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PALEONTOLOGY

The Cretaceous Neornithine record and new Vegaviidae specimens from the López de Bertodano Formation (Upper Maastrichthian) of Vega Island, Antarctic Peninsula

GEOVANE A. DE SOUZA, BRUNO A. BULAK, MARINA B. SOARES, JULIANA M. SAYÃO, LUIZ CARLOS WEINSCHÜTZ, ALESSANDRO BATEZELLI & ALEXANDER W.A. KELLNER

Abstract: A worldwide revision of the Cretaceous record of Neornithes (crown birds) revealed that unambiguous neornithine taxa are extremely scarce, with only a few showing diagnostic features to be confidently assigned to that group. Here we report two new neornithine specimens from Vega Island (López de Bertodano Formation). The first is a synsacrum (MN 7832-V) that shows a complex pattern of transversal diverticula intercepting the canalis synsacri, as in extant neornithines. Micro-CT scanning revealed a camerate pattern of trabeculae typical of neornithines. It further shows the oldest occurrence of lumbosacral canals in Neornithes, which are related to a balance sensing system acting in the control of walking and perching. The second specimen (MN 7833-V) is a distal portion of a tarsometatarsus sharing with *Vegavis iaai* a straight apical border of the crista plantaris lateralis. Osteohistologically the tarsometatarsus shows a thick and highly vascularized cortex that lacks any growth marks, resembling *Polarornis gregorii*. The cortex is osteosclerotic as in other extinct and extant diving neornithines. These new specimens increase the occurrences of the Cretaceous avian material recovered from the Upper Cretaceous strata of the James Ross Sub-Basin, suggesting that a Vegaviidae-dominated avian assemblage was present in the Antarctic Peninsula during the upper Maastrichtian.

Key words: Mesozoic birds, Neornithes, *Vegavis*, Antarctica, James Ross.

INTRODUCTION

Research in Antarctica has been increasing worldwide with constant investment and collaboration among researchers from different countries (e.g., Sampaio 2022), resulting in projects with increasing complexity (e.g., Simões et al. 2022). Despite the several challenges to developing studies in this region, there has been a steady increase of scientific activity in the area (e.g., Kellner 2022, Santos et al. 2022), which includes the search for fossil vertebrates (e.g., Reguero et al. 2022), including extinct birds.

Among the most interesting deposits for paleontology in Antarctica are the layers of Upper Cretaceous-Paleogene sequence that filled the James Ross Sub-Basin, in the northeastern margin of the Antarctic Peninsula. These beds are considered the most significant sedimentary sequence from high latitudes for this time interval and have yielded a diverse fossil assemblage from terrestrial and marine environments such as araucariacean (Césari et al. 2001), angiosperms (Roberts et al. 2014), scleractinian corals (Videira-Santos et al. 2020), serpulid worms and molluscans (e.g., Olivero et al. 1986, Crame & Luther 1997, Olivero 2012a, Raffi et al. 2019), crustaceans (Pinheiro et al. 2020), chondrichthyans (e.g., Otero et al. 2014), osteichthyans (e.g., Richter & Ward 1990), plesiosaurs (e.g., Chatterjee & Small 1989, Kellner et al. 2011, O'Gorman 2012, O'Gorman et al. 2019, Brum et al. 2022), mosasaurs (Martin et al. 2002, Novas et al. 2002a, Martin 2006), pterosaurs (Kellner et al. 2019), and avian and non-avian dinosaurs (Chatterjee 1989, Noriega & Tambussi 1995, Case & Tambussi 1999, Case et al. 2000, 2006, 2007, Case 2001, Cordes 2001, 2002, Novas et al. 2002b, Clarke et al. 2005, Chatterjee et al. 2006, Tambussi & Acosta Hospitaleche 2007, Reguero et al. 2013, Roberts et al. 2014, Brum et al. 2023). All these discoveries have contributed to a better understanding of the Weddellian Biogeographic Province biota (*sensu* Zinsmeister 1979) that occurred in the Patagonia-Antarctica-New Zealand-Australia corridor during the Late Cretaceous-Eocene. Among the Mesozoic taxa found in James Ross Sub-Basin, birds comprise some of the most interesting records (Chatterjee 2002, Clarke et al. 2005, Tambussi & Acosta Hospitaleche 2007, Roberts et al. 2014). Two nominal species have been recognized: *Vegavis iaai* Clarke et al. 2005 and *Polarornis gregorii* Chatterjee 2002. Besides them, an array of fragmentary remains of uncertain affinities have been reported (e.g., Ornithurae indet., Aves indet., Neornithes indet., Charadriiformes indet. Case & Tambussi 1999, Roberts et al. 2014, Case 2001, Cordes 2001, 2002). *Vegavis* and the putative neornithine *Polarornis* help in depicting the radiation of crown neornithines through the Maastrichtian, near the K-Pg extinction (e.g., Clarke et al. 2005). Along with *Asteriornis maastrichtensis* Field et al. 2020, from the upper Maastrichtian of Belgium, these are the only pre-Cenozoic fossils unambiguously assigned to crown birds (Field et al. 2020).

Here we present a review of the Mesozoic neornithines (equivalent to the bird crown group) with emphasis on the Antarctic fossils from the James Ross Sub-Basin and their role in a broader neornithine evolutionary context. We further report new bird specimens from the López de Bertodano Formation, comprising a partial synsacrum and a fragmentary tarsometatarsus collected from 40 m above the levels where *Vegavis* remains were recovered.

Institutional abbreviations

GPMK – Geologisch-Paläontologisches Institut und Museum, Germany, **MACN-PV –** Museo Argentino de Ciencias Naturales, Argentina, **MLP –** División Paleontología Vertebrados of the Museo de La Plata, Argentina, **MN-A** – Museu Nacional, Aves collection, Universidade Federal do Rio de Janeiro, Brazil, **MN-V –** Museu Nacional, Paleovertebrate Collection, Universidade Federal do Rio de Janeiro, Brazil, **MPM –** Paleontological Collection, Museo Regional Provincial "Padre Molina", Argentina, **NHMM** – Natuurhistorisch Museum Maastricht, Netherlands, **PIN –** The Borissiak Paleontological Institute of the Russian Academy of Sciences, Russia, **SDSM** – South Dakota School of Mines and Technology, USA, **TMM** – Texas Memorial Museum, USA, **TTU –** Museum of Texas Tech University, Paleontology collection, USA, **YPM –** Yale Peabody Museum of Natural History, USA.

MESOZOIC NEORNITHINES

Despite the significant improvement in the understanding of Mesozoic birds during the last decades, the fossil record of the crown group of birds (i.e, Neornithes) from this era is limited worldwide. Based on the fossil record and molecular data, the split between stem and crown birds is postulated to have occurred in the Late Cretaceous around 90-100 Mya (e.g., Hedges et al. 1996, Cracraft 2001, Agnolín et al. 2006, Ericson et al. 2006, Worthy et al. 2017) or earlier in the Early Cretaceous (Cooper & Penny 1997, Paton et al. 2002, Brown et al. 2008). Nevertheless, with few exceptions (e.g., *Asteriornis*, *Vegavis*), unambiguous stem-representatives of the three main neornithine clades Panpalaeognathae (ratites and tinamous), Pangalloanserae (landfowl and waterfowl), and Neoaves (all the remaining crown birds) from this time are mostly represented by highly fragmentary and poorly preserved specimens, sparking controversy about their classification (Fig. 1) (Agnolín & Novas 2012). The underrepresentation of neornithines during the Cretaceous may result from their lower abundance in the Mesozoic ecosystems relative to other contemporaneous avian lineages, such as Hesperornithiformes, Enantiornithiformes, and Ichthyornithiformes (Chiappe 1996, Clarke & Chiappe 2001, Alvarenga & Nava 2005, Fountaine et al. 2005, O'Connor & Forster 2010) rather than any taphonomic bias, as it was argued (e.g., Cooper & Penny 1997, Bleiweiss 1998, Pacheco et al. 2011). As a result, the origin and early evolution of the crown birds are still poorly understood. Notwithstanding, relevant Cretaceous records of neornithines are found in both northern and southern higher paleolatitudes.

The global paleogeographic maps of Figure 2 show the localities with records of Cretaceous Neornithes. The information concerning the known Mesozoic neornithines taxa and putative neornithines is summarized in Table I.

Northern Hemisphere neornithines - In the Northern Hemisphere, some well-preserved specimens help us to elucidate the gross anatomy of the first neornithines. The most impressive Mesozoic neornithine, in terms of preservation, is *Asteriornis maastrichthensis* Field et al. 2020 from the upper Maastrichtian (66.8–66.7 Mya) of Belgium. It comprises a nearly

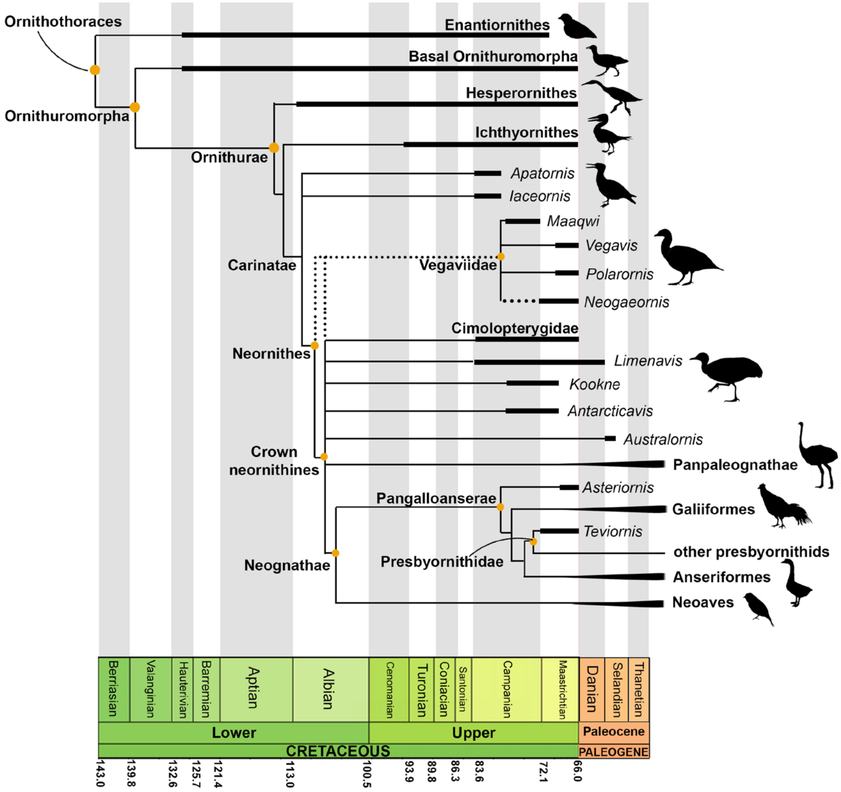

Figure 1. A generalized time-calibrated phylogeny of Mesozoic birds. The time of divergences of the non-neornithine nodes follows Wang & Lloyd (2016). The split of neornithines in the Early Cretaceous follows Hedges et al. (1996) and Ericson et al. (2006). The positioning of the neornithines is according to Clarke (2004) for *Apatornis celer* and *Iaceornis marshi*, McLachlan et al. (2017) and Field et al. (2020) for Vegaviidae, De Pietri et al. (2016) for *Teviornis gobiensis*. *Neogaeornis wetzelli*, *Limenavis patagonica*, *Kookne yeutensis*, *Antarcticavis capelambensis*, and *Australornis lovei* were not submitted to any cladistic analyses. The black horizontal thick lines represent approximated temporal ranges of each taxon. Dotted lines indicate alternative positions of Vegaviidae.

complete 3D-preserved skull and postcranial materials (NHMM 2013 008). The combination of galliform (landfowl) and anseriform (waterfowl) features of *Asteriornis* support its affinities within Pangalloanserae (Field et al. 2020).

