Review of the putative Phorusrhacidae from the Cretaceous and Paleogene of Antarctica: new records of ratites and pelagornithid birds

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Abstract: Remains referred to Phorusrhacidae from the Cretaceous and Paleogene of the Antarctic Peninsula, and mainly known through informal and succinct descriptions, are re-assigned here to other bird lineages recorded in the Antarctic continent. New records of ratites, pelagornithid birds, and penguins are added to the Upper Eocene avifauna of Seymour Island. Moreover, the original allocation for an alleged cursorial seriema-like bird from the Maastrichtian of Vega Island is refuted, and its affinities with foot-propelled diving birds are indicated. The indeterminate Pelagornithidae specimen represents the largest pseudo-toothed bird known so far. It is concluded that there is no empirical evidence for the presence of terror birds in Antarctica.

Key words: Antarctica, fossil birds, Cretaceous, Eocene.

Introduction

The phorusrhacids, commonly known as "terror birds", constitute one of the most characteristic avifaunal elements of the Cenozoic of South America. Their adaptive radiation resulted in about 18 species (Alvarenga and Höfling 2003; Alvarenga *et al*. 2010, 2011), including medium-sized forms as well as the largest cursorial carnivorous birds ever. Their extremely large skulls with hooked beaks and powerful claws on their hindlimbs have allowed to propose them, together with the large borhyaenid marsupials (Wroe *et al*. 2004), as the top predators of the Tertiary ecosystems of South America (Tambussi and Noriega 1996; Blanco and Jones 2005; Agnolin 2009; Degrange *et al*. 2010; Alvarenga *et al*. 2010; Tambussi 2011).

Outside South America, remains of Phorusrhacidae are been referred to the Tertiary of Europe, North America, Africa, and Antarctica. However, the only widely accepted phorusrhacid is *Titanis walleri* Brodkorb, 1963 (Chandler 1994, 1997; Baskin 1995; Gould and Quitmyer 2005), from the Pliocene of Texas and Florida
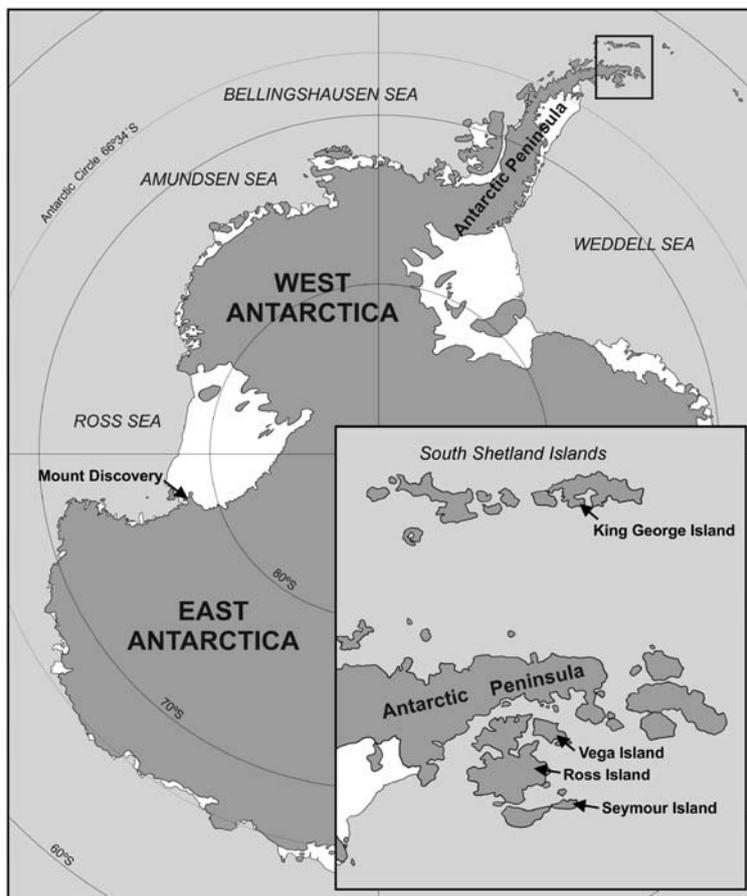
Fig. 1. Location map of Antarctica showing the fossiliferous localities mentioned in the text.

(McFadden *et al*. 2007). Mourer-Chauviré (1981) and Peters (1987) considered the family Ameghinornithidae, from the Paleogene of France and Germany, as the Old World representatives of Phorusrhacidae. This proposal has been rejected by Alva-renga and Höfling (2003) and Mayr (2005, 2007) because this family is considered as a basal Cariamae (Mayr 2007; Agnolin 2009). However, two recent findings indicate a more complex biogeographic history for the basal Cariamae than that previously assumed. These are: some remains from the Upper Paleocene of Brazil, which may present a close affinity with the European idiornithid genus *Elaphrocnemus* (Mayr *et al*. 2011, Idiornithidae affinities of some old Patagonian remains traditionally assigned to Phorusrhacidae were also mentioned by Agnolin 2004, 2009), and the possible presence of a phorusrhacid bird in the Lower–Middle Eocene of Algeria, North Africa (Mourer-Chauviré *et al*. 2011).

Finally, very few and fragmentary remains were useful to indicate the presence of the terror birds in Antarctica during the Cretaceous–Eocene times (Case *et al*.

1987, 2006; Tambussi and Noriega 1996; Chavez 2007; Tambussi and Acosta Hospitaleche 2007). With the exception of the premaxillary fragment described by Case *et al*. (1987), other putative phorusrhacids have not been formally described or figured. Nevertheless, despite the lack of a formal analysis, the assignment to this group of birds has been constantly present in the bibliography (*e.g*., Tambussi and Noriega 1996; Reguero *et al*. 2002; Alvarenga and Höfling 2003; Tambussi and Acosta Hospitaleche 2007; Case 2006; Chavez 2007; Agnolin 2009; Alvarenga *et al*. 2011; Mourer-Chauviré *et al*. 2011). A detailed restudy of these specimens is performed here, showing that they can be referred to other, already recorded in Antarctica, bird lineages.

