems to be slightly increased in the reconstruction, mainly when considering the conserved mandible; the appearance of this skull seems to be more similar to that of *Psilopterus bachmanni* (Fig. 26I) than that represented in Kraglievich's (1946:109) restoration. (Julia Clark, pers. inf., 1999).

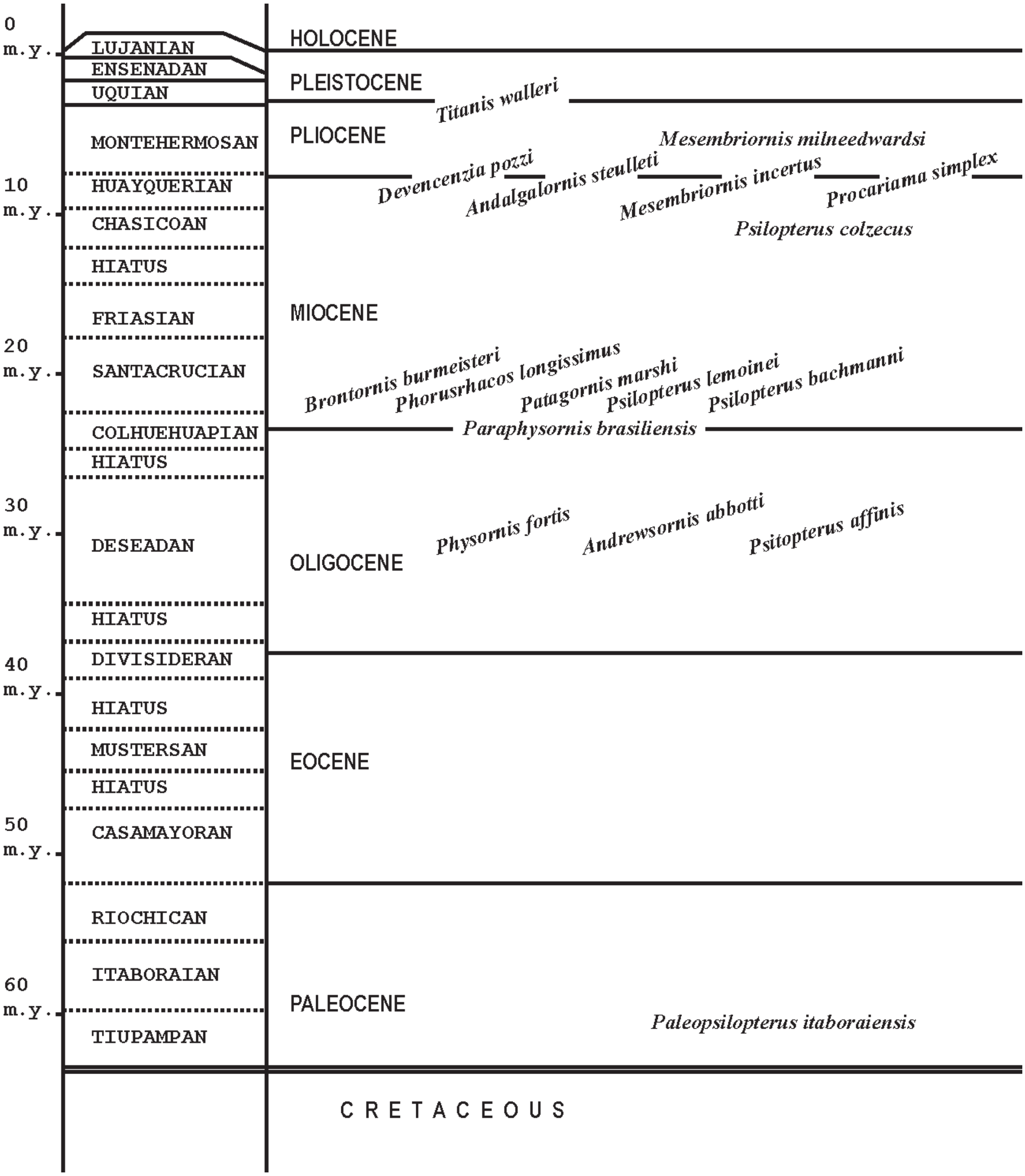

FIGURE 34. Geologic time-table with the distribution of the 17 species (13 genera) of the Phorusrhacidae under consideration herein, within the diverse periods of the Cenozoic. Column on the left represents the South American mammal age, based on Tonni (1980), Mac Fadden (1985) and Marshal *et al.* (1986).

