

Review of the Cretaceous avian diversity of Antarctica: a changing scenario for the evolution of early Neornithine birds

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Abstract The worldwide record of Cretaceous Neornithes and Neornithine-like birds is both controversial and poorly understood. However, in recent years, the Antarctic continent has yielded a substantial number of Maastrichtian avian specimens, contributing significantly to our understanding of the early evolution of this group. Simultaneously, the keen interest and collaborative efforts of various paleornithologists have resulted in a wealth of knowledge, which we have thoroughly reviewed, updated, and discussed in the context of recent discoveries.

Keywords Maastrichtian, Antarctic Peninsula, Vega Island, Seymour (Marambio) Island, Neornithes, birds

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1 Introduction

Over the past few decades, the discovery of numerous Cretaceous avian remains has significantly enhanced our understanding of the early evolution of the group. The predominant birds of the Mesozoic era are the Enantiornithes (Miller et al., 2023), distinguished by a distinctive combination of features. These features include a reverse coraco-scapular articulation, characterized by a convex scapular articular surface of the coracoid and a concave coracoid facet of the scapula. Additionally, both the

dorsal and ventral margins of the scapula are straight, the furcular rami are laterally excavated, the proximal margin of the humerus is centrally concave, the minor metacarpal projects further distally than the major metacarpal, and the trochanter and femoral head exhibit equivalent proximal extension. Other distinguishing features comprise metatarsal IV being narrower than metatarsals II and III, the trochlea of metatarsal II being wider than that of metatarsal III, the width of the sternal margin of the coracoid being half to one-third the length of the coracoid, the penultimate pedal phalanx being longer than the proximal ones, and the cranial margin of the alular metacarpal being broadly convex (Wang and Zhou, 2020). On the contrary, the fossil record of neornithines (crown-birds) is more contentious, primarily attributable to

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the fragmentary nature of the majority of findings, taphonomic artifacts, and the lack of many features essential for reliable systematic allocation (Hope, 2002; Longrich et al., 2011). A limited number of specimens constitute exceptions to this pattern, offering certainty in their stratigraphic provenance and being represented by partially articulated skeletons. Although the systematic position and relationships of these species with other bird groups have not been fully resolved, the Maastrichtian specimens that are most crucial for comprehending the origin and early evolution of the Neornithes include *Vegavis iaai* Clarke, Tambussi, Noriega, Erickson and Ketchum 2005 from the López de Bertodano Formation (LBF), Vega Island, Antarctica, *Polarornis gregorii* Chatterjee 2002 from the LBF (Seymour (Marambio) Island, Antarctica), *Antarcticavis capelambensis* Cordes-Person, Acosta Hospitaleche, Case and Martin 2020 from the Cape Lamb Member of Snow Hill Island Formation (Vega Island, Antarctica) and *Asteriornis maastrichtensis* Field, Benito, Chen, Jagt and Ksepka 2020 from the Maastricht Formation of Belgium. With the single exception of *Asteriornis*, the aforementioned species were discovered in the James Ross Basin (Antarctica) and will be revised in the present contribution. The finding of additional avian remains in these strata (Bender et al., 2023; Irazoqui et al., 2023) has spurred the intensification of fieldwork in the James Ross Basin, leading to new discoveries and promising results. This paper provides a compilation of data, an update of the available information, and offers paleobiological commentaries.

2 Stratigraphic and geographical frameworks

The James Ross Basin encompasses over 6000 m of marine and volcanoclastic sections, spanning from the Early Cretaceous to Paleogene. These sections are integral components of the extensive back-arc Larsen Basin, developed to the east of a magmatic arc situated along the northeastern tip of the Antarctic Peninsula. The Cretaceous section of the James Ross Basin is divided into two major sedimentary successions: the coarse-grained, deep marine sediments of the Gustav Group (Barremian–Coniacian) and the fine-grained sediments of the Marambio Group (Milanese et al., 2020). The Marambio Group (Santonian–Danian) represents the shelf expansion infill, after the Coniacian tectonic inversion stage of the basin. Three transgressive–regressive sequences characterized by the kossmaticeratic ammonites content (N for *Natalites*; NG for *Neograhamites* and *Gunnarites*; and MG for *Maorites* and *Grossouvrites*) have been proposed for the Santonian–Danian Marambio succession (Olivero, 2012; Olivero and Medina, 2000).

The transgressive–regressive N, NG, and MG sequences of more than 3000 m thick, have been proposed for the Santonian–Danian Marambio succession (Olivero,

2012; Olivero and Medina, 2000), at least in the southeast of the James Ross Basin: the Rabot Formation (N sequence), Snow Hill Island Formation and Haslum Crag Sandstones (NG sequence), and the LBF (MG sequence).

The Snow Hill Island Formation with upper Campanian–lower Maastrichtian succession (Milanese et al., 2019) is exposed throughout the James Ross Basin, encompassing ~1000 m of mostly unconsolidated mudstones and fine sandstones (e.g., Milanese et al., 2020). In the northwest sector of the basin, the Snow Hill Island Formation is divided into two members: the Gamma Member and the Cabo Lamb Member, the latter one is well exposed in the Cabo Lamb locality, on Vega Island (Figure 1a). Deposits of the LBF corresponding to the Sandwich Bluff Member, which lies unconformably on the Cape Lamb Member, and carries numerous remains of fossil vertebrates (Table 1) are also exposed in this area. The Sandwich Bluff Member has been correlated with the upper Maastrichtian levels of the LBF which outcrops in Seymour (Marambio) Island (e.g., Figure 2 in Milanese et al., 2020, and bibliography cited therein).