All other neornithine reports from the Northern Hemisphere are highly fragmentary and thus of controversial identification, they could be regarded either as ornithurines close related to the crown birds or as true neornithines (Hope 1999, 2002, Bono et al. 2016, Mayr 2017, Mayr et al. 2018). Among them, *Teviornis gobiensis* Kurochkin, Dyke & Karhu 2002 possesses a set of features only present in neornithines. The specimen PIN 44991-1 was recovered from the Maastrichtian of Mongolia (Nemegt Formation) and it is represented by a crushed distal humerus, scapholunare, pisiform, carpometacarpus and phalanges (Kurochkin et al. 2002). *Teviornis* was originally assigned as the sister taxon of Anseriformes Presbyornithidae. Although its systematic position has been questioned (e.g., Clarke & Norell 2004), a recent reevaluation of *Teviornis* characters revealed a combination of features only found in presbyornithids (De Pietri et al. 2016).

Other incomplete material that was initially referred to Ornithurae and later relocated to crown birds comprises a right coracoid RBCM. EH2008.011.01120.001, collected in the upper Campanian Northumberland Formation, in British Columbia, Canada (Dyke et al. 2011). It was preserved in a concretionary mudstone nodule that, after further preparation, revealed novel details of its anatomy. A humerus, radius, and ulna were discovered in the same nodule, adjacent to the coracoid, leading to the erection of a new species named *Maaqwi cascadensis* (McLachlan et al. 2017). The robustness of the bone cortices of *Maaqwi* suggested that it was

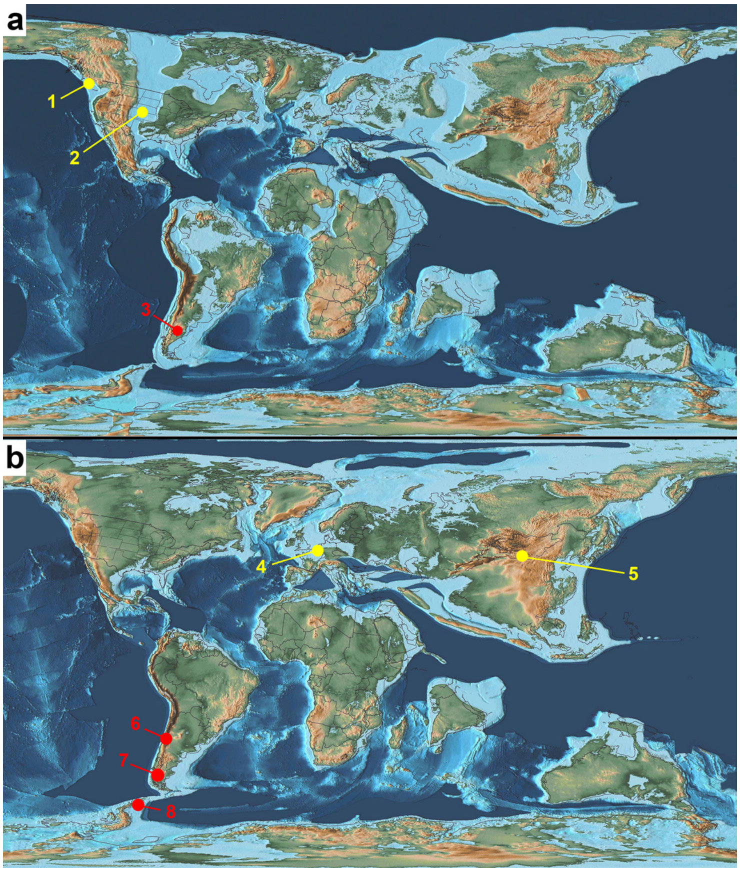

Figure 2. Global paleogeographic maps showing the localities with records of Cretaceous Neornithes. (a) Early Campanian, (b) Late Campanian-Maastrichtian. 1 - Northumberland Formation, British Columbia, Canada (*Maaqwi*), 2 - Niobrara Formation, Kansas, US (*Apatornis* and *Iaceornis*) but see the text to alternative position for these taxa outside Neornithes, 3 - Allen Formation, Rio Negro, Argentina (*Limenavis* and *Lamarqueavis*), 4 - Maastricht Formation, Belgium (*Asteriornis*), 5 - Nemegt Formation, Mongolia (*Teviornis*, af. Phalacrocoracidae, af. Charadriiformes), 6 - Quiriquina Formation, Chile (*Neogaeornis*), 7 - Chorrillo Formation, Santa Cruz, Argentina (*Kookne*, stratigraphic unit ranges from late Campanian to Maastrichtian), 8 - Cape Lamb Member of the Snow Hill Island Formation, Vega Island, Antarctica (*Vegavis*, Neornithes indet., and Charadriiformes indet.) and López de Bertodano Formation, Seymour Island, Antarctica (*Polarornis*). Yellow dots mean the Northern Hemisphere neornithines and red dots indicate the Southern Hemisphere neornithines. Plate tectonic maps of Early Campanian (~80 Mya) and Maastrichtian (~70 Mya) by C. R. Scotese (2001), PALEOMAP Project (www.scotese.com).

adapted to diving, like modern loons and grebes (McLachlan et al. 2017). Despite the fragmentary nature of *Maaqwi*, it was possible to perform a cladistic analysis which recovered the specimen within Vegaviidae, a recently proposed clade composed of diving foot-propelled birds endemic of Gondwana (Agnolín et al. 2017). All remaining vegaviids come from Gondwana, implying that *Maaqwi* is the only Laurasian representative of the group. Vegaviidae has been recovered crownward of Ichthyornithes and Hesperornithes, and in different positions across Aves (e.g., McLachlan et al. 2017, Field et al. 2020), as discussed later.

A third specimen composed of a relatively complete skeleton (YPM 1734) from the early Campanian Niobrara Formation (USA) shows the presence of ribs, scapulae, coracoids, partial furcula, sternum, and a partial forelimb. It was long considered to belong to the ichthyornithine *Apatornis celer* based on weak diagnostic avian features (e.g., keeled sternum, Marsh 1880). However, several features found in YPM 1734 were also present in *Telmabates antiquus* Howard 1955 from the Eocene Sarmiento Formation of Patagonia (originally considered as phoenicopteriform, but now presbyiornithid). The specimen YPM 1734 presents a combination of basal ornithurine and derived neoavian features (e.g., short, angular, and expanded sternal end of the coracoid, and expanded dorsal trochlea on the carpometacarpus, Howard 1955). Later, a set of features present in YPM 1734, such as the short coracoid glenoid, laterally protruding distal end of the scapular glenoid, and an elongated acromion, was used to consolidate the specimen within anseriforms (Hope 2002). Recently, the hypodigm YPM 1734 was separated from the isolated holotype synsacrum of *Apatornis* (YPM 1451) and erected as a new taxon, *Laceornis marshi* Clake 2004. In the phylogeny of Clarke (2004), *Apatornis* was recovered as an Ornithurae outside Aves, whereas *Laceornis* was nested within a more advanced position than *Ichthyornis*, but outside crown birds, thus no longer considered as a presbyiornithid neornithine.

The Cimolopterygidae forms an entire clade of avian species predominantly found in the non-marine Cretaceous sediments of Wyoming, USA. Originally, the clade included *Cimolopteryx rara* (Marsh 1892), *Ceramornis major* (Brodkorb 1963a), *Cimolopteryx maxima* (Brodkorb 1963a), *Cimolopteryx minima* (Brodkorb 1963a), an array of ornithurine remains from the Maastrichtian of Saskatchewan referred to *Cimolopteryx* sp. (e.g., SMNH P1927.936, Tokaryk & James 1989; UALVP 55089, Mohr et al. 2021), and indeterminate ornithurine bone fragments (Longrich 2009). Recently, *Lamarqueavis australis* was formally assigned to Cimolopterygidae by Agnolín (2010), representing the only cimolopterygid from the Southern Hemisphere. Mayr (2017) offers an alternative perspective, suggesting that *Lamarqueavis* more closely resembles some gruiform birds, such as trumpeters (Psophiidae) and the early Cenozoic Messelornithidae, although the fossil remains are too fragmentary for a conclusive classification. Agnolín (2010) also proposed the taxonomic reassignment of two additional species, namely *L. minima* and *L. petra*, whereby they were transferred from *Cimolopteryx* to *Lamarqueavis*. *Lamarqueavis minima* is based on the holotype UCMP 53976, a right coracoid discovered in the Lance Formation of Wyoming (Brodkorb 1963a). Likewise, the classification of *L. petra* relies upon the holotype (AMNH 21911), a left coracoid also recovered from the Lance Formation (Hope 2002).

The phylogenetic relationship of Cimolopterygidae has been neglected by many authors (Agnolín 2010). In the past, it was regarded as a non-neornithine ornithurine or as a stem neornithine bird. However, Longrich et al. (2011)

Table I. List of Neornithes and putative neornithines of the Mesozoic. Asterisks indicate holotype number.

