The fossil record of birds from the James Ross Basin, West Antarctica

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Abstract   The fossil record of birds from Antarctica is concentrated in the James Ross Basin, located in north-east of the Antarctic Peninsula. Birds are here represented by an extensive Paleogene record of penguins (Sphenisciformes) and Cretaceous–Paleogene record of Anseriformes, followed by other groups with a minor representation (Procellariiformes, Falconiformes, and Pelagornithidae), and others previously assigned controversially to "Ratites", Threskiornithidae, Charadriiformes, Gruiformes, Phoenicopteriformes, and Gaviiformes. We provide a complete update of these records, commenting on the importance of some of these remains for the evolution of the major clades.

1   Introduction

Fossil birds have a limited record compared to that of other vertebrates. The intrinsic nature of their bones, which are light and fragile, causes them to be easily destroyed during taphonomic processes. Therefore, in most cases, birds are known in the fossil record through disarticulated and highly fragmentary remains, which makes systematic assignments difficult.

However, some bird groups, due to the secondary loss of pneumaticity, have a richer fossil record. This is the case for diving birds. Other factors, more related to the

environment in which they live, or to their way of life, such as the colonial habit of many species, also may favor the preservation of their remains. The large accumulations of skeletal elements in the same place are a feature of penguin rookeries or surrounding sites. To date all bird remains from Antarctica, save for one undescribed fossil (Cordes, 2001, 2002) from Vega Island of uncertain phylogenetic position (Roberts et al., 2014), have been identified as part of the radiation of crown birds Neornithes.

Antarctica yields a comparatively rich fossil record of aquatic diving birds for key time intervals from the Cretaceous to early Paleogene and nearly all of this record is from the James Ross Basin. Penguins, Sphenisciformes, are the most abundant remains. As expected, groups such as Procellariiformes and Pelagornithidae with more fragile,

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lightly-built skeletal elements, are more poorly represented in this record overall (Cenizo et al., 2015; Acosta Hospitaleche and Gelfo, 2017).

Here, we first provide a brief summary of the fossiliferous units of the James Ross Basin, with particular emphasis on the areas and strata from which bird remains have been collected. More detail on these sites and units on Seymour and Vega Islands can be found in, for example, Marenssi et al. (1998), Olivero (2012), Montes et al. (2013), and Roberts et al. (2014). Subsequently, we detail the records of major clades of birds represented in this basin, commenting on the importance of these records for the evolution of each group.

2   Provenance

The James Ross Basin was defined by Elliot (1988) and comprises extensive outcrops of middle Mesozoic and lower Cenozoic sedimentary units. This basin is developed to the east of the Antarctic Peninsula, near its northern tip. Subsidence of this basin allowed for the deposition of more than 5 km of marine sedimentary rock through the Late Jurassic to the latest Eocene/?Oligocene (e.g., Crame et al., 1991; Pirrie et al., 1991; Riding et al., 1998; Marenssi et al., 2002).It contains one of the most complete Jurassic–Paleogene sedimentary successions in the Southern Hemisphere, as well as a Cretaceous/Paleogene (K-T) boundary section on Seymour Island (e.g., Crame et al., 1991; Whitham, 1993; Pirrie et al., 1997; Riding et al., 1998).

Basin fill crops out mainly in the north sector of the James Ross insular group which includes: James Ross, Vega, Snow Hill, Cockburn, and Seymour Islands, where rock ages vary from deposits of Jurassic (Kimmeridgian) age to latest Eocene (Marenssi et al., 2012). The upper Cretaceous–lower Paleogene strata of this basin comprise a thick sequence of marine sedimentary rocks divided into three lithostratigraphic groups: the basal Gustav Group (Aptian–Coniacian), the intermediate Marambio Group (Santonian–Danian), and the upper Seymour Island Group (Paleogene; Rinaldi, 1982; Marenssi et al., 2012).