The early Maastrichtian–Danian LBF was composed by ~1000 m of marine, sandy to clayey siltstones interpreted as a transgressive shelf succession (Macellari, 1988). At Seymour (Marambio) Island there is a complete exposure of the LBF (Figure 1c), which contains the Cretaceous–Paleogene (K–Pg) boundary within its upper section (Scasso et al., 2020). Macellari (1988) divided the LBF into two informal sections, the lower “Rotularia units” section, which comprises 5 units, and the upper “Molluscan units”, divided into 4 units. The lower section of LBF (= 2 to 6 Rotularia units) spans ~600 m thick and was interpreted as deposited in shallow marine to estuarine environments (e.g., Macellari, 1988; Olivero et al., 2008). The upper LBF section (= 7 to 10 Molluscan units) is ~500 m thick and constitutes a monotonous succession of mudstones and glauconitic silty to very fine-grained sandstones that record an increasing abundance of mollusks, with the common occurrence of marine reptiles (Macellari, 1988; Zinsmeister and Macellari, 1988). Units 7 (250 m thick) and 8 (~100 m thick) were considered middle shelf facies, meanwhile, the lower part of Unit 9 was interpreted as outer shelf facies (Macellari, 1988; Olivero, 2012; Scasso et al., 2020). The lower section of this unit decreases in grain size and is mainly composed of glauconitic stratified sandy siltstones (Macellari, 1988). The upper levels of Unit 9 are composed of structureless, very fine-grained sandstones with abundant concretions, interpreted as a regressive shelf succession (Macellari, 1988; Olivero, 2012). Several fossil vertebrates come from the lower beds of this unit (Figures 1c and 1e, Table 1), which is related to one of the major flooding stages of the James Ross Basin (O’Gorman et al., 2023). The overlying Unit 10 of LBF was probably accumulated in a middle to inner shelf environment (Macellari, 1988). The K–Pg boundary is between Units 9 and 10, and is characterized by an iridium anomaly (Elliot et al., 1994).

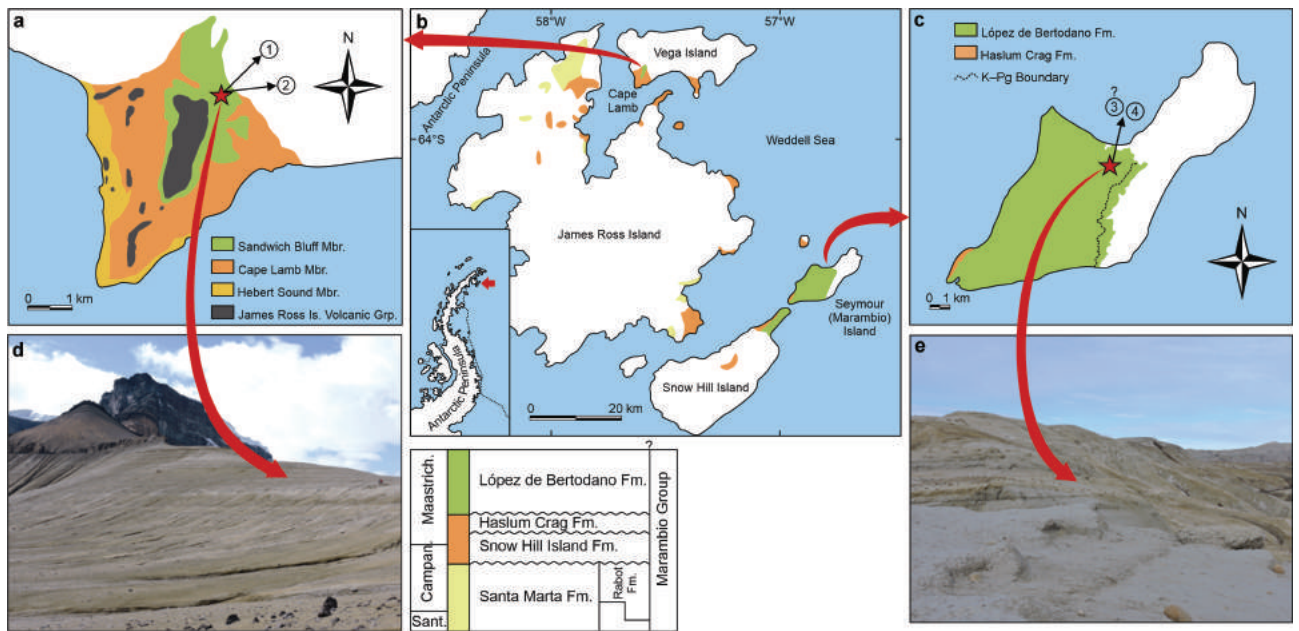


Figure 1 Provenience of the main fossil material of Antarctic Cretaceous birds. **a**, Cape Lamb area at Vega Island; **b**, James Ross Archipelago; **c**, Seymour (Marambio) Island; **d** and **e**, images of field outcrops showing the bird-bearing levels of the López de Bertodano Formation on Vega and Seymour islands, respectively. 1–4 location of the fossil birds: 1, *Antarcticavis capelambensis* SDSM 78147 (holotype), locality V9945 (Cordes-Person et al., 2020; Table 1); 2, *Vegavis iaii* MLP-PV 93-I-3-1 (holotype), locality VEG 9303 (Césari et al., 2001, Table1); 3, *Polarornis gregorii* TTU P 9265, uncertain locality (e.g., Chatterjee, 2002; see discussion in the main text); 4, MLP-PV 08-XI-30-44 and other materials currently under study (Irazoqui et al., 2023).