Materials and methods

Institutional abbreviations. — FMNH, Field Museum of Natural History, Chicago, USA; KUPV, Kansas University, Vertebrate Paleontology Collection, Lawrence, USA; MACN, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, USA; MLP, Museo de La Plata, La Plata, Argentina; MMMP, Museo Municipal de Mar del Plata, Mar del Plata, Argentina; MNHN, Museo Nacional de Historia Natural, Santiago, Chile; NHMUK, Natural History Museum, London, United Kingdom; OCP.DEK/GE, Office Chérifien des Phosphates, Direction des Exploitations de Khouribga, Service de Géologie, Morocco; UCR, University of California, Riverside, USA; UNSM, University of Nebraska State Museum, Lincoln, USA; USNM, National Museum of Natural History, Washington, USA.

The systematic criteria for Ratitae (*i.e.*, Apterygidae, Rheidae, Struthionidae, Casuariidae, Dromaiidae, Dinornithidae, and Aepyornithidae) follows the phylogenetic analysis performed by Bourdon *et al*. (2009) supporting the monophyly of the group, with the tinamous (Tinamidae) as their closest living relatives. Within the Phorusrhacidae, the taxonomical proposal of Alvarenga and Höfling (2003) is adopted and, for the Pelagornithidae, the works of Bourdon (2005, 2011), Bourdon *et al*. (2010), and Mayr (2011) are mainly followed.

The osteological terminology follows Baumel and Witmer (1993) and Livezey and Zusi (2006), all the measurements are in millimeters. The anatomical comparisons were based on specimens representing both extinct and extant species deposited in the MLP and MACN (see Appendix 1). For additional comparison the Pelagornithidae specimens figured in Hopson (1964), Harrison and Walker (1976, 1977), Walsh and Hume (2001), Bourdon (2005, 2006, 2011), Mayr and Rubilar-Rogers (2010), and Bourdon *et al*. (2010); the Dinornithidae specimens in Owen (1879), and Worthy and Holdaway (2002); and the Casuariidae specimens in Richardson (1991) were consulted.

Systematic paleontology

Class Aves Linnaeus, 1758
Cohort Palaeognathae Pycraft, 1900
Subcohort Ratitae Merrem, 1813
Ratitae gen. et sp. indet.
(Fig. 2A)

Referred material. — UCR 22175; fragmentary corpus ossis premaxillaris.

Locality and horizon. — Uppermost levels of the Submeseta Allomember (RV-8405 locality, Case *et al*. 1987; Upper Eocene, about 32–36 million years ago, see Dutton *et al*. 2002; Reguero *et al*. 2002), La Meseta Formation, *Anthropornis nordenskjoeldi* Biozone (Tambussi *et al*. 2006), Seymour Island (Marambio), Antarctic Peninsula (Fig. 1).

Measurements. — Maximum length preserved: 77.29; maximum width preserved: 35.42; maximum height preserved: 31.83.

Description and comparisons. — The fragment of os premaxillare shows a complete apex rostri; caudally, the bone is preserved until the beginning of the apertura nasi ossea, dorsally limited by a fragmentary processus frontalis premaxillare. The Antarctic material shows the following combination of features exclusively found in Ratitae birds (Fig. 2A–D): (1) corpus ossis premaxillaris relatively smaller but stout, poorly pneumatized and with thick bony walls (see Case *et al*. 1987: fig. 2, image 3; contrasting with a more elongated corpus present in the Tinamidae); (2) in lateral view, os premaxillare short and low; (3) apex rostri slightly sharpened and poorly ventraly projected (a similar condition can be seen in Casuariidae, Dromaiidae, Tinamidae and some Dinornithidae, in other Ratitae the apex is broad, rounded and not ventrally projected; *e.g*., *Rhea*, *Struthio*); (4) apertura nasi ossea very close to the apex rostri (more caudally placed in Tinamidae); (5) narrow processus frontalis premaxillare (unambiguous synapomorphy for Casuariidae + Dromaiidae in Bourdon *et al*. 2010, character 30); (6) osseous surface perforated by numerous foramina neurovascularia (this feature seems less developed in UCR 22175 than in the known Ratitae); (7) in ventral view, narrow and shallow os premaxillare (a similar condition can be seen in Casuariidae and Tinamidae), developing a poorly excavated central longitudinal sulcus (reduced or lost in Tinamidae); (8) cristae tomiales poorly developed; (9) conspicuous nasolabial grooves (*sensu* Hieronymus and Witmer 2010) dorsolaterally placed converging with the apertura nasi ossea. This last feature is one of the most remarkable characters observed in the Antarctic material, given that the presence of the marked grooves cranial to the apertura nasi ossea was noted as a synapomorphy of palaeognathous birds (apomorphically lost or reduced in some Tinamidae, see Mayr and Clarke 2003, charater 4) indicating that the compound rhamphotheca
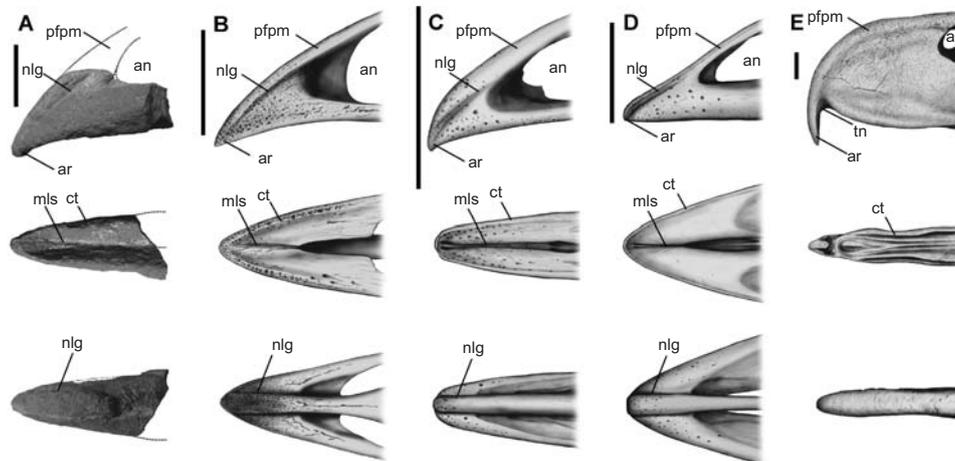
Fig. 2. Comparative morphology of the corpus ossis premaxillaris in some Ratitae and Phorusrhacid birds. **A**. Indeterminate Antarctic Ratitae UCR 22175 (MLP cast). **B**. Dinornithidae *Pachyornis elephantopus* (Owen, 1856), after Owen (1879). **C**. Casuariidae *Casuarius bennetti* Gould, 1857. **D**. Dromaiidae *Dromaius novaehollandiae* (Latham, 1790). **E**. Phorusrhacidae *Andalgalornis steulleti* (Kraglievich, 1931) FMNH P14357. Top, middle and bottom rows: lateral, ventral, and dorsal views, respectively. Abbreviations: an – apertura nasi ossea; ar – apex rostri; ct – crista tomialis; mls – medio-longitudinal sulcus; nlg – nasolabial grooves; pfpm – processus frontalis premaxillare; tn – tomial notch. Scale bars are 30 mm.