The Marambio Group (Rinaldi, 1982) constitutes a thick succession of sandstones and pelites (Marenssi et al., 2012) with the following formations, from bottom to top, the Santa Marta, Rabot (lateral equivalent of the upper part of the Santa Marta), Snow Hill Island, Haslum Crag Sandstone (sensu Olivero et al., 2007), López de Bertodano, and Sobral (Marenssi et al., 2002; Olivero, 2012; Montes et al., 2013). The Paleogene Seymour Island Group overlies this group (Elliot and Trautman, 1982) and corresponds to the last unit filling the James Ross Basin. It encompasses the Cross Valley, La Meseta, and Submeseta formations (Montes et al., 2013) that were deposited within incised valleys on an emerging offshore platform (Marenssi et al., 2012).

The fossil record of birds in the James Ross Basin is restricted to Seymour and Vega Islands. Seymour Island is located in the north-eastern sector of the Antarctic Peninsula, in the Weddell Sea and approximately 100 km southeast of the northern tip of the peninsula (Figure 1). In this island, the units of the James Ross Basin represent an almost continuous sequence from the Maastrichtian to the Eocene/?earliest Oligocene (Marenssi et al., 2012). Post-Oligocene basaltic dykes and post-Miocene glacimarine deposits are also represented (Marenssi et al., 2012). The fossil record of birds from Seymour Island includes remains from the López de Bertodano, Cross Valley, La Meseta, and Submeseta formations of the Marambio and Seymour Island Groups.

Vega Island is a few kilometers to the south of the tip of the Antarctic Peninsula and has the second richest records of birds from Antarctica after Seymour Island. Sedimentary strata exposed on Cape Lamb are assigned to the Marambio Group (Rinaldi, 1982). Specifically, the Snow Hill Island and the López de Bertodano formations of this group (Pirrie et al., 1997) have produced articulated bird remains as well as isolated elements.

2.1   Snow Hill Island Formation

It comprises four units named as Hamilton Point Member, Sanctuary Cliffs Member, Karlsen Cliffs Member, Gamma Member (upper Campanian), and Cape Lamb Member (lower Maastrichtian). The Snow Hill Island Formation constitutes the basal unit of the transgressive part of the NG Sequence as defined by Olivero (2012), which is upper Campanian–lower Maastrichtian in age.

On Vega Island, the Cape Lamb Member is unconformably covered by transgressive mudstones of the mid to upper Maastrichtian López de Bertodano Formation (MG Sequence sensu Olivero, 2012). Some bird fossils without confident taxonomic assignment (Acosta Hospitaleche and Gelfo, 2015) were collected in strata assigned to the Cape Lamb Member (originally described as Member B and assigned to the López de Bertodano Formation in Pirrie et al., 1991).

2.2   López de Bertodano Formation

This unit of 1150 m thickness of siliciclastic sediments (sandy shales and sandstones) with less abundant carbonate horizons constitutes the uppermost part of the Marambio Group (Macellari, 1988). This formation was deposited between the lower Maastrichtian and the lower Danian (Macellari, 1986, 1988; Olivero and Medina, 2000; Crame et al., 2004; Olivero, 2012).