Table 1 Avian specimens from the Cretaceous of Antarctica mentioned in the text

Taxa	Repository number	Stratigraphic provenance	Geographic provenance	Reference
<i>Antarcticavis capelambensis</i>	SDSM 78147, SDSM C-642	Cape Lamb Member, Snow Hill Island Formation	Cape Lamb, Vega Island (Locality V9945, 63°52'39.41"S; 57°36'18.76"W)	Cordes-Person et al., 2020
<i>Polarornis gregorii</i>	TTU P 9265	Unit 9, López de Bertodano Formation	Seymour Island	Chatterjee, 2002
<i>Polarornis</i> sp.	MLP-PV 96-I-6-2	Unit 9, López de Bertodano Formation	Seymour Island (Locality IAA 10/13)	Acosta Hospitaleche and Gelfo, 2015; Reguero et al., 2013
	MLP-PV 98-I-10-47	Cape Lamb Member, Snow Hills Formation	Cape Lamb, Vega Island (Locality VEG IAA 2/98)	
	MLP-PV 98-I-10-50	Cape Lamb Member, Snow Hill Island Formation	Cape Lamb, Vega Island (Locality VEG IAA 2/98)	
	MLP-PV 98-I-10-52	Cape Lamb Member, Snow Hill Island Formation	Cape Lamb, Vega Island (Locality VEG IAA 2/98)	
Gaviiformes-like indet.	MLP-PV 98-I-10-76	Cape Lamb Member, Snow Hills Formation	Cape Lamb, Vega Island (Locality VEG IAA 2/98)	Acosta Hospitaleche and Gelfo, 2015
	MLP-PV 98-I-10-51	Cape Lamb Member, Snow Hill Island Formation	Cape Lamb, Vega Island (Locality VEG IAA 2/98)	
	MLP-PV 98-I-10-60	Cape Lamb Member, Snow Hill Island Formation	Cape Lamb, Vega Island (Locality VEG IAA 2/98)	
	MLP-PV 98-I-10-61	Cape Lamb Member, Snow Hill Island Formation	Cape Lamb, Vega Island (Locality VEG IAA 2/98)	

Continued				
Taxa	Repository number	Stratigraphic provenance	Geographic provenance	Reference
Gaviiformes-like indet.	MLP-PV 98-I-10-48	Sandwich Bluff Member, López de Bertodano Formation	Cape Lamb, Vega Island (Locality VEG IAA 1/98)	Acosta Hospitaleche and Gelfo, 2015
	MLP-PV 98-I-10-59	Sandwich Bluff Member, López de Bertodano Formation	Cape Lamb, Vega Island (Locality VEG IAA 1/98)	
Other undetermined and highly fragmentary remains	MLP-PV 98-I-10-54	Cape Lamb Member, Snow Hill Island Formation	Cape Lamb, Vega Island (Locality VEG IAA 2/98)	Acosta Hospitaleche and Gelfo, 2015
	MLP-PV 98-I-10-27	Cape Lamb Member, Snow Hill Island Formation	Cape Lamb, Vega Island (Locality VEG IAA 2/98)	
	MLP-PV 98-I-10-53	Cape Lamb Member, Snow Hill Island Formation	Cape Lamb, Vega Island (Locality VEG IAA 2/98)	
	MLP-PV 98-I-10-49	Cape Lamb Member, Snow Hill Island Formation	Cape Lamb, Vega Island (Locality VEG IAA 2/98)	
	MLP-PV 00-I-10-1	Unit 9, López de Bertodano Formation	Cape Lamb, Vega Island (Locality IAA 10/13)	
<i>Vegavis iaai</i>	MLP-PV 93-I-3-1, 93-I-3-1 CA	Sandwich Bluff Member, López de Bertodano Formation	Cape lamb, Vega Island (Locality VEG 9303, 63°52'14"S; 57°34'28"W)	Clarke et al., 2005
	MACN-PV 19748	Sandwich Bluff Member, López de Bertodano Formation	Cape lamb, Vega Island (Locality VEG 9303, 63°52'14"S; 57°34'28"W)	Acosta Hospitaleche and Worthy, 2021; Clarke et al., 2016
<i>Vegavis</i> sp.	SDSM 78247	Sandwich Bluff Member, López de Bertodano Formation	Cape Lamb, Vega Island (Locality V2005-3, "plesiosaur papoose")	West et al., 2019
ornithurine indet.	AMNH FARB 3920	Cape Lamb Member, Snow Hill Island Formation	Cape Lamb, Vega Island	Roberts et al., 2014
unidentified bird	AMNH FARB 30898	Sandwich Bluff Member, López de Bertodano Formation	Cape Lamb, Vega Island	Roberts et al., 2014
ornithurine indet. cf. <i>Vegavis</i> ?	AMNH FARB 30913	Sandwich Bluff Member, López de Bertodano Formation	Cape Lamb, Vega Island	Roberts et al. 2014
Neornithes indet.	MLP-PV 08-XI-30-44	Unit 9, López de Bertodano Formation	Seymour Island (64°15'43"S; 56°43'49.20"W)	Irazoqui et al., 2023

3 Material and methods

Examined materials are housed in the vertebrates collections of the Museo de La Plata (MLP-PV); Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN-PV) of the Ciudad Autónoma de Buenos Aires; Repositorio Antártico de Colecciones Paleontológicas y Geológicas (IAA Pv), Argentina; American Museum of Natural History, Fossil Amphibians, Reptiles and Birds (AMNH FARB); and South Dakota School of Mines and Technology (SDSM), Museum of Texas Tech University (TTU P), USA (Table 1).