has a unique shape in this avian lineage (Parkes and Clark 1966; Cracraft 1974). Initially this character was also mentioned as a synapomorphy of "Pelecaniformes" + Procellariiformes by Cracraft (1988:349, character 3) but currently is considered as an apomorphy of a more comprehensive group, the "Waterbird assemblage" (Aequornithes *sensu* Mayr 2010, see also Mayr and Clarke 2003; Mayr 2003; Ericson *et al.* 2006; Hackett *et al.* 2008; Hieronymus and Witmer 2010; including Procellariiformes, "Pelecaniformes", "Ciconiiformes", Sphenisciformes, Scopidae, Balaenicipitidae, and Threskiornithidae). Other non-related group that exhibits the abovementioned groove is Pelagornithidae (*e.g.*, Bourdon *et al.* 2010; Mayr and Rubilar-Rogers 2010). Even though the presence of these last two groups of birds have been referred to the same stratigraphic unit bearing UCR 22175 (for a summary of these records see Tambussi and Acosta Hospitaleche 2007), such material coincides only with the morphology seen in Ratitae. The combination of both premaxillary grooves, and the general shape of the os premaxillare clearly distinguishes UCR 22175 from Aequornithes and Pelagornithidae. The most notable differences are: (1) short and relatively solid os premaxillare (*vs.* extremelly elongated and very pneumatic) with a thin processus frontalis premaxillare (*vs.* robust); (2) apertura nasi ossea close to apex rostri (*vs.* placed very caudally, next to the zona flexoria craniofacialis); (3) poorly developed cristae tomiales (sharp in many Aequornithes); (4) much shorter nasolabial grooves and more dorsally positioned, obliquely converging with the tomial

edges on the cranial end (*vs.* elongated grooves placed near and parallel to the tomial edges); (5) nasolabial grooves limiting a narrow, low and craniocaudally elongated "nail" that extends more caudally than both apertura nasi ossea (*vs.* robust, broad and dorsally rounded "nail", whose caudal end is limited by a culminolabial groove *sensu* Hieronymus and Witmer 2010); (6) slightly sharp apex rostri and poorly ventrally projected (*vs.* strongly developed as a sharp ventral hook in many Aequornithes; *i.e.*, typical hamulus rostri maxillare *sensu* Livezey and Zusi 2006); (7) no tomial projections (characteristic of Pelagornithidae); and (8) shallow palatal surface.

Additionally, according to reported measures, as well as the described morphology, the material has greater affinities with the group of larger Ratitae than the relatively smaller South American Tinamidae.

Remarks. — In the original description, Case *et al.* (1987) noted the possible inclusion of UCR 22175 within Phorusrhacidae indicating that "The laterally compressed dorsal portion of the beak, the anterior rostral expansion, the lateral grooves on the premaxilla, and the bilateral sinuses are features which have previously been described in phororhacoids" (Case *et al.* 1987: 1281). However, the characters used by these authors are, in some cases, non-diagnostic for Phorusrhacidae; in other cases allow, on the contrary, the exclusion from this group and the assignment to the Ratitae birds, as previously justified. Nevertheless, it is included here a list of the main characters that allow to exclude the material from Seymour Island from Phorusrhacidae (Fig. 2): (1) poorly developed os premaxillare, dorsoventrally low, craniocaudally short, and slightly compressed laterally (*vs.* great development forming most of the rostrum, being very voluminous, high and extremely compress; Ameghino 1895; Andrews 1899; Sinclair and Farr 1932; Patterson and Kraglievich 1960; Mayr 2002; Alvarenga and Höfling 2003; Degrange and Tambussi 2011); (2) slightly craniodorsally recurved os premaxillare (*vs.* strongly to extremely convex, see Ameghino 1895; Andrews 1899; Sinclair and Farr 1932; Alvarenga *et al.* 2011); (3) apex rostri ("anterior rostral expansión" *sensu* Case *et al.* 1987: 1281) with a slight ventral projection (*vs.* projects prominently as a sharp ventral hook, see Ameghino 1895; Sinclair and Farr 1932; Mayr 2002; Alvarenga and Höfling 2003; Bertelli *et al.* 2007; Agnolin 2009; Alvarenga *et al.* 2011; presence of true hamulus rostri maxillare); (4) marked dorsolateral nasolabial grooves ("lateral grooves" *sensu* Case *et al.* 1987: 1281) cranial to the apertura nasi ossea (absent in all known phorusrhacid birds, where the only present grooves are in the labial edge [ventrolateral] of the apex rostri, ventrally ending near of beginning of the cristae tomiales, see Andrews 1899; Bertelli *et al.* 2007; these grooves are not homologous to those described for UCR 22175); (5) in lateral view, ventral tomial margin of the os maxillare essentially straight (the terror birds exhibit un conspicuous tomial notch, see Andrews 1899; Sinclair and Farr 1932; see Fig. 2E); (6) thick outer bone surface profusely pierced by foramina neurovascularia (*vs.* thin and compact surface lacking foram-