Taxon	Collection number	Referred specimens	Provenance	Age	Taxonomy	References
Antarcticavis capelambensis	SDSM 78147*	-	Antarctica, Snow Hill Island Formation	Late Campanian-Early Maastrichtian	Pangalloanserae	Cordes 2001, 2002, Cordes-Person et al. 2020
Apatornis celer	YPM 1451*	-	USA, Niobrara Formation	Early Campanian	Basal Carinatae?	Marsh 1873, Clarke 2004
Asteriornis maastrichthensis	NHMM 2013 008*	-	Belgium, Maastricht Formation	Late Maastrichtian	Pangalloanserae	Field et al. 2020
Charadriiformes	MLP 98-I-10-25	-	Antarctica, López de Bertodano Formation	Late Maastrichtian	Neornithes, Charadriiformes indet.	Case & Tambussi 1999, Reguero et al. 2013
Galliform	PVPH 237	-	Argentina, Portezuelo Formation	Turonian-Coniacian	Neornithes cf. Galliformes	Agnolín et al. 2006
Iaceornis marshi	YPM 1734*	-	USA, Niobrara Formation	Early Campanian	Basal Carinatae?	Marsh 1880, Clarke 2004
Kookne yeutensis	MPM 21550*	-	Argentina, Chorrillo Formation	Maastrichtian	Anseriformes	Novas et al. 2019
Cimolopteryx rara	YMP 1805*	-	USA, Lance Formation	Maastrichtian	Neornithes Cimolopterygidae	Marsh 1892, Agnolín 2010
Ceramornis major	UCMP V-5620*	-	USA, Lance Formation	Maastrichtian	Neornithes Cimolopterygidae	Brodkorb 1963a, Agnolín 2010
Lamarqueavis australis	MML 207*	-	Argentina, Allen Formation	Campanian-Maastrichtian	Neornithes Cimolopterygidae	Agnolín 2010
Lamarqueavis minima	UCMP 53976*	-	USA, Lance Formation	Maastrichtian	Neornithes Cimolopterygidae	Brodkorb 1963a, Agnolín 2010
Lamarqueavis petra	AMNH 21911*	-	USA, Lance Formation	Maastrichtian	Neornithes Cimolopterygidae	Hope 2002, Agnolín 2010
Lamarqueavis sp.	UALVP 47943	UALVP 47944?	Canada, Dinosaur Park Formation	Late Campanian	Basal Carinatae?	Hope 2002, Longrich 2009
Limenavis patagonica	PVL4730*	MML 206	Argentina, Allen Formation	Campanian-Maastrichtian	Basal Carinatae?	Clarke & Chiappe 2001, Hope 2002, Clarke 2004, Agnolín & Novas 2012
Maaqwi cascadensis	RBCM. EH2008.011.01120.001*	-	Canada, Northumberland Formation	Late Campanian	Pangalloanserae, Vegaviidae	McLachlan et al. 2017
Neogaeornis wetzelli	GMPK 123*	Unnumbered	Chile, Quiriquina Formation	Maastrichtian	Pangalloanserae, Vegaviidae	Lambrecht 1929, Olson 1992, Mayr et al. 2018, Schneider 1940, Acosta Hospitaleche et al. 2023
Neornithes	AMNH 30920	-	Antarctica, López de Bertodano Formation	Late Maastrichtian	Neornithes indet.	Roberts et al. 2014
Neornithes	MACN PV RN 1115	-	Argentina, Los Alamitos Formation	Campanian-Maastrichtian	Neornithes	Agnolín & Martinelli 2009

Table I. Continuation.

Neornithes	MPEF-PV 7758	-	Argentina, La Colonia Formation	Late Campanian–lower Maastrichtian	Neornithes indet.	Acosta Hospitaleche et al. 2023
Neornithes	Unnumbered	-	Mongolia, Nemegt Formation	Early Maastrichtian	Neornithes af. Diomedeidae	Kurochkin 1995
Neornithes	IGM 100/1309	-	Mongolia, Nemegt Formation	Early Maastrichtian	Neornithes indet.	Clarke & Norell 2004
Neornithes	AMNH 30898	-	Antarctica, López de Bertodano Formation	Late Maastrichtian	Neornithes	Roberts et al. 2014
Phalacrocoracidae	Unnumbered	-	Mongolia, Nemegt Formation	Early Maastrichtian	Neornithes af. Phalacrocoracidae	Kurochkin 1995
cf. *Polarornis*	MN 7833-V	-	Antarctica, López de Bertodano Formation	Late Maastrichtian	Pangalloanserae, Vegaviidae	This study
cf. *Polarornis*	?	-	Antarctica, López de Bertodano Formation	Late Maastrichtian	Pangalloanserae, Vegaviidae	Roberts et al. 2014
Polarornis gregorii	TTU P 9265*	MLP 96-I-6-2	Antarctica, López de Bertodano Formation	Maastrichtian	Pangaviiformes	Chatterjee 1989, 1997, 2002, Feduccia 1999, Olson 1992, Hope 2002, Chatterjee 2002, Reguero et al. 2013, Acosta Hospitaleche & Gelfo 2015, Agnolín et al. 2017
Teviornis gobiensis	PIN 44991-1*	-	Mongolia, Nemegt Formation	Maastrichtian	Anseriformes, Plesbyornithidae	Kurochkin et al. 2002
cf. *Vegavis*	AMNH FARB 30913	-	Antarctica, López de Bertodano Formation	Late Maastrichtian	Pangalloanserae, Vegaviidae	Roberts et al. 2014
cf. *Vegavis*	MN 7832-V	-	Antarctica, López de Bertodano Formation	Late Maastrichtian	Pangalloanserae, Vegaviidae	This study
Vegavis iaai	MLP 93-I-3-1*	MACN-PV 19.748	Antarctica, López de Bertodano Formation	Late Maastrichtian	Pangalloanserae, Vegaviidae	Noriega & Tambussi 1995, Hope 2002, Clarke et al. 2005, Chatterjee et al. 2006, Clarke et al. 2016, Agnolín et al. 2017, Marsà et al. 2017, Acosta Hospitaleche & Worthy 202
***Vegavis* sp.**	SDSM 78247	-	Antarctica, López de Bertodano Formation	Late Maastrichtian	Pangalloanserae, Vegaviidae	Case et al. 2006, West et al. 2019

recovered the cimolopterygids in a polytomy nesting in Neornithes, alongside *Crypturellus, Iaceornis*, and Galloanserae. The grade Cimolopterygidae needs a more comprehensive evaluation since its representatives could be related with the origin of the crown neornithines.

Non-Antarctic Southern Hemisphere neornithines - Outside Antarctica, some neornithines came from the Cretaceous of the Southern Hemisphere. Although these fossils are mostly comprised by poorly preserved materials, they furnish important information about the paleobiogeography of the Mesozoic birds. Most records came from South America, mainly from Argentina and Chile (e.g., Olson 1992, Agnolín & Novas 2012, Novas et al. 2019). *Neogaeornis wetzelli* Lambrecht 1929, from the Maastrichtian Quiriquina Formation of Chile, is based on two unrelated tarsometatarsal elements, the holotype (GMPK 123, Olson 1992, Mayr et al. 2018) and another currently lost specimen (Schneider 1940, Acosta Hospitaleche et al. 2023). *Neogaeornis* was originally placed within Podicipediformes, a polyphyletic group comprised of loons, grebes, and taxa today recognized as hesperornithines (Lambrecht 1929). Later, it was assigned to the podicipediform clade Baptornithidae (Brodkorb 1963b, Martin & Tate 1976), and to the Gaviidae (Olson 1992), until being placed in the Vegaviidae, alongside the Antarctic birds *Vegavis* and *Polarornis*, the Paleocene *Australornis lovei* Mayr & Scofield 2014 (Waipara Greensand, New Zealand) and numerous unnamed specimens (Agnolín et al. 2017). The position of *Neogaeornis* within Vegaviidae was based on the presence of a transversely compressed tarsometatarsal shaft and a posteriorly tilted trochlea of metatarsal II.

Kookne yeutensis Novas et al. 2019, from the Maastrichtian Chorrillo Formation of Argentina, is represented by an incomplete right coracoid lacking the sternal end, with damaged proximal end (MPM 21550). It was referred to Ornithurae for having an acrocoracoid process that curves medially to embrace a wide and deep triosseous foramen, and a broad furcular articulation (Novas et al. 2019). The authors pointed out that *Kookne* resembles crown birds by having a humeral articular facet anteriorly displaced relative to the scapular articular facet, scapular and humeral facets well-separated from each other, and acrocoracoid that medially wraps the triosseous foramen, and thus the specimen was referred to Neornithes, tentatively as an anseriform (Novas et al. 2019).

The Campanian-Maastrichtian Allen Formation of Argentina has yielded a fossil association comprising the basal carinatae *Limenavis patagonica* (Clarke & Chiappe 2001) alongside neornithine remains. The neornithines found in this unit consist of a tibiotarsus (PVL4730) dubiously attributed to a charadriiform (Hope 2002) and an isolated but well-preserved left carpometacarpus (MML 206) (Agnolín & Novas 2012). Although MML 206 presents apomorphic features of Neornithes (e.g., ventral rim of the proximal trochlea not in contact with the extensor process, and a shallow infratrochlear fossa), the specimen preserves insufficient data to ascribe it to any particular neornithine lineage (Agnolín & Novas 2012).

In addition, the avian fossil record of Patagonia has revealed itself as a Gondwanan stronghold for neornithines. Additional material includes a galliform-like coracoid (PVPH 237) from the Turonian-Coniacian Portezuelo Formation of Sierra del Portezuelo, Patagonia (Agnolín et al. 2006). It is important to note that, as presented above, the neornithine remains come from beds not older than Maastrichtian, or perhaps Santonian (Hope 2002). All neornithine records of older age (Early Cretaceous) have been questioned (e.g., Padian & Chiappe 1998, Hope 2002). Thus, despite the incomplete nature of the coracoid PVPH 237, it would constitute one of the oldest known Neornithes yet recorded (Agnolín et al. 2006), which would be consistent with divergence times estimated for modern bird groups based on molecular data (Cooper & Penny 1997, Paton et al. 2002, Brown et al. 2008).

Additionally, Agnolín & Martinelli (2009) reported numerous highly fragmentary specimens from the Campanian-Maastrichtian Los Alamitos Formation, Patagonia. The specimens represent different Ornithuromorpha/Ornithurae clades, some of them tentatively assigned to Enantiornithes, Hesperornithes, and Neornithes, reinforcing the presence of a diverse paleoavifauna in the Weddellian Province (Agnolín & Martinelli 2009). Recently, a fragment of distal ulna was collected from the upper Campanian–lower Maastrichtian La Colonia Formation, outcropping at the southeastern margin of the Somún Curá Plateau, Chubut Province, Argentina (Acosta Hospitaleche et al. 2023)

Antarctic neornithines -The Cretaceous neornithines from this continent comprise three nominal species *Polarornis gregorii* Chatterjee, 2002, *Vegavis iaai* Clarke et al. 2005, and *Antarcticavis capelambensis* Cordes-Person et al., 2020. Additionally, there is an array of poorly diagnosable specimens that have been referred to Gaviiformes (Chatterjee et al. 2006, Roberts et al. 2014), Charadriiformes (Case & Tambussi 1999, Case 2001, Cordes 2001, 2002), and Cariamiformes (Case et al. 2006, Tambussi & Acosta Hospitaleche 2007, Roberts et al. 2014).