New specimens from Vega and Seymour (Marambio) islands are under mechanical preparation in laboratories of the Vertebrates Paleontology Department of the La Plata Museum. They will be examined in detail during the current Ph.D. studies of one of the authors (F. Irazoqui).

4 The Antarctic record of Cretaceous birds

4.1 *Antarcticavis capelambensis*

A partial skeleton (SDSM 78147, cast SDSM C-642) collected during the summer field trip to West Antarctica in

1998 in Maastrichtian sediments of the Snow Hill Island Formation (Locality V9945, Cape Lamb, Vega Island; Figure 1a) is the only specimen known of *Antarcticavis capelambensis* (Figure 2). This skeleton is composed of two thoracic vertebrae, the partial sternum, the articulated right coracoid and scapula, the distal left coracoid, the right humerus, a right ulna and radius still articulated, the proximal right carpometacarpus, proximal and distal left carpometacarpus, the synsacrum, both incomplete femora, the proximal right tibiotarsus and fibula, the distal end of both tibiotarsi, and the proximal right tarsometatarsus (Acosta Hospitaleche et al., 2018).

Despite the recovery of many bones from the skeleton, some of them still being articulated, the preservation of the remains is not good enough to facilitate further comparisons. Numerous features, such as the cranially deflected deltopectoral crest of the humerus, the small acrocoracoid and procoracoid process lacking an incisura for *n. supracoracoidei*, and the expanded facies articularis externalis of the coracoid, relate *Antarcticavis* and the neornithine birds. However, as this specimen belong to an adult bird, certain features such as the enlargement and pneumatization of the humeral head (only partially observed), along with the absence of a supratendinal bridge



Figure 2 *Antarcticavis capelambensis* SDSM 78147 (holotype). **a**, two articulated thoracic vertebrae in lateral view; **b**, sternal keel in lateral view; **c**, right coracoid in ventral view; **d**, synsacrum and right femur in right view; **e**, proximal and distal halves of left humerus in caudal view; **f**, right humerus in cranial view; **g**, right scapula and coracoid in dorso-medial view; **h**, left coracoid in ventral view; **i**, left radius and ulna in dorsal view; **j**, proximal end of right ulna in ventral view; **k**, distal end of right tibiotarsus in caudal view; **l**, proximal end of right carpometacarpus in ventral view; **m**, proximal end of left carpometacarpus in ventral view; **n**, left femur in caudal view; **o**, proximal end of right tibiotarsus and fibula in cranial; **p**, distal end of right tibiotarsus in cranial view; **q**, proximal end of right tarsometatarsus in cranial view. Scale bar represents 10 mm.

in the tibiotarsus, introduce uncertainties regarding its taxonomic assignment to Neornithes (the Figure 5E in Cordes-Person et al., 2020).

During a preliminary examination, the skeleton SDSM 78147 has been assigned to Charadriiformes based on the pleurocoelus of the thoracic vertebrae, and the expanded lateral edge of the posterior coracoid (Cordes, 2002). Some years later, however, the affiliations of this specimen faced challenges. Its incorporation into the data matrix of Wang et al. (2017), prompted a new proposal, interpreting it as a derived Ornithomorpha, likely an Ornithurae, and subsequently naming it *Antarcticavis capelambensis* (Cordes-Person et al., 2020). Although *Antarcticavis* was basally nested in a clade with *Vegavis iaai*, precise phylogenetic positioning faced limitations due to the suboptimal preservation of the bones (Cordes-Person et al., 2020). *Antarcticavis capelambensis* is a new species characterized by the combination of the following features: synsacrum with 11 ankylosed vertebrae, os metacarpalis alularis with a ball-like distal articulation, and the absence of the foramen n. supracoracoidei, elongated preacetabular ilium, tibiotarsus without an ossified pons supratendinous, and a sulcus cartilaginis tibialis developed, with distal articulation caudally extended. Besides, the condylus lateralis

is wider than the medialis, and sulcus intercondylaris is about one third of the cranial surface width. Notably, the fibula is not reduced, and the tarsometatarsus exhibits a well-developed sulcus hypotarsi (Cordes-Person et al., 2020). These features serve to differentiate *Antarcticavis* from other Cretaceous birds from Antarctica like *Polarornis gregorii* and *Vegavis iaai*.

4.2 *Polarornis gregorii*

A partial skeleton (TTU P 9265) recovered from the Maastrichtian levels of Unit 9, LBF on Seymour (Marambio) Island, which bears a resemblance to common loons (Figure 3) was briefly outlined in a short abstract by Chatterjee (1989) and subsequently expanded in Chatterjee (2002). It is important to note that the geographical position indicated on the map by Chatterjee (2002, Figure 1 in the paper) does not align with any of the sites where the Unit 9 is exposed. Our field experience suggests that TTU P 9265 likely come from a nearby locality where the bird-bearing levels of Unit 9 are exposed, near the northern coast of the island (Figure 1c). It is worth mentioning that older levels of the LBF emerge further west in this area on Seymour (Marambio) Island (e.g., Macellari, 1988; Montes et al., 2019).