ina neurovascularia but scarred by highly branched deep vascular grooves, see Ameghino 1895; Andrews 1899; Degrange and Tambussi 2011); (7) in ventral view, wide and low cristae tomiales (*vs.* very narrow and sharp, see Ameghino 1895; Andrews 1899; Degrange and Tambussi 2011); (8) shallow ventral surface with a slight and cranially bifurcated central longitudinal groove (*vs.* deep and complex ventral surface with one to three conspicuous tubercula that develop ridges towards the caudal end, see Ameghino 1895; Andrews 1899; reduced or absent in *Psilopterus* specimens, Sinclair and Farr 1932; Patterson and Kraglievich 1960); (9) in caudal view (where the bone is broken, see Case *et al*. 1987: fig. 2, image 3) there are two bilateral sinuses surrounded by thick layers of bone (in the same region of the os premaxillare in Phorusrhacidae it has been described the presence of single large sinus with trabecular structure and surrounded by thin and compact bone, see Degrange and Tambussi 2011). Finally, Case *et al*. (1987) noted that the specimen shows a feature that could be unique among phorusrhacids: "The external nares extend anteriorly, forward of the anterior rostral expansion" (Case *et al*. 1987: 1281). This is a feature that definitively excludes UCR 22175 from the terror birds, where the apertura nasi ossea is very dorsocaudally positioned, being at a considerable distance of the apex rostri (Ameghino 1895; Andrews 1899; Sinclair and Farr 1932; Patterson and Kraglievich 1960; Agnolin 2009; Degrange and Tambussi 2011; Fig. 2E).

The characters listed for Phorusrhacidae are present in all members of the family, although its development tends to increase from the small and primitive specimens of *Psilopterus* (Sinclair and Farr 1932; Degrange and Tambussi 2011) to the most derived and giant ones belonging to the genera *Onactornis* and *Kelenken* (Cabrera 1939; Bertelli *et al*. 2007).

On the other hand, Alvarenga and Höfling (2003) also noted possible phorusrhacid affinities for the material from Seymour Island indicating similarities with the mandibular symphysis of the giant Brontornithinae. In this regard, Alvarenga *et al*. (2011:191) recently noted: "… that is certainly a mandibular symphysis of a huge phorusrhacid, closely related to the *Brontornis* genus"; however, this conjecture has never been proven with a formal comparison. As previously justified, UCR 22175 undoubtedly belong to a fragment of os premaxillare, moreover, all of the features listed by Alvarenga and Höfling (2003) in the diagnosis of the Brontonithinae are absent in the studied material. The Antarctic specimen differs from Brontornithinae in its considerably smaller size, the presence of subparallel tomial edges (*vs.* strongly divergent, see Alvarenga and Höfling 2003: fig. 7B–C), a "dorsal" surface of the putative "symphysis" much narrower and comparatively deeper (showing a V-shaped edge in cross section, *vs.* very wide U-shape edge in Brontornithinae) exhibiting a well-developed middle-longitudinal sulcus, and the lateral profile of UCR 22175 is also much lower than the one known for the Brontornithinae. Hence, any affinity of this specimen with the terror bird can be ruled out.

Cohort Neognathae Pycraft, 1900
Order Odontopterygiformes Howard, 1957
Family Pelagornithidae Fürbringer, 1888
Pelagornithidae gen. et sp. indet.
(Fig. 3A)

Referred material. — UCR 22176; distal end of a right tarsometatarsus.

Locality and horizon. — Uppermost levels of the Submeseta Allomember (RV 8702 locality; Upper Eocene, about 32–36 million years ago, see Dutton *et al*. 2002; Reguero *et al*. 2002), La Meseta Formation, *Anthropornis nordenskjoeldi* Biozone (Tambussi *et al*. 2006), Seymour Island (Marambio), Antarctic Peninsula (Fig. 1).

Measurements. — See Table 1.