Mesembriornis incertus (Rovereto, 1914) comb. n.

Prophororhacos incertus Rovereto, 1914; Brodkorb, 1967.

Type – A dorsal vertebra; a fragment of the omal portion of the left coracoid; each the right, humerus, ulna and part of the radius; distal part of the right tarsometatarsus and phalanges 1 of digits III and IV and phalanx 3 of digit II (MACN-6934).

Hypodigm – Type; the fragment of a cervical vertebra (MACN-6931); a tibiotarsus associated to the fibula, tarsometatarsus (Fig. 33F and 33G) and complete dig-

TABLE 9. Measurements of the Mesembriornithinae (cm). Numbers in brackets are estimates on incomplete bones.

	Mesembriornis incertus		*Mesembriornis australis*	
	MACN-6934 (type)	FM-P14422	MACN-5944	MMP-S1551
Skull				
Total length	–	–	–	44.0
Width at base	–	–	–	14.3
Height of maxilla	–	–	–	8.0
Mandible				
Total length	–	–	–	34.2
Length of symphysis	–	–	–	8.2
Hight base symphysis	–	–	–	3.4
Femur				
Total length	–	–	25.2	27.7
Proximal width	–	–	–	8.5
Distal width	–	–	–	8.7
Tibiotarsus				
Total length	–	(37.0)	42.1	45.8
Width middle diaphysis	–	2.6	3.2	3.2
Distal width	–	3.9	5.2	5.7
Tarsometatarsus				
Total length	–	31.5	36.0	(37.5)
Proximal width	–	4.3	6.3	6.1
Width middle diaphysis	–	1.9	2.7	2.5
Width middle trochlea	2.1	2.1	2.7	–

[1] Type of *Hermosiornis rapax* Kraglievich, 1946.

its I and II, all from the right side (FM-P14422); a left tarsometatarsus, with the proximal portion missing, and phalanges 1 and 2 of digit II (MACN-6737).

Horizon and Locality – The Upper Miocene to the Lower Pliocene, of Argentina (Huayquerian): Catamarca Province (Andalgala, Corral Quemado).

Diagnosis – Much smaller than *M. milneedwardsi*.

Measurements – Table 9.

Illustrations – Rovereto (1914).

Remarks – As commented by Patterson & Kraglievivh (1960:20), the "second specimen of *Procariama*" described by Rovereto (1914) is part of the same specimen that this author described as *Phororhacos incertus*, thus being added to the originally described type material (distal tarsometatarsus associated to the phalanges). The possibility of confusing material between these two species of similar sizes and the same geological age serves as a warning.

CONCLUSIONS

The family Phorusrhacidae belonging to the order Ralliformes, suborder Cariamae, consists of 13 genera and 17 species recognized nowadays, all being medium or large built birds, some of which even gigantic, rivalling with the largest already existing birds.

All are extinct. Their fossils are known as dating from the Middle Paleocene up to the limit Pliocene-Pleistocene (Fig. 34).

They certainly diversified at the end of the Cretaceous or beginning of the Cenozoic in South America, when this continental mass was insulated, separated from the remaining portions of the earth originating from the ancient supercontinent of Gondwana.They constituted an endemism very peculiar to South America, where they were the most spectacular land carnivores during most of the Tertiary. After South America became linked to North America, which occured with the raising of the isthmus of Panama, in the Upper Pliocene, the family also reached North America, where from at least one species is known (*Titanis walleri*).

Within the suborder Cariamae, the families Cariamidae, Idiornithidae and Bathornithidae are the closest to the Phorusrhacidae, and the identification of some fossil remains could be difficult if based on few segments of skeletons. Outstanding amongst the main characteristics of the family Phorusrhacidae are: the large or gigantic build; the narrow body, especially the upper maxilla, thorax and pelvis; the bulky and especially high upper maxilla, with the pointed, strong and curved apex; the existance of basipterigoid processes in the skull; the absence of uncinate processes on the ribs; the atrophiated cranial half of the pubis; the reduction of the wings and loss of the ability to fly; the extreme reduction of the acrocoracoid and procoracoid processes of the coracoid.