Polarornis gregorii (TTU P 9265) comprises a partial skull, posterior cervical vertebrae, sternal fragment and ribs, femora, proximal tibiotarsus and fibula. The specimen was found in the late Campanian-Maastrichtian Lopéz de Bertodano Formation, Seymour Island, Antarctica in 1983. TTU P 9265 was assumed to belong to a stem-loon (Gaviiformes, Chatterjee, 1989, 1997, 2002, Olson 1992, Hope 2002), hesperornithid (Feduccia 1999), or as synonymous with the Chilean bird *Neogaeornis* (Olson 1992), until Acosta Hospitaleche & Gelfo (2015) recovered it within Pangaviiformes. Later, a distal femur and two proximal tiobiotarsi (MLP 96-I-6-2) were referred to *Polarornis* (Reguero et al. 2013, Acosta Hospitaleche & Gelfo 2015, Agnolín et al. 2017).

Another relevant taxon is *Antarcticavis capelambensis* (SDSM 78147) from the Cape Lamb Member (Late Campanian-Early Maastrichtian) of the Snow Hill Island Formation cropping out in Vega Island (Cordes-Person et al. 2020). The holotype consists of dorsal vertebrae, rib fragments, synsacrum, coracoids, partial sternum, sternal ribs, humeri, proximal radius and ulnae, carpometacarpi, ilium, femora, tibiotarsi, fibula, and tarsometatarsus. SDSM 78147 was originally referred to the crown birds Charadriiformes (Cordes 2001, 2002), until Cordes-Person and colleagues (2020) offered a formal publication with Zoobank's registration number, erecting the taxon *Antarcticavis capelambensis*. In this paper, the authors recovered *Antarcticavis* as a sister taxon of *Vegavis*+Galloanserae.

Vegavis iaai is the most complete Cretaceous neornithine found, followed by *Asteriornis*. The first *Vegavis* specimen, MLP 93-I-3-1, was preserved in a carbonatic concretion collected during the 1992/93' Antarctic Field expedition, supported by the Instituto Antártico Argentino (IAA), in the Sandwich Bluff Member of the López de Bertodano Formation, Vega Island. It was initially assigned to the anseriform family Presbyornithidae (Noriega & Tambussi 1995). The first identification was based on right coracoid, complete right humerus, proximal end of left humerus, distal end of right radius, synsacrum, proximal and distal ends of both femora, left tibiotarsus, proximal end of right (left of Noriega & Tambussi 1995) tarsometatarsus, distal end of left (right of Noriega & Tambussi 1995) tarsometatarsus, ribs and undetermined fragments published in the 1995 paper by Noriega & Tambussi (1995). Later, the matrix was mechanically removed to expose the five thoracic vertebrae, two cervical vertebrae, left scapula, right ulna, all pelvic bones, right and left fibulae and left? tarsometatarsal shaft (Fig. 3), which resulted in the formal description and naming of *Vegavis iaai*, including a phylogenetic analysis that recovered the holotype within the crown anseriform clade Anatoidea (Clarke et al. 2005).

Conversely, the phylogenetic affinities of *Vegavis* remain somewhat obscure (Ksepka & Clarke 2015, Ericson et al. 2006, Prum et al. 2015). Such uncertainty regarding the phylogenetic

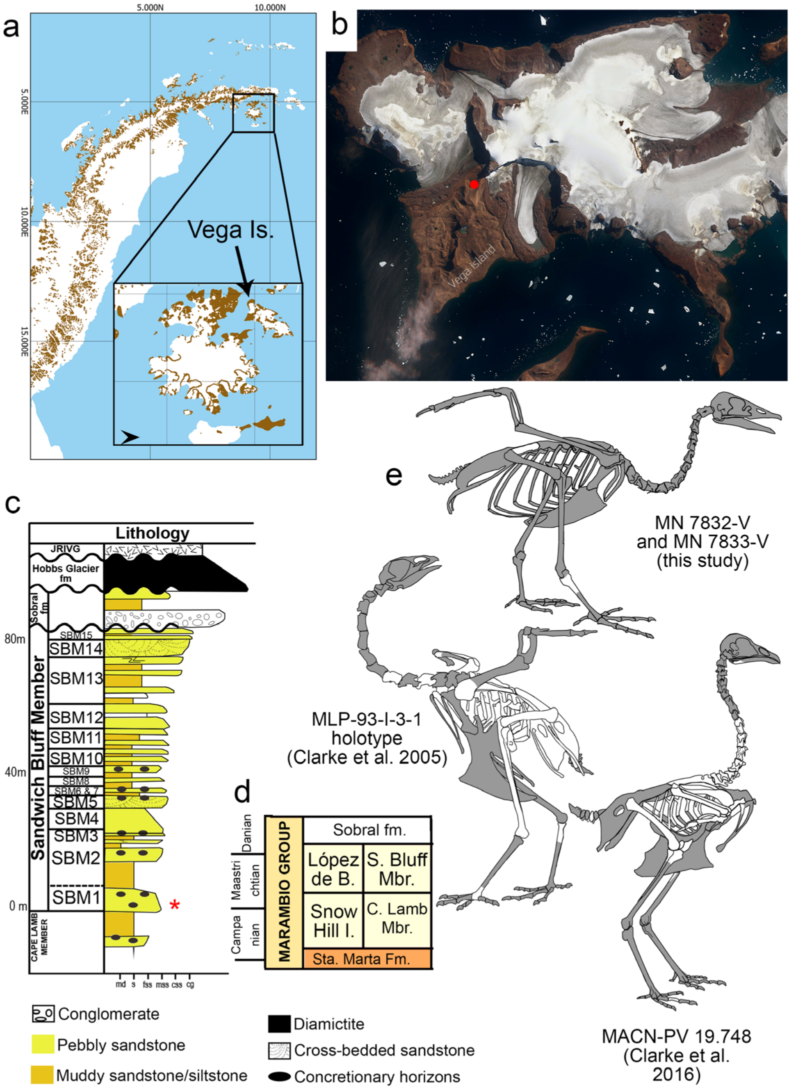

Figure 3. Map of the Antarctic Peninsula showing location of Vega Island (**a**). Copernicus Sentinel-2 image of ice-free portion of Cape Lamb, in Vega Island showing the locality (red dot) where the specimens studied here were collected (**b**). Stratigraphic interpretation of the Sandwich Bluff Member of the López de Bertodano Formation modified from Roberts et al. (2014) showing the levels where previous *Vegavis* specimens were found (marked by the red star) (**c**). Stratigraphic chart of the Marambio Group, James Ross Basin (**d**). Simplified schematic drawings showing all specimens unambiguously assigned to *Vegavis iaai* and the new avian materials studied here (white silhouettes indicate the preserved bones). See text for more details. Credit of figure **b**: European Union, Copernicus Sentinel-2 imagery. Abbreviations: SBM, Sandwich Bluff lithostratigraphic units recognized by Roberts et al. (2014), JRIVG, James Ross Island Volcanic Group.

position of *Vegavis* remains (Agnolín et al. 2017, Worthy et al. 2017) even after the description of a second concretion containing more materials attributed to this species (Clarke et al. 2016). This new specimen, MACN-PV 19.748 (previously MLP 93-I-3-2), was collected by the same 1992/93 expedition but was only studied in the 2000s. It comprises a pterygoid, caudal portion of mandible, syrinx, cervical and thoracic series and part of the caudal series, coracoids, scapula, furcula, humerus, ulna, radius, radiale, ulnare, carpometacarpus, manual phalanges II-1 and II-2 in articulation, femora, patella, tibiotarsus, fibula, pedal phalanges, ribs, and a possible ceratobranchial element from the hyoid (Fig. 3). MACN-PV 19.748 was also treated as a presbyornithid (Hope 2002) or as a small sympatric, gracile specimen of *Polarornis* (Chatterjee et al. 2006). Later, MACN-PV 19.748 was described using micro-CT scanning and assigned to *Vegavis* in the 2016 paper by Clarke and colleagues, being remarkable by preserving the oldest known syrinx in the fossil record (Clarke et al. 2016).

In 2017, Agnolín and colleagues proposed the taxonomic name Vegaviidae, grouping *Vegavis*, *Polarornis*, the controversial *Neogaeornis wetzeli*, the Paleocene *Australornis lovei* and several unnamed specimens. By employing a version of Worthy's basal avian analysis (Worthy et al. 2017), 'vegaviids' were retrieved as a clade sister to Anseriformes. However, this hypothesis has not been widely accepted by paleornithologists. Mayr et al. (2018) disputed the placement of *Neogaeornis*, *Australornis* and most of the Tertiary unnamed specimens in Vegaviidae based on qualitative data, correctly observing that many characters shared with anseriforms are ambiguously present or also found in various neoavians that were not incorporated in Worthy's matrix.

West et al. (2019) re-evaluate an isolated partial femur SDSM 78247 collected 12 m up section from the horizon that yielded *Vegavis* (Sandwich Bluff Member of the López de Bertodano Formation). The specimen was initially reported as a Cenozoic Phorusrhacidae ('terror birds') or a representative of the extant Cariamidae (seriemas) within Cariamiformes (Case et al. 2006). However, the presence of a deep, round ligament scar on the proximocaudal surface and elongated scar on its distolateral margin suggest that this isolated femur was more similar to *Vegavis* than other birds (West et al. 2019). However, among the features that separate SDSM 78247 from *Vegavis*, the most remarkable is its size, approaching nearly twice that of the *Vegavis* femora (West et al. 2019). This feature led the authors to assign SDSM 78247 to a new, unnamed, larger-bodied species within the genus *Vegavis* (West et al. 2019). Curiously, the paleohistological analysis performed by Marsà and colleagues (2017) on *V. iaai* MACN-PV 19.748 pointed out that the specimen was close to, or even had reached, the somatic maturity at the time of death, based on the maturity of limb bones (humerus and femur), characterized by slow growth rates. Thus, even if there was wide variation in size within this species, it would not be expected that an individual could double in size once reaching the barrier of the adult stage, arguing in favor of two distinct species within the genus *Vegavis*.

After the sedimentary matrix of the holotype MLP 93-I-3-1 was removed, it was submitted to CT-scanning which resulted in the redescription with new observations of the anatomy of *Vegavis* (Acosta Hospitaleche & Worthy 2021). Although it enables the scoring of new characters into the cladistic matrix of Field and colleagues (2020), no improvement in the phylogenetic relationship of *Vegavis* was acquired (Acosta Hospitaleche & Worthy 2021). Álvarez-Herrera et al. (2023) have recently provided a description of the lower jaw of the specimen MACN-PV 19.748. Their analysis revealed that the anatomical characteristics of the articular region align more closely with those of neoavians, which contrasts with the anseriform signature of its postcranial skeleton.