The identified stratigraphic levels are different in Seymour and Vega islands. In the first one, two informal divisions named as "*Rotularia* units 1–6" and "Molluscan units 7–10" were recognized after their characteristic macrofossils. A shallow marine environment near to an estuary was inferred for the lower '*Rotularia* units', whereas
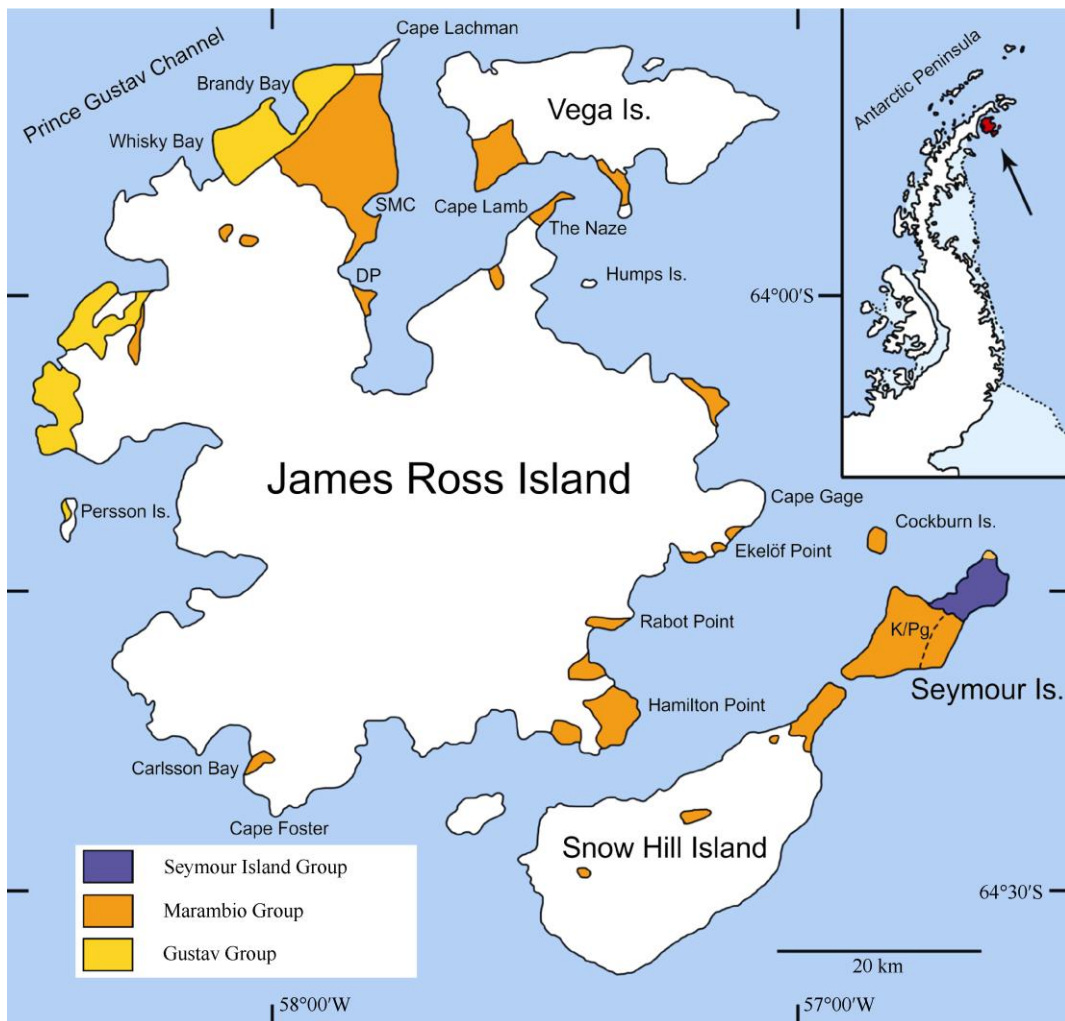
Figure 1 Location map of the James Ross Basin islands.

middle to outer shelf settings was proposed for the upper 'Molluscan units' (Macellari, 1988; Olivero et al., 2008). After that, Unit 1 of the 'Rotularia units' was reassigned to the underlying Snow Hill Island Formation (Crame et al., 2004; Olivero, 2012). The K/Pg boundary was located close to the base of Unit 10 (Macellari, 1988; Elliot et al., 1994; Zinsmeister, 1998; Witts et al., 2016), indicated by the presence of a laterally continues 40 cm thick glauconitic horizon, beneath which the last records of *Rotularia* and ammonites appear (Macellari, 1988). The most productive levels for fossils are the 'molluscan units', particularly Units 8 and 9, that carry the fossil birds (Chatterjee, 2002; Chatterjee et al., 2006; Clarke et al., 2016). However, a partial skeleton was recently recovered from the Paleocene portion of the upper-most Lopez de Bertodano Formation (Unit 10; Tambussi et al., 2019)

On Vega Island, the Member C described by Pirrie et al. (1991) was assigned to the López de Bertodano Formation, and renamed as Sandwich Bluff Member, belonging to the same unit (Crame et al., 1999). From these levels (SBM 1; Roberts et al., 2014), partial skeletons (Noriega and

Tambussi, 1995; Clarke et al., 2005; Clarke et al., 2016) as well as isolated remains (SBM ~11–12; Roberts et al., 2014) were recovered (e.g., Case and Tambussi, 1999).