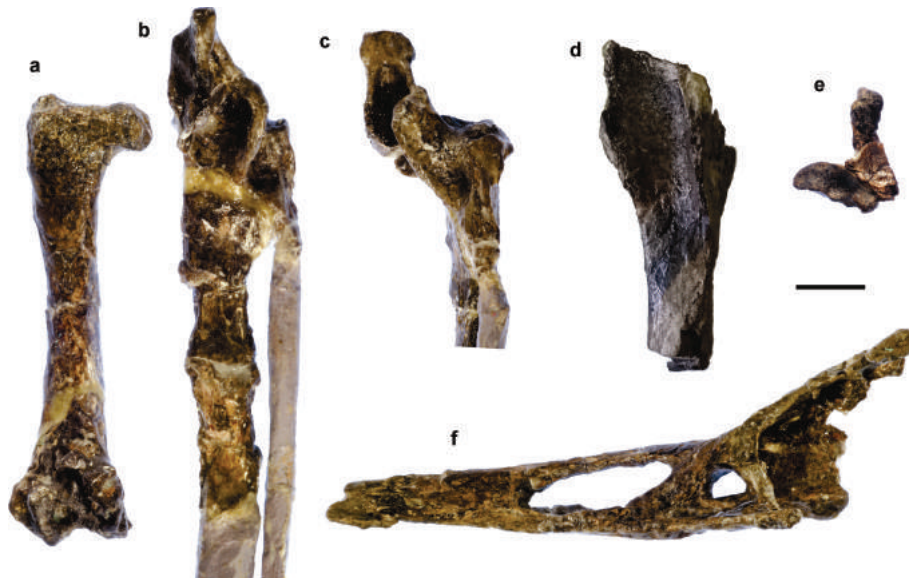


Figure 3 *Polarornis gregorii* TTU P 9265 (holotype) and MLP-PV 96-I-6-2. **a**, left femur in caudal view; **b**, proximal left tibiotarsus in cranial view; **c**, proximal left tibiotarsus in lateral view; **d**, proximal left tibiotarsus in cranial view; **e**, undetermined bone fragment; **f**, skull in lateral view. Scale bar represents 10 mm.

Chatterjee (2002) provides only schematic drawings for the description of the incomplete skull, four cervical vertebrae, a sternal fragment, the left femur, a fragment of the right femur, and the proximal left tibiotarsus that constituted the holotype of *Polarornis gregorii* Chatterjee 2002.

The initial phylogenetic proposal grouped *Polarornis* with *Gavia* based on the following synapomorphies: orbital process of quadrate with the medial surface sharply concave

and an overhanging ridge, mandibular articular surface of the quadrate with a prominent caudal projection, femur strongly arched and with a proximal end anteromedially compressed, elongated cnemial crest and lateral cnemial crest distally widen (Chatterjee, 2002). However, it is important to note that the taxonomic content of the data matrix used in the analysis considered only four neognathous birds, and none of which were birds with aquatic habits like Podicipedidae or Anatidae, which would

have allowed the recognition of convergent characters. Consequently, the sister-taxa relationship between *Gavia* and *Polarornis* may be somewhat inevitable in this context, potentially influencing the phylogenetic hypothesis proposed by Chatterjee (2002).

Another species that Chatterjee (2002) suggested might be related to loons is *Neogaeornis wetzeli* Lambrecht 1929 (Lambrecht, 1929), represented by a tarsometatarsus from the contemporaneous Quiriquina Formation in Chile. Notably, this species has been also considered as a senior synonym of *Polarornis* (Olson, 1992).

In subsequent years, a second skeleton from the late Cretaceous levels of Vega Island was identified as a smaller species of *Polarornis* (Chatterjee et al., 2006). However, it is essential to clarify that this material was, the same second concretion that was collected with the holotype of *Vegavis iaai* during 1993 (as described in Section 4.3), later designated as the second partial skeleton (MACN-PV 19748) of *Vegavis iaai* in Clarke et al. (2016).

Other materials, including a small sedimentary block containing an incomplete skeleton (MLP-PV 96-I-6-2), were collected from Unit 9 of the LBF on Seymour (Marambio) Island. The specimen, assigned to *Polarornis* sp., comprises the distal end of a left femur, proximal end, partial left and right tibiotarsi shaft, proximal half of right fibula, and a pedal phalanx (Acosta Hospitaleche and Gelfo, 2015; Reguero et al., 2013). Additionally, isolated and very fragmentary materials (MLP-PV 98-I-10-47, incomplete tarsometatarsus; MLP-PV 98-I-10-50, incomplete right tarsometatarsus; MLP-PV 98-I-10-52, incomplete left tarsometatarsus; MLP-PV 98-I-10-76, incomplete right tarsometatarsus; MLP-PV 98-I-10-51, proximal end of left femur; MLP-PV 98-I-10-60 and MLP-PV 98-I-10-61, distal end and partial corpus of pedal phalanges; MLP-PV 98-I-10-48, distal end of left tibiotarsus; MLP-PV 98-I-10-59, diaphysis of left tibiotarsus) from Vega Island (Sandwich Bluff Member, LBF) might belong to *Gaviiformes* according to Acosta Hospitaleche and Gelfo (2015) or some other *Gaviiformes*-like group that remains undetermined. A similar situation applies to poorly preserved remains from the Sandwich Bluff Member of the LBF, Vega Island (MLP-PV 98-I-10-54, incomplete left tarsometatarsus; MLP-PV 98-I-10-27, incomplete right tarsometatarsus; MLP-PV 98-I-10-53, distal end of left tibiotarsus; MLP-PV 98-I-10-49, distal end of right tibiotarsus) and from the Unit 9 of the LBF, Seymour (Marambio) Island (MLP-PV 00-I-10-1, pedal phalanx). Unfortunately, it is not possible to advance in the systematic determination of these remains until more complete material can be examined.