Vegavis is recovered either together with Galliformes and Anseriformes within Pangalloanserae (Worthy et al. 2017, Acosta Hospitaleche & Worthy 2021), in its own family Vegaviidae also including *Polarornis*, *Australornis lovei* Mayr & Scofield 2014, and *Neogaeornis wetzeli* Lambrecht 1929 as the sister group to crown Anseriformes (Agnolín et al. 2017), or as a sister clade of Pangalloanserae+Panneoaves within Panneognathae (Field et al. 2020). The difficulty of allocating *Vegavis* within Pangalloanserae is expected because this species represents one of the earliest radiations of neornithine birds, exhibiting a combination of plesiomorphic neornithine features and derived ones, typical of neoavians (Álvarez-Herrera et al. 2023). Although there is still some debate about which taxa are assigned to Vegaviidae (Mayr et al. 2018, Acosta Hospitaleche & Worthy 2021), the close relationship between *Vegavis* and *Polarornis* as members of the monophyletic clade Vegaviidae remains well supported (Mayr et al. 2018). In this work, we follow the proposal of Agnolín et al. (2017), considering Vegaviidae as a valid clade.

Dozens of isolated bird fossils have been reported from the Cape Lamb Member of the Snow Hill Island Fm. and the Sandwich Bluff Member of the Lopéz de Bertodano Fm. on Vega Island, mostly comprised of fragments. From Cape Lamb Member, we point out an incomplete tarsometatarsus (MLP 98-I-10-25) (Case & Tambussi 1999, Reguero et al. 2013) and incomplete trunk vertebrae (AMNH 30920) (Roberts et al. 2014), all of them have been tentatively referred to Charadriiformes. From Sandwich Member, we can cite an incomplete coracoid (AMNH 30898) provisionally referred to Aves (Roberts et al. 2014), a thoracic vertebra (AMNH FARB 30920) of an unidentified ornithurine bird (Roberts et al. 2014), a distal tarsometatarsus (AMNH FARB 30913) referred to cf. *Vegavis* (Roberts et al. 2014), and an avian femur and tibia from the same level as *V. iaai* (Coria et al. 2015). Nonetheless, in most cases, the taxonomic identification of these specimens cannot be verified due to the incomplete nature of the available materials and the lack of comprehensive descriptions.

Geological and geographical setting

The material studied here was collected in Vega Island during the 2018/19' austral summer by the PALEOANTAR project that is coordinated by the Museu Nacional/UFRJ, Brazil. Vega is a small island located northeast of James Ross Island, in the Weddell Sea, eastern flank of the Antarctic Peninsula (Fig. 3). Cape Lamb is the southern sector of the island, where sedimentary sequences that filled the James Ross Sub-Basin crop out (Del Valle et al. 1992). Among the three main lithostratigraphic units of the basin, only the Santonian-Danian Marambio Group is represented in the Cape Lamb area (e.g., Crame et al. 1991). Marambio Group is subdivided into Santa Marta (Santonian to Middle Campanian), Snow Hill Island (Upper Campanian to Lower Maastrichtian), and López de Bertodano (Lower Maastrichtian to Lower Danian) formations (Crame et al. 2004, Olivero 2012b, Roberts et al. 2014).

Previous bird remains from Vega Island were found in the upper Cape Lamb Member (upper Campanian-lower Maastrichtian), which corresponds to the top levels of Snow Hill Island Fm., and in the Sandwich Bluff Member (upper Maastrichtian), which corresponds to beds of the López de Bertodano Fm. cropping out in Vega (Case & Tambussi 1999, Chatterjee et al. 2006, Clarke et al. 2005, Case et al. 2006). Both units are regarded as progradational deltaic wedges to near-shore marine deposits (Crame et al. 1991, 2004, Olivero 2012a, Roberts et al. 2014).

Roberts and colleagues (2014) subsequently subdivided the Sandwich Bluff Member into fifteen discrete lithostratigraphic units, termed Units SBM1 to SBM15. Some of these lithostratigraphic units represent concretionary horizons bearing spherical-subspherical and fossil nucleated concretions. The vegaviid specimens MACN-PV 19.748 and MLP 93-I-3-1 were collected from the SBM1. Unlike the other specimens of *Vegavis* reported in the literature, the specimens here studied were not found inside carbonatic concretions, but on a distinct bench of poorly indurated siltstone. We tentatively assigned the specimens to the horizon SBM8, however, it cannot be ruled out that the specimens may have rolled down from upper strata (particularly horizons SBM11 and SBM 12) (Fig. 3).

MATERIALS AND METHODS

Material and anatomical nomenclature

The material is housed in the Paleovertebrate collection of the Museu Nacional of Universidade Federal do Rio de Janeiro (UFRJ), Brazil. The specimens consist of three fused synsacral vertebrae lacking the respective centra (MN 7832-V) and a fragment of long bone (MN 7833-V), identified as a distal portion of a tarsometatarsus.

Measurements were taken with a digital caliper Vernier 0-150 mm. Photographs were taken using the digital camera Nikon D7200. The anatomical plates were constructed with Adobe Photoshop® CS6. We adopted the anatomical terms and views of Baumel et al. (1993) for osteological description. Comparative material includes photographs and 3D models of *Vegavis* and *Polarornis* from the literature (Chatterjee 2002, Clarke et al. 2005, 2016, Acosta Hospitaleche & Worthy 2021). Extant dry skeletons examined first-hand and used for comparisons were *Spheniscus magellanicus*, *Rhea americana*, *Anhinga anhinga*, and *Vanellus chilensis* from the Aves Collection (MNA) of Museu Nacional/UFRJ.

Micro-CT scanning and tridimensional reconstructions

The synsacrum (MN 7832-V) was scanned at the Laboratório de Sedimentologia e Petrologia of the Pontifícia Universidade Católica do Rio Grande do Sul (PUCRS), Porto Alegre (Brazil), using 110 kV and 72 µA. The scan resulted in 2,012 tomographic slices, with a voxel size of 21.87 µm. Digital preparation and volume rendering was performed using 3D Slicer image computing software version 4.10 freely available in slicer.org.

Microstructural analysis

The protocol of thin section preparation and paleohistological analysis was modified from Lamm (2007). The long bone (MN 7833-V) was embedded in epoxy resin Rp031 to produce resin blocks that protected it against saw trepidation. Although midshafts offer better information about the growth record and lead to underestimated skeletochronology (Stein & Sander 2009), MN 7833-V preserved no midshaft. Therefore, the section was done by a precision router (Dremel®, Racine, WI, USA), as close as possible to the middle part. The resin block containing the bone was fixed on a histological slide using epoxy resin Rp031. After the hardening, the block was polished to millimeter thickness using a lap wheel Politriz Aropol® VV200-PU and sandpapers Norton Saint-Gobain® T277 with P100, P600, and P1200 lines/inch sequentially. Finally, the other side was thinned and polished using the same sandpaper series. The histological slide was analyzed using a ZEISS Axioscope 5 Phase Contrast Microscope under conventional white-light reflection and transmitted circularly polarized light with 4×, 20×, or 40× objectives. Images were acquired with an Axiocam 202 mono video camera using the interface program ZEN® software. The histological terms used in the description follow Buffrénil et al. (2021). Microstructural measurements were made in ImageJ Software (Schneider et al. 2012).

Because MN 7833-V exhibits moderate cortical thickness, we calculated the Relative Bone Thickness (RBT, Wall, 1983) and compared it to other fossil and extant birds (e.g., Smith & Clarke 2014). RBT was calculated by dividing the mean thickness of cortex by mean diameter of the total cross-section and then multiplying by 100 (Bühler 1986, Chinsamy 1993). Five sets of measurements were taken in the cross-sectional area approaching 40° from each other to obtain the mean thickness of the cortex. However, the incompleteness of the shaft prevented us from calculating the RBT at the midshaft level, which would be ideal. The histological slide was deposited in the Paleovertebrate collection of Museu Nacional/UFRJ.

RESULTS

Systematic Paleontology

Aves Linnaeus 1758
Ornithurae Haeckel 1866
Panneognathae Gauthier & de Queiroz 2001
Vegaviidae Agnolín et al. 2017
Vegavis iaai Clarke et al. 2005
cf. V. iaai

Material – MN 7832-V, three fused synsacral vertebrae lacking the corpus vertebrae.

Locality and horizon – Sandwich Bluff, Sandwich Bluff Member, SBM8, 9, 10, 11 or 12 of Roberts et al. (2014), approximately 40 m above the level where *Vegavis* specimens were recovered, López de Bertodano Formation outcropping in Cape Lamb, Vega Island, Antarctic Peninsula. Upper Maastrichtian (~ 66-68 Mya).

Description and comparisons – The specimen MN 7832-V consists of three fused synsacral neural arches 3.7 mm in length (Fig. 4). It lacks the corpus vertebrae and the most of the processus transversi. Despite its incompleteness, there are no signals of taphonomic deformation. The inner surface of the neural spines has a nacreous aspect, ranging from dusky- to dark-red colors (Fig. 4d). The proccessus spinosum and ossified tendons are ankylosed into a crista spinosa sinsacri, which is low but exceeds dorsally the processus transversi in lateral view. In *Vegavis*, the crista spinosa exceeds dorsally the processus transversi in synsacral vertebrae 4th to 8th, similarly to MN 7832-V. The dorsal surface of the crista is straight. The crista decreases in both height and thickness caudally. Two longitudinal sulci extend side by side to the crista. MN 7832-V preserves three proximalmost portions of the processus transversi. Each processus is dorsoventrally tall and mediolaterally short, being laterally rather than caudolaterally or laterocaudally projected. A laterally projected processus also occurs in the preacetabular vertebrae synsacrales in *Vegavis* (Acosta Hospitaleche & Worthy 2021). In MN 7832-V, the processus transversi lack the end that articulates with the os coxae. The processus transversi are separated by deep concave intervertebral spaces in lateral view. In the floor of these spaces, ventral to each processus transversus lies a series of small foramina intervertebralia (Fig. 4g and h). Each intervertebral space bears a small foramen. Similar foramina occur in vertebrae synsacrales 5th to 7th (apparently also in 4th and 9th) of the *Vegavis* holotype (MLP 93-I-3-1) (Acosta Hospitaleche & Worthy 2021). The smaller size and low density of foramina resemble extant diving birds such as the examined sphenicid *Spheniscus magellanicus* (MNA 32383, MNA 2858), the suliform *Anhinga anhinga* (MNA 22863, MNA 26347), rather than cursorial terrestrial Neornithes such as the ratite *Rhea americana* (MNA 7679) and the charadriid *Vanellus chilensis* (MNA7004), reinforcing the interpretation of adaptations for a foot-propelled diving ecology for MN 7832-V and *Vegavis*.