2.3 Cross Valley Formation

It is a lenticular body of 195 m thick that fills in a narrow valley with volcaniclastic deposits representing the incised valley system, including estuarine, shallow marine and deltaic facies (Marenssi et al., 2012). The main outcrop is located in the central sector of the Seymour Island, but an accessory outcrop exposes in the northeastern area of the island, between Gorrochategui Cape and Larsen Cove. A strong erosive unconformity marks the base of the Cross Valley Formation where it contacts the Sobral Formation and likely where it also the López de Bertodano Formation (Santillana and Marenssi, 1997).

The micropaleontological data allow the estimation of a Paleocene age for this formation (Palamarczuk et al., 1984). Dinoflagellates date the lower part of the sequence to the Selandian (Wrenn and Hart, 1988; Santillana et al., 2007), and the top to the upper Thanetian (Askin, 1988).

Isotopic chemostratigraphic data supports these ages (Dingle and Lavelle, 1998; Santillana, 2007).

Three allomembers were recognized in this unit, which are named Cross Valley A, B, and C, with C the top-most unit (Marenssi et al., 1999, 2012; Montes et al., 2007, 2013). A partial skeleton comprising the oldest penguin from Antarctica was collected from this last subunit C (Tambussi et al., 2005).

2.4   La Meseta and Submeseta formations

These two units are treated together because they are closely related regarding their definitions, and share also a common history. The La Meseta Formation was the term employed by Rinaldi et al. (1978) to designate the Tertiary marine sedimentary rocks cropping out on the northeastern part of the Seymour Island. This unit had been originally described by Trautman (1976) and designated as Marambio Formation, name that quickly fell into disuse and was replaced by La Meseta Formation, looking to avoid misunderstandings with the Marambio Group (Elliot and Trautman, 1982).

The first studies on this formation differentiate three informal members, which were designated from base to top as I, II, and III. However, a posterior detailed study allowed to distinguish seven levels named Tertiary Eocene La Meseta (TELM) and re-numbered as TELM 1–7 (Sadler, 1988).

A different approach was made by Marenssi and Santillana (1994), in which the scheme was conceptually modified, proposing subdivisions based on unconformity-bounded (allostratigraphic) units. These units were named as Valle de Las focas, Acantilados (Acantilados I and II sensu Montes et al., 2013), Campamento, Cuccullaea I, Cuccullaea II, and Submeseta Allomembers (Marenssi et al., 1998). A complete detail of the correlations between the units proposed by different authors during the last years can be consulted in Marenssi et al. (1998), where the La Meseta Alloformation is also defined as a 720 m thick clastic unit whose extension is equivalent with that one of the La Meseta Formation.

The purpose of that new proposal was to emphasize the importance of the discontinuities of the base, the top, and within this unit, for an adequate interpretation of the depositional system. The basal unconformity has a diachronous surface, whereas the uppermost unconformity has an irregular erosion surface, with overlying glaciomarine deposits filling shallow channels (Marenssi et al., 1998).

Finally, some years later, the magnitude of these discontinuities allowed to Montes et al. (2013) to consider the Submeseta Allomember (the uppermost part of the La Meseta Formation sensu Marenssi et al., 1998) as the Submeseta Alloformation. It comprises three allomembers, named from the base as Submeseta I, Submeseta II, and Submeseta III (Montes et al., 2013).