Description and comparison. — Bourdon *et al*. (2010) noted that, within the family Pelagornithidae, commonly known as "pseudo-toothed" or "bony-toothed" birds, two morphological types can be clearly distinguished. The first one, the "*Dasornis* morphotype" (including *Odontopterix* and *Macrodontopteryx*, see synonyms in Mayr 2008; Bourdon *et al*. 2010; but also see Mayr 2011) comprises *Dasornis emuinus* (Bowerbank, 1854), *D. toliapica* (Owen, 1873) and *D. abdoun* Bourdon *et al*., 2010 from the Upper Paleocene–Lower Eocene of Morocco (Bourdon 2005, 2006; Bourdon *et al*. 2010) and Lower Eocene of England (only the first two, Harrison and Walker 1976; Mayr 2008). The second form corresponds to the "*Pelagornis*/*Osteodontornis* morphotype" (synonymy and possible specimens referable in Olson 1985; Warheit 2002; Mayr 2009; Bourdon *et al*. 2010; Bourdon 2011) from the Upper Eocene to Upper Pliocene strata of North America, North Africa, South America and Europe (*e.g*., Lartet 1857; Howard

Table 1

Comparative measurement of Pelagornithidae with known tarsometatarsal distal end. Data take from: a – Bourdon *et al*. 2010; b – Harrison and Walker 1977; c – Mayr and Rubilar-Rogers 2010; d – Hopson 1964; e – Olson 1985.

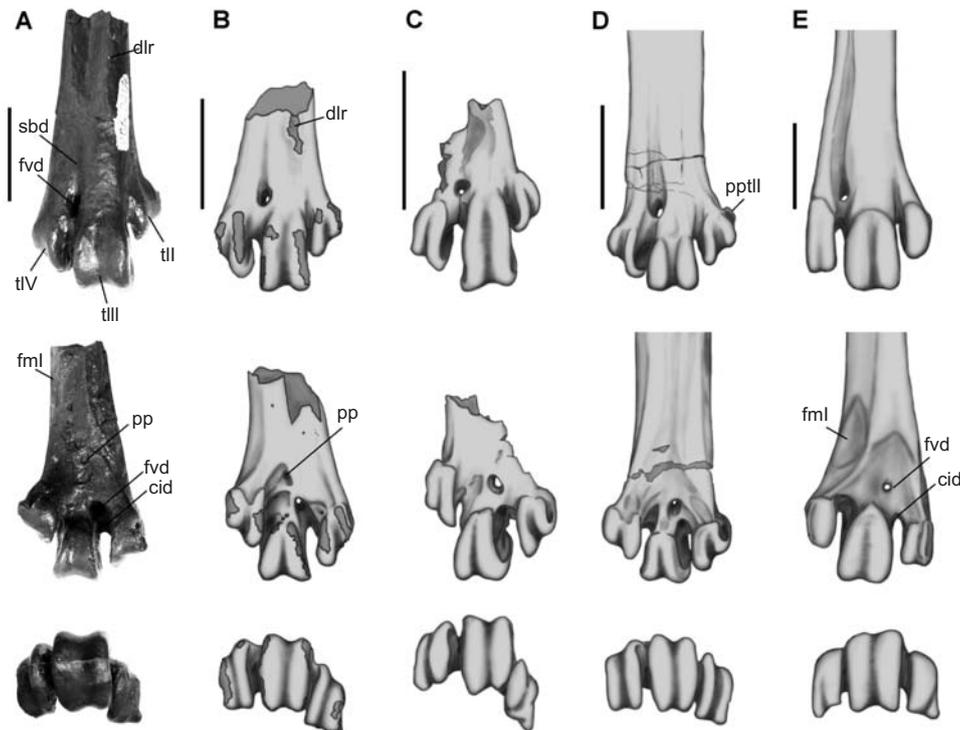|	Distal width (specimen)	Stratigraphic range	Provenance
Pelagornithidae indet.	38.53 (UCR 22176)	Upper Eocene	Antarctica
Odontopteryx (*Dasornis*) *toliapica*	15.70 (OCP.DEK/GE 1146)[a]	Upper Paleocene–Lower Eocene	Morocco
	17.50* (OCP.DEK/GE 1235)[a]	Upper Paleocene–Lower Eocene	
Dasornis emuinus	21.30 (OCP.DEK/GE 1252)[a]	Upper Paleocene–Lower Eocene	
	25.30 (OCP.DEK/GE 1106)[a]	Upper Paleocene–Lower Eocene	
	27.10 (BMNH A894)[b]	Lower Eocene	England
?*Palaeochenoides mioceanus*	34.70 (MCZ 2514)[d]	Lower Miocene[d] or Upper Oligocene[e]	USA
Tympanonesiotes wetmorei	~24.50 (USNM 16809)[d]	Lower Miocene[d] or Upper Oligocene[e]	
Pelagornis chilensis	37.3 (MNHN SGO.PV 1061)[c]	Middle Miocene–Lower Pliocene	Chile

Fig. 3. Comparative morphology of the right tarsometatarsal distal end in some Pelagornithidae and Phorusrhacid birds. **A**. Indeterminate Antarctic Pelagornithidae UCR 22176 (MLP cast). **B**. *Palaeo-chenoides miocaenus* MCZ 2514 (after Hopson 1964, reversed for comparison). **C**. *Dasornis emuinus* NHMUK 894 (after Harrison and Walker 1977). **D**. *Pelagornis chilensis* MNHN SGO.PV 1061 (after Mayr and Rubilar-Rogers 2010). **E**. *Patagornis marshi* Moreno and Mercerat, 1891 NHMUK-A516 (after Andrews 1899). Top, middle and bottom rows: dorsal, plantar, and distal views, respectively. Abbreviations: cid – canalis interosseus distale; dlr – dorsal longitudinal ridges; fmI – fossa metatarsi I; fvd – foramen vasculare distale; pp – plantar "pit"; pptII – plantar proyection of trochlea metatarsi II; sbd – sulcus musculi extensoris brevis digiti IV; tII – trochlea metatarsi II; tIII – trochlea metatarsi III; tIV – trochlea metatarsi IV. Scale bars are 30 mm.

1957, 1978; Howard and White 1962; Hopson 1964; Olson 1984, 1985; Goedert 1989; Olson and Rasmussen 2001; Stidham 2004; Chavez *et al*. 2007; Mayr *et al*. 2008; Mourer-Chauviré and Geraads 2008).