Externally, the contacts between vertebrae are indiscernible. However, the absence of corpus vertebrae exposes, in ventral view, the roof of the canalis synsacri, enabling us to examine the inner structure of the neural arches (Fig. 4d and i). Internally, a sulcus extends longitudinally over the roof of the canalis synsacri, likely accommodating the spinal cord canal. The divisions of the vertebrae are represented by small recesses, identified as lumbosacral transverse canals, that intercept transversally the canal synsacri (Fig. 4i). The functional hypothesis about such canals is that they are part of a secondary balance sensing system, working similarly to the semicircular

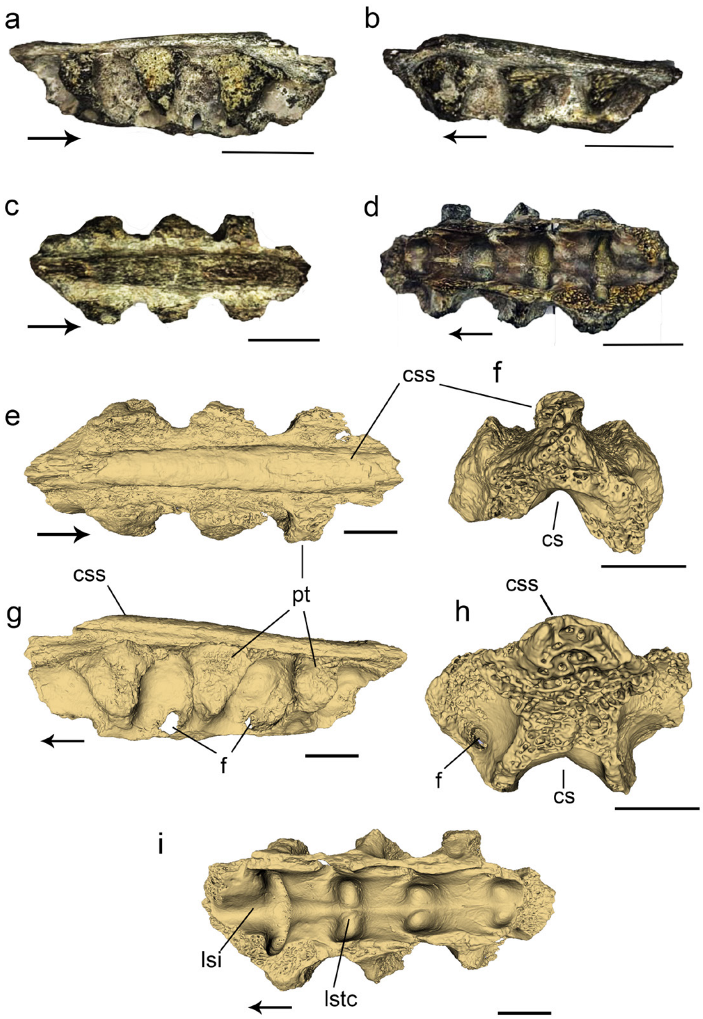

Figure 4. Synsacrum MN 7832-V (**a-i**), photographs of the specimen in (**a**) right lateral, (**b**) left lateral, (**c**) dorsal, and (**d**) ventral view. Micro CT-scan of MN 7832-V in (**e**) dorsal, (**f**) anterior, (**g**) left lateral, (**h**) posterior, and (**i**) ventral views. Scale bar for (**a-d**) = 10mm, (**e-i**) 5mm. Arrows indicate anterior side. Abbreviations: **cs**, canalis synsacri, **css**, crista spinosa synsacri, **f**, foramina intervertebralia, **lsi**, lumbosacral intumescence, **lstc**, lumbosacral transverse canals, **pt**, processus transversus.

channels of the inner ear, involved in the control of walking and perching (Stanchak et al. 2020, Jadwiszczak et al. 2022). These canals are found in most neornithine groups (Jalgersma 1951) and, up to now, the oldest record of lumbosacral canals in a synsacrum was reported in a Maastrichthian Ornithurae FMNH PA 741 from Madagascar (O'Connor & Forster 2010). Thus, in the fossil Neornithes context, the specimen MV 7832-V exhibits the oldest record of the lumbosacral canals, since before they were only reported in early Sphenisciformes penguins from the Eocene of Seymour Island, Antarctic Peninsula (Jadwiszczak et al. 2022). The canalis synsacri expands cranially, which likely corresponds to the lumbosacral intumescence (= bulla intumescentia lumbosacralis) (Fig. 4d and i) that contains the glycogen body (cranium inferior of Barkow 1856). In living birds, this glycogen body is placed medially between two lateral rami of the spinal cord that bifurcate at the level of lumbosacral vertebrae. This feature is present in all crown birds, neornithines, ichthyornithids, and hesperornithids (Acosta Hospitaleche & Worthy 2021). In *Vegavis*, the lumbosacral intumescence reaches its maximum width around the 6th and 7th vertebrae (Acosta Hospitaleche & Worthy 2021).

Comparison among ornithurines is restricted by the small number of specimens in which the synsacrum is preserved. The crista synsacri of MN 7832-V differs from the ornithurine UA

9601 by having a mediolaterally broader crest, whereas in UA 9601, the crest is sharp. Instead, the dorsal surface of the crista synsacri of MN 7832-V is flattened similar to *Apatornis* (YPM 1451). The ornithurine UA 9601 lacks the sulci bounding laterally the crista synsacri seen in MN 7832-V and in the anteriormost synsacral vertebrae of *Apatornis*. In UA 9601, the lumbosacral intumescence occurs around the 4th and 5th vertebrae, whereas in *Vegavis* and *Apatornis* it occurs in the 6th and 7th, which we assume to be similar to MN 7832-V. A single large foramen intervertebralis facing laterally lies on the lateral surface of the 4th vertebra in UA 9601 and *Apatornis*, whereas in *Vegavis* and MN 7832-V, the foramina occur on the processus transversi of the 5th, 6th, and 7th vertebrae. The morphology of MN 7832-V is consistent with its referral to *Vegavis*. Based on the morphological comparisons performed here, MN 7832-V is assigned to *Vegavis*, most likely representing the 5th to 7th vertebra synsacrales. Furthermore, both *Vegavis* and MN 7832-V possess a pattern of synsacral pneumaticity similar to that of diving birds, reinforcing the hypothesis of a diving ecology for this species.

Ornithurae Haeckel 1866
Panneognathae Gauthier & de Queiroz 2001
Vegaviidae Agnolín et al. 2017
Polarornis gregorii Chatterjee 1989
cf. *Polaronis gregorii*

Material – MN 7833-V, isolated fragment of a tarsometatarsus? (Fig. 5a).

Locality and horizon – Sandwich Bluff, Sandwich Bluff Member, SBM8, 9, 10, 11 or 12 of (sensu Roberts et al. 2014), approximately 40 m above the level where *Vegavis* specimens were recovered, López de Bertodano Formation outcropping in Cape Lamb, Vega Island, Antarctic Peninsula. Upper Maastrichtian (~66-68 Mya).

Description and comparisons

MN 7833-V consists of a small fragment (3.5 mm) of a rod-like bone with a diameter of 8.8 mm, lacking its proximal and distal ends. The specimen was found with no association with the synsacrum MN 7832-V. The incompleteness of the bone precludes its precise identification (Fig. 5a), but some features are informative. The partial diaphysis has a longitudinal and sharp crest extending along the shaft, but its presumably distal portion is broken. The apical margin of the crest is straight and roughly parallel to the shaft surface. As it extends along the shaft, the crest deflects and gradually merges onto the shaft surface. One of the surfaces of the crest is convex and continuous with the shaft, whereas the opposite surface is concave, which gives to the shaft a half salinon-shape to the transverse section in distal view. Above the crest level, the shaft exhibits a roughly circular cross-section. The combination of straight shaft, roughly circular shape in transversal section, and the presence of a sharp and bowed crest suggests that the specimen represents a hind limb long bone. The preserved shaft is elongated and robust, possessing a thick cortex, similar in proportions to the avian tibiotarsus or tarsometatarsus. In comparison with partially chronocorrelated birds, the crest of MN 7833-V superficially resembles the crista fibularis or tuberositas retinaculi extensoris of the tibiotarsus of *Vegavis* (Acosta Hospitaleche & Worthy 2021). These crests are sharp and have rounded apical edges as in MN 7833-V. However, they are lower in *Vegavis*, protruding briefly from the shaft to immediately merge into the bone surface. In addition, the apical margins of these crests are not parallel to the shaft as in MN 7833-V. Instead, the crest of MN 7833-V is more similar to the crista plantaris lateralis (crista dorsalis lateralis of Acosta Hospitaleche & Worthy 2021) of the tarsometatarsus of *Vegavis*. In both MN