Those forms assigned to the family Phorusrhacidae from the Lower Tertiary of Europe and North America do not belong to this family; they present certain plesiomorphic similarities and are represented by only a few segments of the skeleton, which do not permit an adequate comparison, thus requiring a deeper revision in their phylogenetic afinities.

Moreover, some of the South American forms described based on only few segments of the skeleton, that do not allow for arriving at an effective conclusion as to their classification, even though several authors have already related them therein, are excluded from the family Phorusrhacidae. Included in this case are: *Riacama caliginea* Ameghino, 1899, *Smiliornis penetrans* Ameghino, 1899, *Pseudolarus guaraniticus* Ameghino, 1899, *Pseudolarus eocaenus* Ameghino, 1899 and *Lophiornis obliquus* Ameghino, 1891.

The proposed final classification is:

Order Ralliformes Reichenbach, 1852
Suborder Cariamae Fürbringer, 1888
Family Phorusrhacidae Ameghino, 1899

1 – Subfamily Brontornithinae Moreno & Mercerat, 1891
Genus *Brontornis* Moreno & Mercerat, 1891
B. burmeisteri Moreno & Mercerat, 1891
Genus *Physornis* Ameghino, 1895
P. fortis Ameghino, 1895
Genus *Paraphysornis* Alvarenga, 1993
P. brasiliensis (Alvarenga, 1982)

2 – Subfamily Phorusrhacinae Ameghino, 1889
Genus *Phorusrhacos* Ameghino, 1889
P. longissimus Ameghino, 1899
Genus *Devincenzia* Kraglievich, 1932
D. pozzi (Kraglievich, 1931)
Genus *Titanis* Brodkorb, 1963
T. walleri Brodkorb, 1963

3 – Subfamily Patagornithinae Mercerat, 1897
Genus *Patagornis* Moreno & Mercerat, 1891
P. marshi Moreno & Mercerat, 1891
Genus *Andrewsornis* Patterson, 1941
A. abbotti Paterson, 1941
Genus *Andalgalornis* Patterson & Kraglievich, 1960
A. steulleti (Kraglievich, 1931)

4 – Subfamily Psilopterinae Dolgopol de Saez, 1927
Genus *Psilopterus* Moreno & Mercerat, 1891
P. bachmanni (Moreno & Mercerat, 1891)
P. lemoinei (Moreno & Mercerat, 1891)
P. affinis (Ameghino, 1899)
P. colzecus Tonni & Tambussi, 1988
Genus *Procariama* Rovereto, 1914
P. simplex Rovereto, 1914
Genus *Paleopsilopterus* Alvarenga, 1985
P. itaboraiensis Alvarenga, 1985

5 – Subfamily Mesembriornithinae Kraglievich, 1932
Genus *Mesembriornis* Moreno, 1889
M. milneedwardsi Moreno, 1889
M. incertus (Rovereto, 1914)

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RESUMO

Foram estudados os fósseis de aves atribuídos à família Phorusrhacidae depositados em diversos museus da América do

Sul, da América do Norte e da Europa, com o objetivo principal de caracterizar esta família e reorganizar o estado caótico que até então envolvia a nomenclatura e classificação destas aves. A reconstituição de algumas espécies é feita, com o propósito de formar uma idéia sobre o tamanho, massa corpórea, postura e hábitos com base no esqueleto das mesmas. As formas européias, Ameghinornis minor *e* Aenigmavis sapea *são refutadas como pertencentes à esta família. São refutadas ainda várias formas do Terciário da Argentina, descritas com base em segmentos de esqueleto, insuficientes para uma plena identificação como é o caso dos gêneros* Cunampaia, Smiliornis, Pseudolarus, Lophiornis *e* Riacama, *freqüentemente referidos como pertencentes aos Phorusrhacidae. A família Phorusrhacidae certamente originou-se na América do Sul pelo final do Cretáceo, como resultado de um endemismo formado pelo isolamento dessa porção de terra. Pelo final do Plioceno, com a emersão do istmo do Panamá, a família estendeu-se até a América do Norte onde pelo menos uma espécie,* Titanis walleri *que talvez represente a última conhecida desta família, que extinguiu-se no início do Pleistoceno. A revisão sistemática foi conduzida com inúmeros problemas de nomenclatura e a família Phorusrhacidae passa então a ser constituída de cinco subfamílias, ou seja: Brontornithinae, Phorusrhacinae, Patagornithinae, Psilopterinae e Mesembriornithinae, nas quais se distribuem 13 gêneros e 17 espécies. Os caracteres de todos os táxons são descritos e finalmente é apresentada uma distribuição geocronológica de todas as espécies.*

Palavras-chave: Phorusrhacidae, Ralliformes, Gruiformes, Terciário, Aves gigantes.