　　Within the pelagornithids, in which the distal end of the tarsometatarsus is known, UCR 22176 resembles those included within the *Dasornis* morphotype, and differs from the *Pelagornis/Osteodontornis* morphotype in the following combination of features (Fig. 3): (1) corpus tarsometatarsi slender, almost square in transverse section (Bourdon *et al*. 2010); (2) trochlea metatarsi II strongly displaced proximally and, in distal view, plantarly projected (Bourdon *et al*. 2010; Mayr and Rubilar-Rogers 2010); (3) on the plantar surface, truncated prox-imo-medial edge of the trochlea metatarsi II (lacks the typical plantar projection

observed in *Pelagornis*; see specimens in Walsh and Hume 2001; Bourdon *et al*. 2010; Mayr and Rubilar-Rogers 2010); (4) trochleae metatarsorum II and IV more narrow and less excavated; (5) in dorsal view, trochlea metatarsi III no laterally directed (Mayr and Rubilar-Rogers 2010); (6) in plantar view, trochlea metatarsi III with a laterally inclined and sharp apex (Bourdon 2005; Bourdon *et al*. 2010); and (7) in dorsal view, foramen vasculare distale large and higher than wide, proximally continued by a deep sulcus musculi extensoris brevis digiti IV (Bourdon *et al*. 2010). Likewise, some few characters are reminiscent to the *Pelagornis*/*Osteodontornis* morphotype, rather than with the *Dasornis* morphotype: (1) in plantar view, the foramen vasculare distale is recessed, more distally positioned, and opens closer to the canalis interosseus distalis (Bourdon 2005; Mayr and Rubilar-Rogers 2010; Mayr 2011); and (2) the trochlea metatarsi III is wider and lower, not elongated. It is possible that these latter features indicate a slightly more derived condition of UCR 22176 with respect to the specimens included in the *Dasornis* morphotype, this inference is consistent with its more modern stratigraphic location (Upper Eocene *vs.* Upper Paleocene–Lower Eocene for *Dasornis* specimens, Bourdon 2005, 2006; Bourdon *et al*. 2010; Mayr *et al.* 2008; Mayr 2009). Other authors have already mentioned that the *Dasornis* morphotype was more generalist, while a more specialized condition for soaring flight with relatively shorter and stouter legs is evident in the *Pelagornis*/*Osteodontornis* morphotype (Olson 1985; Mayr *et al*. 2008; Mayr 2009; Bourdon *et al*. 2010; Mayr and Smith 2010).

It is remarkable that within the pelagornithids, the Seymour Island material has close affinity with the specimen referred by Hopson (1964) to *Palaeochenoides miocaenus* Shufeldt, 1916 reported for deposits of South Carolina in the North Atlantic coast, and tentatively referred to the Early Miocene by this author (although it probably belong to Late Oligocene according to Olson 1985; see also Mayr and Rubilar-Rogers 2010). Both specimens share intermediate characters between the primitive *Dasornis* morphotype and the most derived *Pelagornis*/*Osteodontornis* (*e.g*., degree of plantar displacement of trochlea metatarsi II, dorso-plantar compression of corpus metatarsi, and width of the sulcus musculi extensoris brevis digiti IV). In addition, Hopson (1964: 11) describes for the material referred as *P. miocaenus* the presence on the plantar side of the bone of a "… large subtriangular pit…" placed "some 9 mm above the center of the middle trochlea, and 4 mm dorsomedial to the distal foramen". This possible foramen pneumaticum is similar in shape and position in UCR 22176 (Fig. 3A–B; a similar condition can be found in some Anseriformes, *i.e*., Anhimidae, Anatidae).

According to the reported proportions for pelagornithids whose tarsometatarsal distal end is known, the distal width observed in UCR22176 is the largest known for this family (see Table 1), even surpassing to *Pelagornis chilensis* Mayr and Rubilar-Rogers, 2010, the largest bony-toothed bird previously known. Furthermore, the size could be proportionally larger if it is considered that the

paleogene forms of *Dasornis* morphotype show a lateromedially much narrower tarsometatarsus than the very wide and dorsoplantarly compressed tarsometatarsus of the neogene *Pelagornis/Osteodontornis* (Mayr and Rubilar-Rogers 2010; Bourdon *et al*. 2010).

Remarks. — The material here studied was originally presented by Case *et al*. (2006) in a poster displayed in the 66th Annual Meeting of the Society of Vertebrate Paleontology (Ottawa, Canada), but omitted from the published abstract. However, given the importance of its first assignment to Phorusrhacidae, as the constant mention in the bibliography (*e.g*., Tambussi and Noriega 1996; Reguero *et al*. 2002; Alvarenga and Höfling 2003; Tambussi and Acosta-Hospitaleche 2007; Chavez 2007; Agnolin 2009; Alvarenga *et al*. 2011; Mourer-Chauviré *et al*. 2011), it is appropriate to clarify here this unusual situation. In the original abstract, Case *et al*. (2006) presented a left femur from the Maastrichtian (López de Bartodano Formation) of the Vega Island in Antarctic Peninsula (Fig. 1), as belonging to a cursorial bird that they have related to cariamids and phorusrhacids (see below). However, in the poster presented in the meeting, the authors added three specimens referred to Phorusrhacidae from the Upper Eocene (Submeseta Allomember, La Meseta Formation) of Seymour Island corresponding to a tibiotarsus, a cervical vertebra, and the tarsometatarsal end UCR 22176 before described. Subsequently, Tambussi and Acosta Hospitaleche (2007) noted that the assignment of the first two specimens should be revised (see below), nevertheless, regarding the tarsometatarsal distal end, they indicated an "unquestionable phorusrhacid affinities, similar in size to *Patagornis marshii*" (Tambussi and Acosta Hospitaleche 2007:607). In this regard, as indicated, the material UCR 22176 can be assigned with certainty to the family Pelagornithidae. Moreover, the presence of the following characters allow to exclude it from the Phorusrhacidae and Cariamidae (Fig. 3): (1) very thin-walled shaft; (2) shallow fossa metatarsi I, situated on the medial surface and more proximal; (3) in dorsal view, grooved trochlea metatarsi II with the lateral margin distally extending (*vs.* not grooved and distally rounded); (4) trochlea metatarsi II more proximally placed and much more plantarly projected; (5) wide foramen vasculare distale; (6) distal opening of the canalis interosseus distale more plantarly positioned and very close to the foramen vasculare distale; (7) presence of a prominent longitudinal ridges on the dorsal surface, placed in the medial side of the midline of the bone on the trochlea metatarsi III (Fig. 3A–B, dlr; this may represent an autapomorphy for the family as it has not been observed in another group of birds, see also Hopson 1964).