The current state of knowledge allows further comparisons with all the *Vegavis* specimens, the holotype of *Antarcticavis*, and some other non-Antarctic Cretaceous neornithine-like birds, providing a new perspective to analyze the phylogenetic relationships of *Polarornis*. However, several outstanding questions remain regarding

the anatomy and the original interpretation and codification of the morphological character-states of *Polarornis*. This is partly because this species was studied primarily from images and the detailed description provided by Chatterjee (2002) is confusing in some respects when the fossils are examined directly.

4.3 *Vegavis iaai*

Vegavis iaai is represented by the holotype (MLP-PV 93-I-3-1, Figures 4–6), a second partial skeleton (MACN-PV 19748, Figures 5 and 6, formerly MLP-PV 93-I-3-2), and an isolated femur (SDSM 78247). The holotype is based on a partial skeleton that was found in the Sandwich Bluff Member of the LBF, exposed at the locality IAA VEG 9303 of the Vega Island (Figure 1a) by members

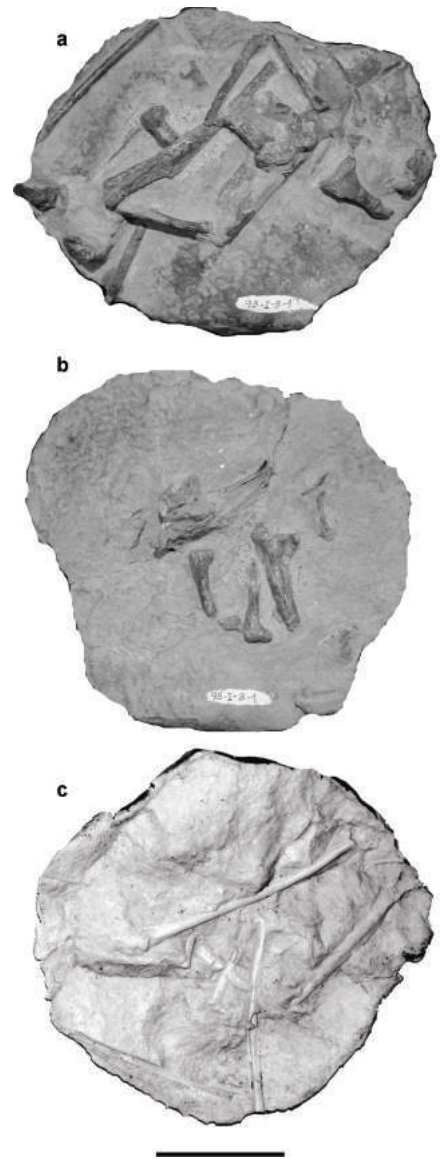


Figure 4 *Vegavis iaai* MLP-PV 93-I-3-1. **a–b**, holotype within the sedimentary concretion before mechanical extraction of the bones; **c**, latex peel MLP-PV 93-I-3-1 CA.



Figure 5 *Vegavis iaai* MLP-PV 93-I-3-1 (a–c, h, k, m–o) and MACN-PV 19748 (d–g, i–j, l). a, ninth cervical vertebra in dorsal view; b, third thoracic vertebra in cranial view; c, fourth thoracic vertebra in cranial view; d, cervical vertebra in dorsal? view; e, articular region of right mandible in medial view; f, caudal vertebra in dorsal? view; g, left pterygoid; h, left scapula in lateral view; i, left scapula in lateral view; j, thoracic vertebra series in dorsal view; k, right ossa coxae in medial view; l, left coracoid in ventral view; m, right coracoid in ventral view; n, left ossa coxae in medial view; o, synsacrum in ventral view. Scale bar represents 10 mm.

of the Instituto Antártico Argentino (Clarke et al., 2005, 2016; West et al., 2019). Despite that, the preliminary examination was made with most of the bones included into matrix in a concretion divided into two halves (Figure 4), and affinities with the Anseriformes were recognized, mainly based on the anatomy of the right humerus and the left tibiotarsus (Figure 6). In consequence, the fossil was

assigned to Presbyornithidae (Noriega and Tambussi, 1995). A latex peel 93-I-3-1 CA (Figure 4c), currently housed with the holotype, was made at this instance on one of the halves, in which also part of the left humerus, distal right radius, right coracoid, synsacrum, proximal and distal ends of both femora, proximal left and distal right tarsometatarsi, and six ribs were exposed.



Figure 6 *Vegavis iaai* MLP-PV 93-I-3-1 (a, c, e-i, k-l, n-o, q-s) and MACN-PV 19748 (b, d, j, m, p). a, right humerus in cranial view; b, right humerus in caudal view; c, radius in dorsal? view; d, articulated right radius and ulna; e, proximal left humerus in caudal view; f, proximal left humerus in cranial view; g, left ulna in ventral view; h, proximal fragment of right humerus in caudal view; i, left tibiotarsus in caudal view; j, articulated right carpometacarpus and phalanges; further back are cervical and caudal vertebrae together with a possible ceratobranchial element from the hyoid sensu Clarke et al. (2016); and a pedal phalanx distally located to the wing elements; k, proximal left femur in cranial view; l, proximal left femur in caudal view; m, right femur in caudal view; n, proximal right femur in caudal view; o, proximal right femur in cranial view; p, proximal left tibiotarsus in lateral view; q, distal left tarsometatarsus in medial view; r, proximal right tarsometatarsus in cranial view; s, distal left femur in cranial view; t, pedal phalanx. Scale bar represents 10 mm (except for q and r in which it represents 20 mm).