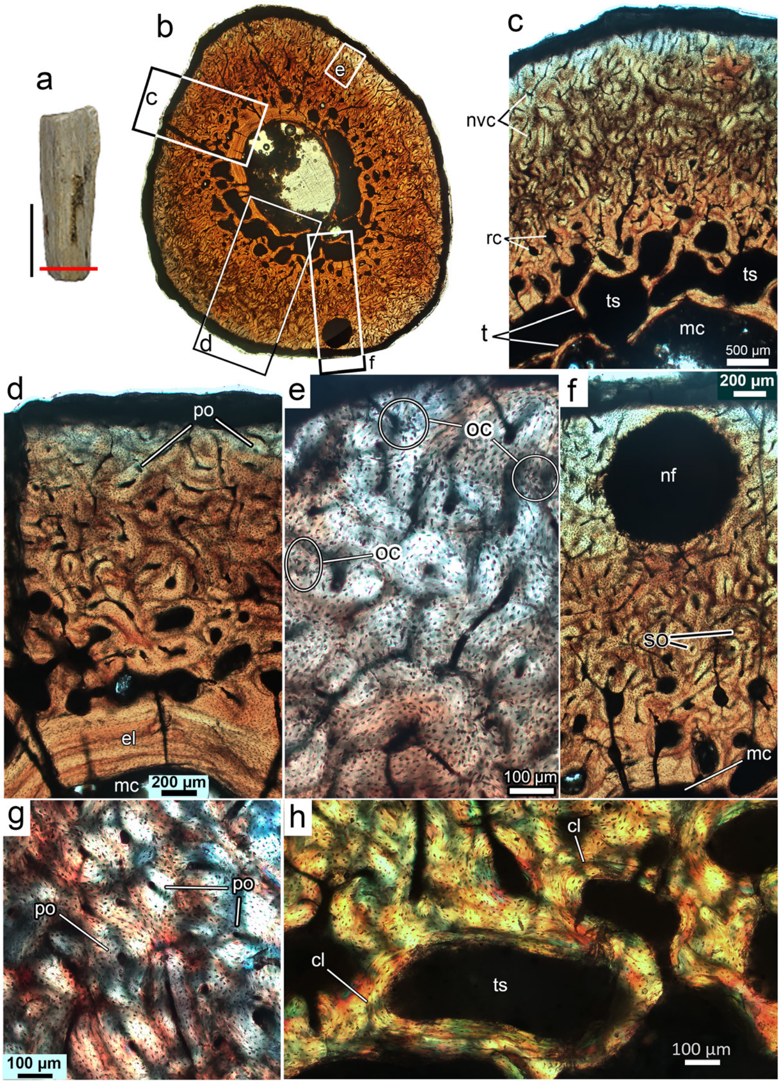

Figure 5. Microstructural pattern of MN 7833-V (**a-h**), proximal fragment of tarsometatarsus MN 7833-V in lateral view (**a**), whole cross section of MN 7833-V (**b**). Two cortical regions showing the large amount of intertrabecular spaces (**c**) and thick endosteal lamella (**d**) in different portions of the perimedullary cortex. High-magnification of the cortex showing the clusters of osteocyte lacunae, which characterize the woven-fibered bone matrix (**e**). Nutrient foramen in subperiosteal cortex (**f**). High magnification of subperiosteal cortex showing the longitudinal primary osteons (**g**). High magnification of trabeculae bounded by cement lines in perimedullary cortex (**h**). Red line in **a** corresponds to the level where the section was made. The outer cortex face upward in **b-g**. Scale bar in **a** is equal to 15 mm. Abbreviations: **cl**, cement line, **el**, endosteal lamellae, **mc**, medullary cavity, **nf**, nutrient foramen, **nvc**, neurovascular canals, **po**, primary osteons, **oc**, osteocyte clusters, **rc**, resorption cavities, **so**, secondary osteon, **t**, trabeculae, **ts**, intertrabecular spaces.

7833-V and *Vegavis* tarsometatarsus, the crests similarly protrude acquiring a more dorsal inclination. Their apical edges are parallel to the straight shaft. The shafts possess a deeply concave sulcus extensorum on one side, whereas they have a convex shaft in the opposite side. The half 'salinon-shaped' cross-section is present in both MN 7833-V and *Vegavis*. However, unlike *Vegavis*, MN 7833-V lacks foramina vasculare proximale laterale et proximale on the floor of sulcus extensori. MN 7833-V may represent a fragment from a more distal part of the shaft of the tarsometatarsus than the one preserved in *Vegavis,* in which the distalmost portion of crista plantaris is missing, preventing us from determining whether the inflection of the crest is similar to MN 7833-V or not.

The anatomy of the crest of MN 7833-V also resembles the crista deltopectoralis of the vegaviids *Vegavis, Maaqwi* (McLachlan et al. 2017, Acosta Hospitaleche & Worthy 2021), and many extant neornithines such as *Gavia adamsii* and *Haliaeetus leucocephalus* (Serrano et al. 2020, Watanabe et al. 2021), with a straight apical margin almost parallel to the shaft. The deflection of the crest within the shaft in lateral view of MN 7833-V approaches angles similar to those of the cited vegaviids. However, MN

7833-V differs from the humerus by having a sinuous apical outline instead straight. Given its morphology, we tentatively identify MN 7833-V as an undetermined vegaviid tarsometatarsus.

Microstructural pattern

The thin section of MN 7833-V revealed a roughly circular cross-section (Fig. 5b). It shows a relatively thick and azonal compact cortex that represents 89.6% of the cross-sectional area (RBT ranging from 32.7% to 37.14%, mean = 34.55±1.957). A wide, roughly circular, and well delimited medullary cavity is present. The cavity is delimited by thick endosteal lamellae (avascular inner circumferential layer of some authors - e.g., Chinsamy-Turan 2005, Màrsa et al. 2017), which indicates that the specimen was a skeletally mature adult at the time of death (Fig. 5b and d).

The cortex is intensely vascularized (Fig. 5). It is filled by globular, and haphazard-oriented osteocyte lacunae, which occur in clusters approaching a high degree of overlapping (Fig. 5e). The primary osteons are arranged in a mixed reticular and longitudinal neurovascular pattern. Primary longitudinal osteons are particularly abundant toward the subperiosteal region (Fig. 5g). The primary osteons are surrounded by flattened osteocyte lacunae, which are concentrically arranged around the inner canals. The longitudinal primary osteons show birefringence under circularly cross-polarized light (Fig. 5b and f). In the subperiosteal cortex lies a large, longitudinal nutrient foramen (Fig. 5e). This foramen houses the arterial supply for the primary diaphyseal growth center during development and it is regarded as indicative of mid-diaphysis in adults (Payton 1934).

Under circularly cross-polarized light most of the cortex exhibits isotropism (i.e., exhibiting transmitted light regardless of the plane of observation, Shapiro & Wu 2019), which occurs when large amounts of matrix are quickly deposited (Buffrénil et al. 2021). The combination of isotropic bone matrix, globular haphazard-oriented and clustered osteocyte lacunae characterize the woven-fibered matrix (de Ricqlès 1976). The woven-fibered bone matrix extensively occupied by longitudinal primary osteons indicates that the bone is of fibrolamellar type (=woven-parallel of Buffrénil et al. 2021). This bone is typical of endothermic tetrapods and is commonly indicative of high, sustained metabolic activity (e.g., de Ricqlès et al. 2008).

The cortex is devoid of any cyclical growth marks (LAG or annuli), suggesting that the specimen exhibited a high and continuous growth rate (Shapiro & Wu 2019, Buffrénil et al. 2021), likely reaching adulthood without any periodic interruption.

The perimedullary cortex of MN 7833-V has enlarged eroded resorption cavities (Fig. Fig 5c and h). The cavities grade to bone trabeculae endosteally. Trabeculae are formed by primary lamellated bone. They are asymmetrically distributed over the cross-section, completely obliterating the endosteal lamella in one of the sides of the section. The resorption cavities decrease in size toward the outer cortex, but they do not extend outside the deep cortex (Fig. 5b, d, f and h). Outwardly, these cavities are replaced by secondary osteons with wide Harversian canals (Fig. 5f and h). The Harvesian canals decrease in diameter outwards (Fig. 5f).

The overall microstructure of MN 7833-V is roughly similar to the pattern seen in the femur of *Polaronis* (Chinsamy et al. 1998), and has some resemblance with the humerus, radius, and femur of *Vegavis* (Clarke et al. 2005, Màrsa et al. 2017).

The cortex of MN 7833-V is highly populated by resorption cavities like the pattern seen in the *Polarornis* TTU 9265. In both MN 7833-V and

Polarornis, these cavities occur in the margins of the medullary cavities. Although *Vegavis*' femur has numerous porosities, they differ in diameter from those of *Polaronis*. The perimedullary cortices of MN 7833-V and *Polarornis* contain numerous Volkman's canals passing through the endosteal lamellae, whereas the *Vegavis* specimens do not exhibit such structures in the endosteal lamellae. In *Vegavis*, the predominant neurovascular pattern is longitudinal, unlike MN 7833-V and *Polarornis*, which have predominantly reticular neurovascular pattern. Furthermore, the specimen MN 7833-V shares with *Polarornis* proportionally thick endosteal lamellae.

MN 7833-V and *Vegavis* femora share perimedullary cortices intensely populated by resorption cavities. However, MN 7833-V differs from all sampled *Vegavis* bones by the presence of a large nutrient foramen in the subperiosteal cortex and proportionally thicker endosteal lamellae. It is difficult to confirm whether these features (especially the thicker endosteal lamellae) may result from intra-elemental histovariability or not.

Although the Cretaceous vegaviid *Maaqwi* has not been histologically analyzed, its broken proximal humerus shows a large nutrient foramen close to the subperiosteal cortex, as in MN 7833-V. *Maaqwi* also possesses a thick cortex (we calculated RBT = 31.54) that is more similar to MN 7833-V (34.55) than *Vegavis* (20 for humerus and 21.6 for femur, Marsà et al. 2017).

The microstructural features of MN 7833-V also resemble *Ichthyornis* (Chinsamy et al. 1998), but it can be easily distinguished from the latter by possessing a considerably thicker cortex. Unlike *Polarornis* and *Vegavis*, the relatively thin bone wall of *Ichthyornis* is more consistent with other non-diving volant birds (Chinsamy et al. 1998).

The vascular pattern, bone type, and absence of LAGs in MN 7833-V are consistent with its placement within Neornithes, but also Ornithurae as a whole. However, these attributes alone are not enough to provide a less inclusive taxonomic assignment of the specimen with confidence. Among the birds herein examined, *Vegavis*, *Polarornis*, and *Maaqwi* shared similar microstructural patterns resulting from adaptation to their diving-ecologies.

Hollow long bones with a cortical thickness comparable to or even thinner than MN 7833-V only occur in theropod dinosaurs, including birds (Erickson 2014). In fact, non-avian theropod bones occasionally occur in horizons SBM7, 12, and 15 (Case et al. 2003, Roberts et al. 2014, Lamanna et al. 2019). However, because ornithurine (those including Neornithes) exhibit extremely high growth rates, they rarely deposit cyclical growth marks during growth, differing from other non-ornithurine theropods that show LAGs (Padian et al. 2001, Chinsamy 2002). Therefore, LAGs have been observed in only few neornithines, including the king penguin (Castanet 2006), kiwi (Bourdon et al. 2009), orange-winged Amazon parrot (Amprino & Godina 1947), extinct Moa (Turvey et al. 2005), and *Gastornis* (Padian et al. 2001). The absence of LAGs in MN 7833-V is thus consistent with ornithurine birds and excluded it from non-ornithurine theropods.

However, the cortex of MN 7833-V is thicker than in most typical volant ornithurines. Thick cortices are present in *Hesperornis*, *Polarornis*, anatids, penguins, and diving charadriiforms, and are associated with their diving ecology (Chinsamy et al. 1998, Smith & Clarke 2014). The cortical thickness varies considerably even among diving birds. This feature can be expressed through comparisons of RBT among extant and extinct taxa. The RBT of tarsometatarsus MN 7833-V (=34.5) is considerably higher than in *Vegavis* (20 – 21.6) (Marsà et al. 2017), some anseriforms (~17.6) (Mendoza & Tambussi 2015), but lower than in *Polarornis* (37) (Chinsamy et al. 1998) and the larger femur of the unnamed species of *Vegavis* SDSM 78247 (37) (West et al. 2019). Instead, the RBT of MN 7833-V approximates to diving charadriiformes (~30) (Smith & Clarke 2014), the Andean ruddy duck *Oxyura ferruginea* (31.42) (Mendoza & Tambussi 2015), *Maaqwi* (31.54), gentoo penguin *Pygoscelis papua* (32.83) (Mendoza & Tambussi 2015), and emperor penguin *Aptenodytes forsteri* (33) (Chinsamy et al. 1998). Therefore, it is important to note that the RBT observed in MN 7833-V is intermediate between sphenicids and highly osteosclerotic anseriforms.