On other putative Antarctic cariamid or phorusrhacid birds

As mentioned above, Case *et al*. (2006) briefly described a left femur from the Maastrichtian (López de Bertodano Formation) of the Vega Island. They noted af-

finities with unrelated modern cursorial predatory birds like cariamids and the Accipitriformes Sagittariidae based on the following alleged apomorphic features (Case *et al*. 2006): "the enlarged and posteriorly prominent tibiofibular crista, the laterally expansive lateral epicondyle, and the highly planar and vertically oriented fibular trochlea". On the basis of these characters, Case *et al*. (2006) conclude that "this specimen may represent a taxon which may be ancestral to both cariamids and phororhacoids or it is the basal cariamid which is then ancestral to the phororhacoids, rather than being their descendant". However, the above opinion appears not to be justified. First, the characters mentioned by these authors are not diagnostic for cariamids and/or phorusrhacid birds, being widely distributed among Neornithes (Mayr and Clarke 2003). Additionally, the material lacks most of the characteristic features observed in these taxa (*e.g*., rectilinear femoral shaft with parallel margins, oblique and deep sulcus patellaris, deep fossa poplitea; very wide condylus medialis with a strong distal orientation, being in caudal view wider than high; in caudal view, great development of the epicondylus medialis; conspicuous osseous bar connecting both condylae; on the trochlea fibularis, wide tuberculum musculi gastrocnemius laterally limited by a marked osseous edge; see also Mourer-Chauviré *et al*. 2011). Furthermore, the presence of other relevant characters has been omitted, for example: (1) wide and craniocaudally strongly flattened distal end, with its margins proximally converging towards the middle of the shaft; (2) curved shaft; (3) shallow and wide sulcus patellaris; (4) shallow sulcus intercondylarys; (5) condylus medialis smaller than the lateralis; (6) very wide trochlea fibularis and laterally strongly projected; (7) prominent and elongated crista supracondylaris medialis; and (8) fovea tendinis musculi tibialis cranialis reduced or absent. Most of the enumerated characters are typically present in Mesozoic and modern foot-propelled diving birds (*i.e*., Hesperornithidae, Baptornithidae, Gaviidae, Podicipedidae, Anhingidae, Phalacrocoracidae; see *e.g*., Owre 1967; Martin and Tate 1976; Cracraft 1982; Galton and Martin 2002).

Also, as noted above, Case *et al*. (2006) added three records to Phorusrhacidae from the Upper Eocene outcrops (La Meseta Formation) of Seymour Island, although they were not mentioned in the published version of the abstract. One of them, the distal tarsometatarsus UCR 22176 was reassigned here to Pelagornithidae. Other specimens, the isolated cervical vertebra and the complete tibiotarsus, have clear spheniscid affinities differing from the terror birds in many features (*e.g*., poor development of the cristae cnemialis lateralis et cranialis, extending to about half the shaft; distal end strongly projected medially; distal opening of the canalis extensorius centrally placed between the condylae; very wide incisura intercondylaris; laterally inclined condylus medialis; horizontal pons supratendineus). Importantly, sphenisciforms specimens are abundant in the La Meseta Formation, being uniquely diverse in terms of both morphology and taxonomy (see Myrcha *et al*. 2002; Jadwiszczak 2006; Tambussi and Acosta-Hospitaleche 2007; Jadwiszczak and Mörs 2011).

Discussion and conclusion

The record of an undetermined Ratitae bird was presented by Tambussi *et al*. (1994) on the basis of a highly eroded tarsometarsal distal end from La Meseta Formation of Seymour Island. Regrettably, the authors did not perform a comparative description, therefore its affinities with the extant or extinct lineages is unknown (see Mayr 2009). On the other hand, Covacevich and Rich (1982) described ichnites allocated to a large ground bird from the Fossil Hill Formation (currently considered Paleocene–Eocene, see Torres 2003) on Fildes Peninsula, King George Island (Fig. 1), Southern Shetlands. These authors suggested that the preserved tridactyl footprints may represent activity records that belong to a representative of Ratitae or Phorusrhacidae. Although this kind of indirect evidence precludes discarding other links, the data here provided suggest that these ichnofossils may belong to the former taxon.