The subsequent partial extraction of the bones (proximal left humerus, right coracoid, partial pelvis, and proximal femora) from the concretion allowed the first analysis in a phylogenetic context, the proposal of a generic and specific name for this specimen, and a new taxonomical proposal. The name *Vegavis iaai* was given to this specimen allocated within Anseriformes, in the clade Anatoidea with Anatidae and *Presbyornis* (Clarke et al., 2005). The comprehensive analysis of Clarke et al. (2005) included the volume rendering of the bones preserved within the matrix using CT scan images for scoring new characters and the analysis of the histological section of the radius for further comparisons with other Anseriformes. The bones included in the second half of the concretion (cervical and thoracic vertebrae, proximal right humerus, right radius, left ulna, left scapula, ribs, synsacrum, pelvis, distal left femur, and both fibulae), were examined through this technique.

The second skeleton, which was still within the sedimentary matrix, was prepared many years later, and assigned to *Vegavis iaai*. Minor variations were observed during the comparisons with the holotype (Figures 5 and 6), mainly referring to the larger size of MACN-PV 19748 (Clarke et al., 2016). This specimen provided a new opportunity to advance in the acknowledgment of the anatomy of basal neornithine birds, based on elements not preserved in the holotype, such as the syrinx, the pterygoid, the posterior portion of the mandible, two articulated portions of the cervical and thoracic vertebrae and free caudals, distal portions of the right ulna and radius together with the radiale and the ulnare, right carpometacarpus with some of the phalanges, and an element preliminarily assigned to the patella (Clarke et al., 2016). The analysis of a more complete dataset including both specimens of *Vegavis iaai*, positioned *Vegavis* within Galloanseres but outside Anseriformes (Worthy et al., 2017).

The new family Vegaviidae was erected by Agnolín et al. (2017) based on the similarities observed among *Vegavis iaai*, *Polarornis gregorii*, *Neogaeornis wetzeli* (a partial tarsometatarsus from the Maastrichtian Quiriquina Formation, Chile), and *Australornis lovei* (a partial coracoid, scapula, and wing from the late early Paleocene Waipara Greensand, New Zealand). Vegaviidae was recovered as a basal clade of Anseriformes characterized with an austral distribution during the late Cretaceous and Paleocene (Agnolín et al., 2017). This idea provoked a quick reaction in most of the paleornithological community, which not only disapproved the taxonomic composition of this clade (Mayr et al., 2018) but also deeply disagreed with many of the anatomical observations made by Agnolín et al. (2017).

However, more recently, *Vegavis* was recovered as the sister taxon of the new species *Maaqwi cascadenis* McLachlan, Kaiser and Longrich 2017, from the Late Campanian Northumberland Formation of Canada. Although no other Vegaviidae (*sensu* Agnolín et al., 2017) was included in the data matrix analyzed by McLachlan et al. (2017), the clade *Maaqwi cascadenis* + *Vegavis iaai*

was interpreted as Vegaviidae (McLachlan et al., 2017). The proposals of Agnolín et al. (2017) and McLachlan et al. (2017) are not comparable regarding their taxonomic composition. In the original proposal (Agnolín et al., 2017), Vegaviidae would be an austral family with a biochron spanning from the Maastrichtian to the Danian. On the contrary, in the second proposal, Vegaviidae would be a family more widely distributed, both geographically and temporally, and certainly not with an austral origin as it was originally proposed (McLachlan et al., 2017). In any case, it should also be considered that this last phylogenetic proposal results from the analysis of a data matrix modified from Longrich et al. (2011) that would be much more appropriate to analyze stem birds rather than Neornithes.

Almost simultaneously, and after three years of hard work, the holotype of *Vegavis* was completely removed from the sedimentary matrix in the División Paleontología Vertebrados of the Museo de La Plata. As a result, a total of 36 new features could be scored in that instance, and a new phylogenetic analysis was performed (Acosta Hospitaleche and Worthy, 2021). Although new anatomical details were described, particularly in the pelvis, synsacrum, tarsometatarsus, and humerus, the phylogenetic results did not show a major resolution in comparison with previous proposals using the same set of characters (Worthy et al., 2017). The results recover *Vegavis* within Galloanseres again (Acosta Hospitaleche and Worthy, 2021), but not within Anseriformes, as was proposed by Clarke et al. (2005, 2016).

A third specimen (SDSM 78247) is represented by an isolated femur (West et al., 2019) that has been previously interpreted as an indeterminate Cariamiformes (Case et al., 2006). It was assigned to *Vegavis* sp. after a detailed examination and the comparison with the holotype MLP-PV 93-I-3-1 and MACN-PV 19748. The differences with *Polarornis* (see next paragraph) were also highlighted by West et al. (2019) taking advantage of the preservation of this bone in all those skeletons.

The phylogenetic position of *Vegavis* was re-evaluated by Field et al. (2020), in the study of *Asteriornis maastrichtensis* from the Maastrichtian of Belgium. Important variations in the phylogenetic position of *Vegavis iaai* were observed, depending on the optimization criteria applied in the analysis and the addition of molecular data in the Bayesian analysis of the same data matrix (modified from Worthy et al., 2017). Under maximum parsimony, *Vegavis* was recovered as the sister taxon to Neornithes; while in the Bayesian analysis, it appears in an unresolved position at the base of Neognathae (Field et al., 2020).