REFERENCES

Alvarenga, H. 1982. Uma gigantesca ave fóssil do Cenozóico brasileiro: *Physornis brasiliensis* sp. n. *Anais da Academia Brasileira de Ciências*, 54:697-712.

Alvarenga, H. 1985a. Um novo Psilopteridae (Aves: Gruiformes) dos sedimentos Terciários de Itaboraí, Rio de Janeiro, Brasil. In: Congresso Brasileiro de Paleontologia, 8. *Anais*. Rio de Janeiro, NME-DNPM, 1983. p.17-20. (Série Geologia, 27)

Alvarenga, H. 1985b. Notas sobre os Cathartidae (Aves) e descrição de um novo gênero do Cenozóico brasileiro. *Anais da Academia Brasileira de Ciências*, 57:349-357.

Alvarenga, H. 1990. Flamingos fósseis da bacia de Taubaté, Estado de São Paulo, Brasil: descrição de nova espécie. *Anais da Academia Brasileira de Ciências* 62:335-345.

Alvarenga, H. 1993. *Paraphysornis* novo gênero para *Physornis brasiliensis* Alvarenga, 1982 (Aves: Phorusrhacidae). *Anais da Academia Brasileira de Ciências*, 65:403-406.

Amadon, D. 1947. An estimated weight of the largest known bird. *Condor*, 49:159-164.

Ameghino, F. 1887. Enumeración sistemática de las espécies de mamíferos fósiles coleccionados por Carlos Ameghino en los terrenos Eocenos de la Patagonia austral y depositados en el Museo de La Plata. *Boletim Museo La Plata*, 1:1-26.

Ameghino, F. 1889. Contribuición al conocimiento de los mamíferos fósiles de la República Argentina. *Actas Academia Nacional Ciencias de Cordoba*, 6:1-1028.

Ameghino, F. 1891a. Mamíferos y aves fósiles Argentinos: espécies nuevas: adiciones y correciones. *Revista Argentina Historia Natural*, 1:240-259.

Ameghino, F. 1891b. Enumeración de las aves fósiles de la República Argentina. *Revista Argentina Historia Natural*, 1:441-453.

Ameghino, F. 1895. Sobre las aves fósiles de Patagonia. *Boletin del Instituto Geografico da Argentina*, 15:501-602.

Ameghino, F. 1898. Sinopsis geológico-paleontológica de la Argentina. *Segundo Censo de la República Argentina*, 1:112-255.

Ameghino, F. 1899. Sinopsis geológico-paleontológica. Suplemento (Adiciones y correciones), La Plata, 13p.

Ameghino, F. 1901. L'age des formations sédimentaires de Patagonie. *Anales de la Sociedad Cientifica Argentina*, 51:65-91.

Andrews, C. 1896. Remarks on the Stereornithes, a group of extinct birds from Patagonia. *Ibis*, 7:1-12.

Andrews, C. 1899. On the extinct birds of Patagonia. *Transactions of the Zoological Society of London*, 15:55-86.

Baskin, J.A. 1995. The giant flightless bird *Titanis walleri* (Aves: Phorusrhacidae) from the Pleistocene coastal plain of south Texas. *Journal of Vertebrate Paleontology*, 15:842-844.

Baumel, J. &. Witmer, L. 1993. Osteologia. In: Baumel, J. ; King, A.; Breazile, J.; Evans, H. & Berge, J. (eds.), *Nomina Anatomica Avium*. 2. ed., Cambridge. Nuttal Ornithological Club. p.45-132. (Publications of the Nuttall Ornithological Club 23)

Brodkorb, P. 1963. A giant flightless bird from the Pleistocene of Florida. *Auk*, 80:111-115.

Brodkorb, P. 1967. Catalogue of fossil birds, Part III (Ralliformes, Ichthyornithiformes, Charadriiformes). *Bulletin of Florida State Museum*, 2:99-220.

Cabrera, A. 1939. Sobre vertebrados fósiles del Plioceno de Adolfo Alsina. *Revista del Museo La Plata*, 2:3-35.