3   Fossil avifauna from the James Ross Basin

3.1   Anseriformes

The first preliminary report of an anseriform bird from late Cretaceous deposits James Ross Basin was by Noriega and Tambussi (1995). These authors published photographs of a humerus from a new partial postcranial skeleton from Sandwich Bluff on Vega Island and noted similarities with Presbyornithidae. At the time the phylogenetic position of Presbyornithidae, known from the early Paleogene of North America, South America and Europe, remained debated. Several authors noted its filter-feeding, duck-like rostrum and "shorebird-like" postcranium suggested a mosaic charadriiform/anseriform identity, indicating it could be a "missing link" between these two major avian subclades (Olson and Feduccia, 1980). However subsequent analyses placed *Presbyornis* firmly in Anseriformes (e.g., Livezey, 1997), and this clade and Charadriiformes (shorebirds) were increasingly recovered in disparate parts of the avian tree, with Charadriiformes well nested within Neoaves (Hackett et al., 2008; Jarvis et al., 2014).

Clarke et al. (2005) used X-ray computed tomography (CT) of the specimen (preserved in a grapefruit-sized concretion) and peels taken of the specimen prior to preparation to recognize a nested set of characters from different parts of the skeleton that located it within Neognathae. The specimen was important because, at the time, only single bones with few preserved characters had been tentatively identified as part of the radiation of all living birds from the Cretaceous. The specimen (MLP 93-I-3-1; Figure 2) was named as the holotype of a new species, *Vegavis iaai*. The character support for its placement within Anatoidea (Anseranatidae [magpie geese] + Anatidae [true ducks and geese]) (Clarke et al., 2005) was reviewed by Ksepka and Clarke (2015).

A second partial skeleton in a nodule (MACN PV 19748) was collected by the same Argentine expedition in 1992 from the same stratigraphic unit on Sandwich Bluff. Meticulously prepared, it was described by Clarke et al. (2016) and referred to the same species, *Vegavis iaai*. This specimen is remarkable in preserving the first known remains of part of the vocal organs of birds (the syrinx) from the Mesozoic. These delicate mineralized cartilage rings have no earlier known fossil record. The syrinx of *Vegavis* shows a left/right asymmetry in these preserved rings that is also seen in some Anatidae but not known in *Presbyornis*, other galloanserines including magpie geese and screamers (Anhimidae), or in Neoaves (Clarke et al., 2016; Figure 2e). These data are consistent with the original phylogenetic placement of *Vegavis* (Clarke et al., 2005).
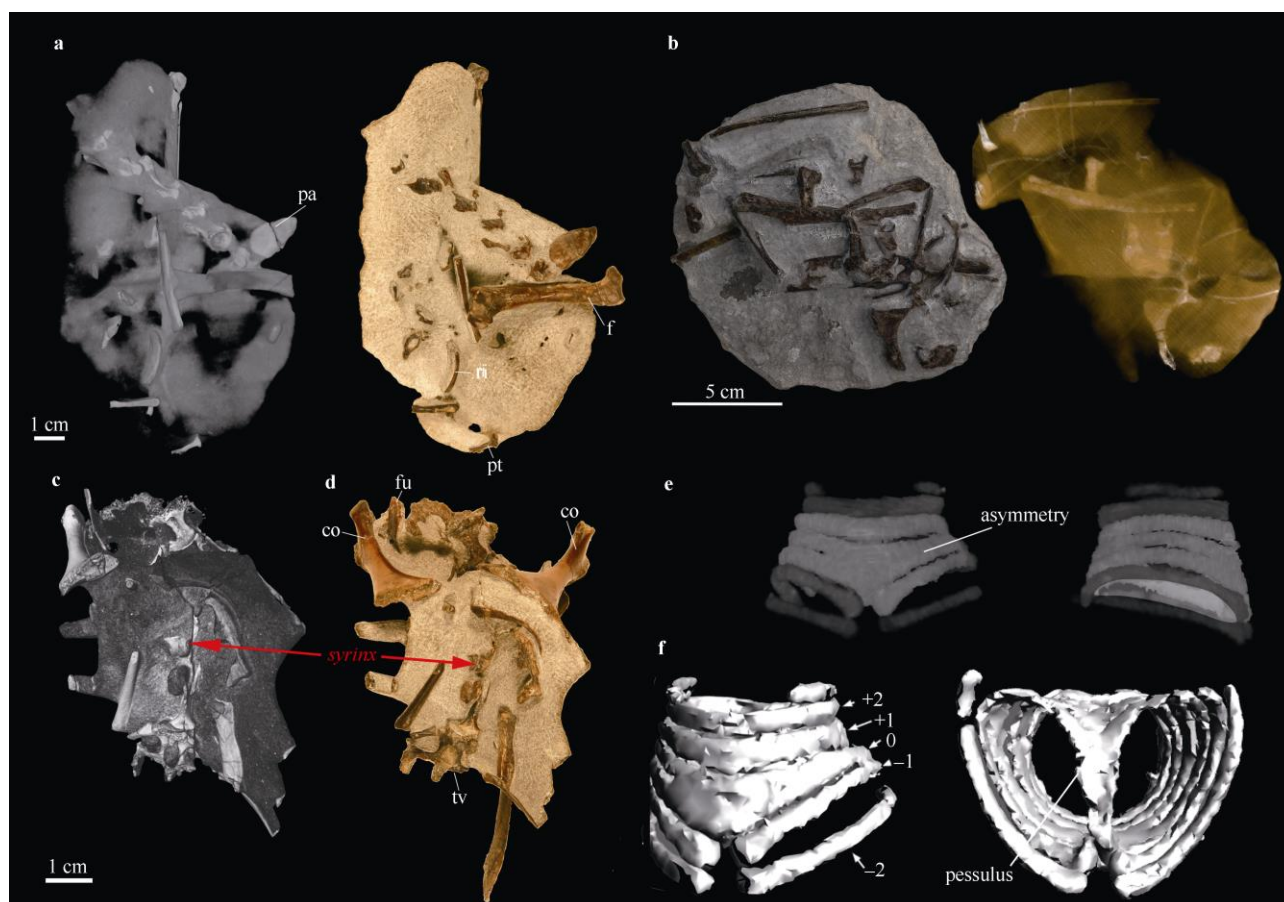
Figure 2 Holotype and referred specimen of anseriform *Vegavis iaai*. **a**, **c–f**, Photograph and rendering from X-ray computed tomography (CT) images of two blocks of the referred specimen MACN-PV 19.748, showing the location of the syrinx and its morphology; **b**, Photograph and CT images of main block of the holotype specimen, MLP 93-I-3-1. Anatomical abbreviations: co, coracoid; f, femur; fu, furcular; pa, patella; pt, pterygoid; ri, rib; tv, thoracic vertebrae. Numbering of syrinx rings referred to reference system of Clarke et al. (2016) with the inferred location of the lateral tympaniform membrane between ring-1 and ring-2.