Although the microstructure of the tarsometatarsus MN 7833-V shows a pattern consistent with ornithurine birds and roughly similar to diving neornithines (especially vegaviids), the anatomy fails to show any feature that enables a less inclusive taxonomic identification of the specimen.

Regardless of both bias inherent to the histological sampling and plasticity of nutrient foramina, and consistent with the morphologic comparisons here provided, we tentatively consider MN 7833-V as an undetermined vegaviid tarsometatarsus, with striking microstructural similarities with *Polarornis*, and thus potentially regarded as belonging to this taxon.

DISCUSSION

The literature shows a dramatic improvement in the number of Mesozoic avian specimens since 1980, expanding our knowledge about the diversity, distribution, and early stages of the evolution of the crown birds. Most of the discoveries come from taxa found in South America, Asia, and Antarctica, adding materials known for a long time from Europe and North America, which also revealed recent findings.

Putative neornithines appear in the fossil record probably in the Coniacian of South America (Agnolín et al. 2006), which could reinforce the Gondwanan origin of the crown neornithines (Cracraft 2001). The fossil record indicates that the group coexisted alongside Enantiornithes, Hesperornithes, Ichthyornithes and their kin in both Northern and Southern Hemispheres. While most non-neornithine avian lineages reached the apex of diversification and abundance before the Late Cretaceous (O'Connor & Forster 2010), the neornithines only represented modest components of the paleocommunities of this time. It is hard to determine whether the apparent paucity of Cretaceous neornithines results from taphonomic bias or paleoecology, but the current data support both hypotheses.

A taphonomic bias has often been argued to explain the relatively low abundance of neornithines in the Mesozoic, with many authors suggesting that the avian fossil record is poor (Cooper & Penny 1997, Cooper & Fortey 1998, Smith & Peterson 2002) or that paleontologists have performed relatively little collecting effort, especially in the Southern Hemisphere (Cooper & Fortey 1998, Cracraft 2001). Other authors, however, suggested that neornithines were simply ecologically less abundant (Fontaine et al. 2005). However, the high number of specimens discovered in South America (Lambrecht 1929, Clarke & Chiappe 2001, Hope 2002, Agnolín et al. 2006, Agnolín & Martinelli 2009, Agnolín 2010, Novas et al. 2019, Acosta Hospitaleche et al. 2023) and the well-preserved *Vegavis* specimens found in Antarctica (Noriega & Tambussi 1995, Hope 2002, Clarke et al. 2005, 2016, Chatterjee et al. 2006, Agnolín et al. 2017, Marsà et al. 2017, Acosta Hospitaleche & Worthy 2021) in the last decades have challenged these traditional assumptions. Furthermore, frequently neornithines and non-neornithine birds occur in the same strata, with rare exceptions (e.g., O’Connor & Foster 2010). They also possess similar habits and sizes, making it improbable that these birds had significantly different preservation potential (Fontaine et al. 2005). This argues against a taphonomic filter acting over the neornithine fossil record.

Although molecular data indicate that the origin of crown birds occurred in the mid-Cretaceous (Cooper & Penny 1997, Paton et al. 2002, Brown et al. 2008), the fossil record shows that only in the Campanian they began to increase slightly in diversity, becoming more abundant in the Maastrichtian. Such a pattern would corroborate the model of evolution of bird lineages throughout vicariance events related to the break-up of Gondwana (Cracraft 2001). The end-Cretaceous encompassed the extinction of all basal avian lineages (Enantiornithes, Hesperornithes, Ichtyornithes and kin) but not the neornithines. Several studies have attempted to list the features of the neornithines that enabled them to survive across the K-Pg boundary (Feduccia 1995, Cooper & Penny 1997, Longrich 2009, Bono et al. 2016, Mayr 2017, Torres et al. 2021). Among the hypotheses, that of the different growth rates between neornithines and non-neornithine avians have gained strength in the last years (Longrich 2009, Bono et al. 2016, Marsà et al. 2017). Although all ornithothoraceans shared bone cortices composed of fast-growing fibrolamellar bone, neornithines differed by usually lacking LAGs, despite growth marks have been observed in the outer cortices of some species (Canoville et al. 2022). This suggests a relatively higher metabolism and continuously sustained growth rates, without annual interruption. However, because neornithines did not comprise predominant elements across the world or were even absent in some Mesozoic paleocommunities (O’Connor & Foster 2010), this higher growth rate seems not to have provided considerable advantage over the non-neornithine birds. Notwithstanding, a fast growth, allied with relatively small body size, may have been advantageous and selectively beneficial through the K-Pg extinction event (Field et al. 2020)

Antarctica has the only Mesozoic sites where neornithines are predominant. In parallel, the identification of basal ornithurines from Vega and Seymour islands (Cordes 2001, Roberts et al. 2014) may be a result of the lack of diagnostic neornithines characters in the aforementioned specimens, what places them on a more inclusive level. The paucity of the “non-neornithine birds” in Antarctica (notably enantiornithines) contrasts with the abundance of Mesozoic neornithines there. Despite the low sampling due to the extreme conditions imposed to fieldwork on the continent and the high weathering acting on the Antarctic fossils, Vega and Seymour Islands have provided abundant neornithine remains. They include one of the best-preserved neornithines of the Mesozoic (Clarke et al. 2005).

The predominance of neornithines in Antarctica suggests that the uninterrupted fast growth rates could be advantageous in these higher latitudes (Longrich 2009, Bono et al. 2016, Marsà et al. 2017), where extreme seasonal changes in luminosity, temperature, and food availability presumably occurred, such as in Antarctica during the end Cretaceous. The possible absence of non-neornithine birds in the Maastrichtian rocks of Vega and Seymour islands may support this statement, which is also corroborated by our findings.

The south polar region and the Southern Hemisphere as a whole were less affected by the Chicxulub impact than the equatorial zones (Cracraft 2001), which may have contributed to their survival through the K-Pg Mass Extinction Event (Case 2001, Chatterjee 2002).

CONCLUSIONS

In the comprehensive global reevaluation of the Late Cretaceous record of Neornithes (crown birds) presented here, it has been ascertained that unequivocal neornithine taxa are notably rare with only a few confidently assigned to that group. In contrast to this scarcity, the sedimentary deposits of the James Ross Sub-Basin in the Antarctic Peninsula exhibit an abundance of neornithine fossilized remains. These findings assume a paramount significance in elucidating the early evolutionary trajectories of neornithines and their resilience during the K-Pg extinction event.

Two new specimens of vegaviids from the Maastrichtian of the Antarctic Peninsula are described in this contribution, a partial synsacrum assigned to *Vegavis* (MN 7832-V) and a tarsometatarsal fragment tentatively assigned to *Polarornis* (MN 7833-V). *Vegavis* is the most representative fossil bird found in the Maastrichtian López de Bertodano Formation. Four specimens are now recognized for this taxon, the holotype (MLP 93-I-3-1), referred materials remarkable by preserving the oldest syrinx known in the fossil record (MACN-PV 19.748), the larger isolated femur (SDSM 78247), and the partial synsacrum (MN 7832-V) here studied. Despite its incompleteness, this specimen records the oldest occurrence of the lumbosacral canals in fossil Neornithes, related to a balance sensing system acting in the control of walking and perching. The tarsometatarsus fragment MN 7833-V shares with *Vegavis* a roughly similar microstructure, but its incompleteness prevents us from confirming the assignment to this taxon. On the other hand, the general osteohistological pattern exhibited by MN 7833-V resembles more that of the vegaviid *Polarornis gregorii*. Furthermore, our findings agree with previous authors that higher latitudes had an avifauna dominated by ornithurines, and especially by neornithines in Antarctica, supporting the hypothesis that crown birds were better fitted to live in these environments than more ancient bird lineages presumably by having higher metabolic and growth rates.

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GEOVANE A. DE SOUZA[1]
https://orcid.org/0000-0003-0979-1526

BRUNO A. BULAK[2]
https://orcid.org/0009-0003-5994-943X

MARINA B. SOARES[2,3]
https://orcid.org/0000-0002-8393-2406

JULIANA M. SAYÃO[2,3]
https://orcid.org/0000-0002-3619-0323

LUIZ CARLOS WEINSCHÜTZ[4]
https://orcid.org/0000-0002-8978-6120

ALESSANDRO BATEZELLI[5]
https://orcid.org/0000-0001-5324-7638

ALEXANDER W.A. KELLNER[2,3]
https://orcid.org/0000-0001-7174-9447

[1]Programa de Pós-Graduação em Zoologia,
Universidade Federal do Rio de Janeiro, Museu
Nacional, Parque da Quinta da Boa Vista, s/n, São
Cristóvão, 20940-040 Rio de Janeiro, RJ, Brazil

[2]Universidade Federal do Rio de Janeiro, Museu
Nacional, Laboratório de Sistemática e Tafonomia de
Vertebrados Fósseis, Quinta da Boa Vista, s/n, São
Cristóvão, 20940-040 Rio de Janeiro, RJ, Brazil

[3]Universidade Federal do Rio de Janeiro, Museu
Nacional, Departamento de Geologia e Paleontologia,
Laboratório de Paleobiologia e Paleogeografia
Antártica, Parque da Quinta da Boa Vista, s/n, São
Cristóvão, 20940-040 Rio de Janeiro, RJ, Brazil

[4]Centro de Pesquisa Paleontológica da UNC
(CENPALEO), Universidade do Contestado, Av.
Nereu Ramos, 89300-000 Mafra, SC, Brazil

[5]Universidade Estadual de Campinas, Instituto
de Geociências, Departamento de Geologia e
Recursos Naturais, Rua João Pandiá Calógeras, 51,
Barão Geraldo, 13083-870 Campinas, SP, Brazil

Correspondence to: **Geovane Alves De Souza**
E-mail: geoosoouza@gmail.com

Author contributions

GAS, BAB, MBS, AB, LCW, JMS, and AWAK conceived and designed the study, GAS, LCW and AB performed fieldwork in the Antarctic Peninsula collecting several fossil vertebrates that are housed in the Museu Nacional/UFRJ, LCW and AB conducted the geological study, GAS, BAB, MBS, and JMS did the osteohistological analysis. All authors reviewed and contributed to the manuscript.