Campbell Jr., K. & Marcus, L. 1992. The relationship of hindlimb bone dimensions to body weight in birds. *Science Series. Natural History Museum of Los Angeles County*, 36:395-412.

Campbell Jr., K. &. Tonni, E. 1980. A new genus of teratorn from the Huayquerian of Argentina (Aves: Teratornithidae). *Contributions in Science. Natural History Museum of Los Angeles County*, 330:59-68.

Case, J.A.; Woodburne, M & Chaney, D. 1987. A gigantic phororhacoid (?) bird from Antarctica. *Journal of Paleontology*, 61:1280-1284.

Carr, G.E. 1981. *An early Pleistocene avifauna from Inglis Florida*. Gainesville, Univ. Florida, 161p. (Ph.D. Dissertation)

Chandler, R.M. 1994. The wing of *Titanis walleri* (Aves: Phorusrhacidae) from the late Blancan of Florida. *Bulletin of Florida Museum of Natural History*, 36:175-180.

Chiappe, L. & Soria, M. 1990. *Phororhacos* Ameghino, 1889 (Aves, Gruiformes): proposed conservation. *Bulletin of Zoological Nomenclature*, 3:198-201.

Cracraft, J. 1968. A review of the Bathornithidae (Aves, Gruiformes), with remarks on the relationships of the suborder Cariamae. *American Museum Novitates*, 2326:1-46.

Cracraft, J. 1971. Systematics and evolution of the Gruiformes (Class Aves) 2. Additional comments on the Bathornithidae, with descriptions of new species. *American Museum Novitates*, 2449:1-14.

Cracraft, J. 1976. The species of moas (Aves: Dinornithidae). *Smithsonian Contributions to Paleobiology*, 27:189-205.

Dolgopol de Saez, M. 1927. Las aves corredoras fósiles del Santacrucense. *Anales de la Sociedad Cientifica Argentina*, 103:145-64.

Gilbert, B.; Martin, L. & Savage, H. 1981. *Avian Osteology*. Laramie, B. Miles Gilbert Publisher. 252p.

Howard, H. 1929. The avifauna of Emeryville shellmound. *University of California Publications in Zoology*, 32:301-394.

Kraglievich, L. 1931. Contribución al conocimiento de las aves fósiles de la época araucoentrerriana. *Physis*, 10:304-315.

Kraglievich, L. 1932. Una gigantesca ave fósil del Uruguay, *Devincenzia gallinali* n. gen. n. sp., tipo de una nueva familia, Devincenziidae, del Orden Stereornithes. *Anales del Museo Historia Natural de Montevideo*, 3:323-55.

Kraglievich, L. 1946. Noticia preliminar acerca de un nuevo y gigantesco Estereornito de la fauna Chapadmalense. *Anales de la Sociedad Cientifica Argentina*, 142:104-121.

Lambrecht, K. 1933. *Handbuch der Paleornithologie*. Berlin, Gebrüder Bornthreger. 1024p.

Livezey, B.C. 1998. A phylogenetic analysis of the Gruiformes (Aves) based on morphological characters, with an emphasis on the rails (Rallidae). *Transactions of the Royal Society of London*, 353:2077-2151.

Loomis, F.B. 1914. *The Deseado formation of Patagonia*. Massachussets, Public Amherst College. 232p.

Lydekker, R. 1891. *Catalogue of the fossil birds in the British Museum (Natural History)*. London, British Museum Publishers. 368p.

Lydekker, R. 1893. On the extinct giant birds of Argentina. *Ibis*, 5:40-47.

MacFadden, B.J. 1985. Essay review of Marshall, Hoffstetter and Pascual, drifting continents, mammals, and time scales: current developments in South America. *Journal of Vertebrate Paleontology*, 5:169-74.

Marshall, L.G.; Cifelli, R.; Drake, R. & Curtis, G. 1986. Vertebrate paleontology, geology, and geochronology of the Tapera de Lopez and Scarritt Pocket, Chubut Province, Argentina. *Journal of Paleontology*, 60:920-951.

Mercerat, A. 1893. *Note sur la géologie de Patagonie*. Buenos Aires. 6p.

Mercerat, A. 1897. Note sur les oiseaux fossiles de la Republique Argentine. *Anales de la Sociedad Cientifica Argentina*, 43:222-240.

Moreno, F.P. 1889. Breve reseña de los progresos del Museo La Plata, durante el segundo semestre de 1888. *Boletin del Museo* La *Plata*, 3:1-44.