Finally, a thoracic vertebra of an unidentified ornithurine bird (AMNH FARB 30920) from the upper Cape Lamb Member, an incomplete coracoid of an unidentified bird (AMNH FARB 30898) from the same level that the *Vegavis* holotype (Sandwich Bluff Member 1 *sensu* Roberts et al., 2014), and a distal tarsometatarsus of an indeterminate ornithurine (AMNH FARB 30913) from the overlying SBM (according to Roberts et al., 2014) could

belong to either *Vegavis* or *Polarornis* (Roberts et al., 2014). They could only be evaluated when more complete materials are available for comparison. The current scenario is promising for the advances in the field for the following years.

5 Current research on new materials and future perspectives

Numerous fossils remain in different stages of preparation and examination and will be communicated shortly. Among them, MLP-PV 08-XI-30-44 (Figure 7) constitutes one of the most important because cranial and postcranial elements were preserved in association with a small sedimentary concretion. This specimen, coming from the base of Unit 9 of the LBF (Figure 1b), comprises the cranium, humerus, ulna, pelvis, synsacrum, tibiotarsus, and minor fragments in association, and it differs from *Vegavis*, *Polarornis*, and *Antarcticavis* (Acosta Hospitaleche et al., 2022). MLP-PV 08-XI-30-44 is the first neornithine-like bird with the neurocranium and posteriormost region of the cranium perfectly preserved allowing the reconstruction of the cranial endocast and a first glimpse into the paleoneuroanatomy of this Cretaceous bird (Irazoqui et al., 2023).



Figure 7 Specimen MLP-PV 08-XI-30-44. **a**, cranium in dorsal view; **b**, pelvis in lateral view; **c**, left tibiotarsus in cranial view; **d**, distal end of right humerus in cranial view. Scale bar represents 10 mm.

Although the phylogenetic affinities are still under evaluation, specimen MLP-PV 08-XI-30-44 was preliminarily assigned to a Neornithes based on the presence of fused and edentulous premaxillae, edentulous and fused dentary forming a mandibular symphysis, the complete fusion of the cranial elements, and tibiotarsus with an ossified supratendinoal bridge. MLP-PV 08-XI-30-44 definitively constitutes a new genus and species belonging to a different guild of the Cretaceous birds from Antarctica that was not previously described, evidenced in the lack of diving adaptations in the whole skeleton.

Besides, as mentioned above, specimen MLP-PV 08-XI-30-44 constitutes the first Cretaceous Neornithes that preserves the braincase bones, including the basicranium and elements of the occipital and otic regions, which could be studied using micro-CT. The endocranial cast shows that the encephalon is well developed along the dorsoventral axis, expanded, and flexed; the cerebellum is dorsally expanded and shows no evidence of cerebellar fissures or sulcus medianus; the sagittal sulcus in the medulla oblongata is reduced to a circular depression. Furthermore, the optic lobes do not protrude laterally in the dorsal view, the interhemispheric fissure is wide and the flocculus is elongated. There is no evidence of wulst. And the wulst may be absent or restricted to the anterior part of the telencephalon, which is not preserved (Irazoqui et al., 2023).

Additionally, three concretions bearing bird bones from the base of Unit 9 of the LBF collected in Seymour (Marambio) Island are pending further studies. Preliminary three-dimensional reconstructions based on computed tomographies were made to evaluate the specimen's completeness. We will focus on them once the mechanical and digital preparation is completed in the laboratories of the División Paleontología Vertebrados of the Museo de La Plata. Similarly, nine unprepared specimens recently collected from the same levels of the LBF, at Vega and Seymour (Marambio) islands are in the first preparation stages.

Unit 9 of the LBF at Seymour (Marambio) Island and the Sandwich Bluff Member of the LBF at Vega Island have proven to be highly fossiliferous levels, due to the discovery of many fossil vertebrates (e.g., Bona et al., 2020; O'Gorman et al., 2023), especially bird specimens. From what we have been able to observe through a preliminary analysis, these levels contain a large amount of new avian fossil remains, which exceeds our expectations. Further studies of all these specimens will allow a more detailed analysis of the anatomy of Cretaceous species already known for Antarctica, elucidate some phylogenetic aspects especially those linked with the early history of Neornithes that was not yet resolved, and recognize the presence of new taxa.

The review and update of the known avian records plus the new findings present a new scenario for the study of the Cretaceous birds. It implies the presence of a higher taxonomic and paleoecological diversity of Neornithes and/or Neornithine-like birds at the end of the Cretaceous

concentrated in a small sampling area. These birds would have covered a wider paleoecological range, including foot-propelled divers (*Vegavis* and *Polarornis*), and flying birds not particularly specialized in diving (e.g., MLP-PV 08-XI-30-44).

Although not completely elucidated yet, the phylogenetic relationships among the birds represented in the James Ross Basin seem more complex than that was previously thought. However, despite this uncertainty, our examination of the known specimens, coupled with the prospect of future discoveries, promises to provide valuable insights for refining the calibration of divergence times. This, in turn, holds the potential to enhance our ability to infer the geographical origins of modern birds. By integrating these Antarctic insights, we can elucidate how these unique specimens contribute to our understanding of the evolutionary timeline and geographic distribution of avian species. It becomes evident that continued exploration and documentation of specimens from this region will play a pivotal role in refining our knowledge. The inclusion of such future findings in subsequent analyses will undoubtedly contribute to a more nuanced calibration of divergence times.

The uncertainties in molecular phylogenies, compounded by the challenges associated with the early radiation of Neornithes, emphasize the need for comprehensive calibrations. The Antarctic specimens discussed herein, alongside future discoveries, represent invaluable assets in this pursuit. The integration of the molecular and paleontological data ensures a more holistic understanding of the intricate processes that have shaped the temporal and geographic origins of modern birds.

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