Likewise, the pelagornithid birds have been already known from Antarctic. They were reported from the Upper Eocene of Seymour Island (Submeseta Allomember, La Meseta Formation), and their remains comprise a medium-distal rostral fragment (MLP 78-X-26-1, Tonni and Cione 1978; Tonni 1980), a fragmentary pars caudalis of a right ramus mandibulae (MLP 83-V-30-1, Tonni and Tambussi 1985), an eroded portion with remains of "teeth" possibly corresponding to a pars intermedia of a ramus mandibulae (MLP 83-V-30-2, Tonni and Tambussi 1985). A possible fourth record found in the Middle Eocene beds from McMurdo Sound, near Mount Discovery in East Antarctica (Fig. 1), is represented by a distal fragment of humeral diaphysis (Stilwell *et al*. 1998; Jones 2000). Even though those remains are poorly preserved, the measurements reported for the known Antarctic materials, together with the reassignment of UCR 22176 to this group of birds, allow to note that, for the Upper Eocene of Seymour Island, at least two different taxa of these birds have coexisted, as previously noted Tonni and Tambussi (1985). It is possible that the specimen here described may be conspecific with the medium-distal rostral fragment (MLP 78-X-26-1) described by Tonni (1980b), nevertheless, this assumption must be corroborated with the discovery of additional materials.

The presence of diving birds in the Cretaceous of Antarctica has been already reported. Feduccia (1999; see also Chavez 2007) commented on the possible record of Hesperornithiform birds from Lower Cretaceous of an undetermined locality in this continent, however, this material has not been figured nor described so far. Likewise, the record of Gaviiformes seems to be abundant in the Maastrichtian deposits from López Bertodano Formation in Seymour Island. *Polarornis gregorii* Chatterjee, 2002 was described from these units and, recently, it has been announced the discovery of a second smaller species belonging to this genus from the Upper Cretaceous of Vega Island (Chatterjee *et al*. 2006).

The analysis of alleged phorusrhacid birds from Antarctica has resulted in the reassignment of these specimens to other groups of birds known from that continent. Consequently, previous reports on the presence of undetermined Ratitae and Pelagornithidae in the Upper Eocene of Antarctica, as well as, possible foot-propelled diving birds from the Upper Cretaceous, find here new evidences.

The Cretaceous–Paleogene deposits of Seymour, Vega, and Ross islands have provided the most important avifauna known for Antarctica; however, their knowledge still remains in a very rudimentary state. With the exception of penguins (*e.g.*, Myrcha *et al*. 2002; Jadwiszczak 2006; Tambussi *et al*. 2006; Jadwiszczak and Mörs 2011), most of the taxa have been reported in abstracts or brief descriptions with poorly figured specimens, providing a partial information that cannot be well contrasted (see bibliography in Tambussi and Acosta Hospitaleche 2007; Chavez 2007). Future efforts to provide formal descriptions of the old collections and new specimens, will allow to develop more robust tools for the interpretation of the paleoecological, paleoenvironmental and paleogeographic patterns of the Cretaceous and Paleogene of Antarctica and their links with those from other continents.

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Appendix 1

Specimens examined in this study. Extant taxa: *Crypturellus parvirostris*, *C. tataupa*, *C. undulatus*, *Eudromia elegans*, *E. formosa*, *Nothoprocta cinerascens*, *N. ornata*, *N. pentlandii*, *Nothura boraquira*, *N. darwinii*, *N. maculosa*, *Rhynchotus rufescens*, *Tinamotis ingoufi*, *T. pentlandii*, *Tinamus solitarius*, *Rhea americana*, *R. pennata*, *Struthio camelus*, *Dromaius novaehollandiae*, *Apteryx australis*, *Anhinga anhinga*, *Phalacrocorax atriceps*, *P. brasilianus*, *Sula variegata*, *S. leucogaster*, *Morus bassanus*, *Fregata magnificens*, *Pelecanus occidentalis*, *Phaethon rubricauda*, *Macronectes giganteus*, *Pachyptila belcheri*, *Oceanites oceanicus*, *Daption capense*, *Diomedea exulans*, *Spheniscus magellanicus*, *Pygoscelis antarctica*, *Eudyptes chrysocome*, *Aptenodytes forsteri*, *Chroicocephalus maculipennis*, *Stercorarius maccormicki*, *Sterna* sp., *Theristicus melanopis*, *Ciconia maguari*, *Gavia immer*, *Podiceps major*, *Rollandia rolland*, *Vultur gryphus*, *Cariama cristata*, *Chunga burmeisteri*, *Coscoroba coscoroba*, *Nomonyx dominicus*, *Mergus serrator*. Fossil taxa: *Andalgalornis atrox* (MLP 604-I, FMNH P14357 cast), "*Hermosiornis rapax*" (MMMP S155), *Mesembriornis incertus* (MLP 627-1, FMNH P14422 cast; MACN 6737; MACN 6934), *Mesembriornis milneedwardsi* (MACN 5944), "*Palaeociconia australis*" (MLP 20-87), *Patagornis marshi* (NHMUK A517, MLP 84-III-9-2), *Phorusrhacos longissimus* (MLP 20-131), "*Devincenzia pozzi*" (MACN 6554), *Procariama simplex* (MACN 6939, MACN 8225), *Psilopterus affinis* (MACN A52-184), *Psilopterus australis* (MLP 20-188), *Psilopterus colzecus* (MLP 76-VI-12-2), "*Psilopterus communis*" (MLP 20-187), *Psilopterus limoinei* (MPM-PV 3650), *Psilopterus* sp. (MLP 20-586), "*Rostrornis floweri*" (MLP 20-112), "Phorusrhacinae" indet. (MACN 18602), "Patagornithinae" indet. (MACN 14374), Dinornithidae indet. (MLP and MACN not cataloged), *Macranhinga paranensis* (MACN 14363, MACN 14358), Pelagornithidae indet. (MLP 78-X-26-1, MLP 83-V-30-1, MLP 83-V-30-2), *Vegavis iaai* (MLP-PV 93-I-3-1), *Hesperornis regalis* (UNSM 1212), *Parahesperornis alexi* (KUVP 2287).