Moreno, F.P. & Mercera, A. 1891. Catálogo de los pájaros fósiles de la República Argentina conservados en el Museo de La Plata. *Anales del Museo de La Plata*, 1:7-71.

Mourer-Chauviré, C. 1981. Première indication de la présence de Phorusrhacidés, famille d'oiseaux géants d'Amérique du Sud, dans le Tertiaire Européen: *Ameghinornis* nov. gen. (Aves, Ralliformes) des Phosphorites du Quercy, France. *Geóbios*, 14:637-647.

Mourer-Chauviré, C. 1983. Les Gruiformes (Aves) des Phosphorites du Quercy (France). I. Sous-ordre Cariamae (Cariamidae et Phorusrhacidae) systématique et biostratigraphie. *Paleovertebrata*, 13:83-143.

Noriega, J. 1995. The avifauna from the "Mesopotamian" (Ituzaingó Formation; Upper Miocene) of Entre Rios Province, Argentina. *Courier Forschungsinstitut Senckenberg*, 181:141-148.

Olson, S. 1985. The fossil record of birds. In: Farner, D.; King, J. & Parkes, K. (eds.). *Avian Biology*. New York, Academic Press. v.8, p.79-252.

Patterson, B. 1941. A new phororhacoid bird from the Deseado formation of Patagonia. *Field Museum of Natural History, Geological Series*, 8:49-54.

Patterson, B. & Kraglievich, L. 1960. Sistemática y nomenclatura de las aves fororracoideas del Plioceno Argentino. *Publicacion del Museo Municipal Ciencias Naturales y Tradicionales de Mar del Plata*, 1:1-51.

Peters, D.S. 1987. Ein "Phorusrhacidae" aus dem Mittel-Eozan von Messel (Aves: Gruiformes: Cariamae). *Documents des Laboratoires de Géologie de Lyon*, 99:71-87.

Richmond, C. 1902. List of generic terms proposed for birds during the years 1890 to 1900, inclusive, to which are added names omitted by Waterhouse in his "Index generum avium". *Proceedings United States National Museum*, 24:663-730.

Rovereto, C. 1914. Los estratos araucanos y sus fósiles. *Anales del Museo Nacional Historia Natural de Buenos Aires*, 25:1-247.

Rusconi, C. 1946. Algunos mamíferos, reptiles y aves del Oligoceno de Mendoza. *Revista de la Sociedad de Historia y Geografia de Cuyo*, 2:1-37.

Sinclair, W. & Farr, M. 1932. Aves of the Santa Cruz beds. In: Scott, W. (ed.) *Reports of the Princeton University expeditions to Patagonia (1896-1899)*. Princeton University. v.7, p.157-191.

Soria, M. & Alvarenga, H. 1989. Nuevos restos de mamíferos de la cuenca de Taubaté, Estado de São Paulo, Brasil. *Anais da Academia Brasileira de Ciências*, 61(2):157-175.

Thiollay, J. 1994. Family Accipitridae (hawks and eagles). In: Hoyo, J.; Elliott, A. & Sargatal, J. (eds.), *Handbook of the birds of the world*. Barcelona, Lynx Edicions. v.2, p.52-205.

Tambussi, C.; Ubilla, M. &. Perea, D. 1999. The youngest large carnassial bird (Phorusrhacidae, Phorusrhacinae) from South America (Pliocene-Early Pleistocene of Uruguay). *Journal of Vertebrate Paleontology*, 19:404-406.

Tonni, E. 1980. The present state of knowledge of the cenozoic birds of Argentina. *Contributions in Science. Natural History Museum of Los Angeles County*, 330:105-114.

Tonni, E. & Tambussi, C. 1988. Un nuevo Psilopterinae (Aves: Ralliformes) del Mioceno tardio de la Provincia de Buenos Aires, Republica Argentina. *Ameghiniana*, 25:155-160.

Wetmore, A. 1944. A new terrestrial vulture from the Upper Eocene deposits of Wyoming. *Annals of the Carnegie Museum*, 30:57-69.

Wetmore, A. 1967. Re-creating Madagascar's giant extinct bird. *National Geographic*, 132:488-493.

Wroe, S. 1998. Bills, bones and bias: did thunder birds eat meat? *Riversleigh Notes*, 40:2-4.

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