Subsequent to these discoveries, there has been debate over the possible affinities of *Vegavis* with a second Late Cretaceous Antarctic taxon, *Polarornis gregorii* (Chatterjee, 1989, 2002), from Seymour Island and with other more fragmentary high latitude taxa from Chile and New Zealand (Agnolin et al., 2017; Mayr et al., 2018a). These two taxa are similar in that they represent hind limb propelled divers; although, *Polarornis* is approximately twice the size of *Vegavis* and lacks several proposed diagnostic features of that taxon (Clarke et al., 2016; see also Gaviidae below). The clade, Vegaviidae was proposed for all of these taxa (Agnolin et al., 2017). However, the New Zealand *Australornis* and the Chilean *Neogaeornis* are markedly different in the humerus, coracoid, and hypotarsus, respectively, from *Vegavis* (Mayr and Scofield, 2014; Clarke et al., 2016; Mayr et al., 2018a). The observed differences would be consistent with referral of these taxa to different major crown bird subclades. Mayr et al. (2015) and Clarke et al. (2016) both found evidence for the affinities of *Australornis* with stem penguins, for example. Unfortunately, the coracoid and hypotarsus of *Polarornis*

remain unknown. Several of these studies have proposed that *Vegavis*, and possibly the similar- but larger-bodied-*Polarornis*, may not be a crown anseriform (Agnolin et al., 2017; Mayr et al., 2018a). However, they do not agree on a location for these taxa within any other clade either in Galloanseres or Neoaves, or on their placement relative to Anseriformes.

Recently, another exceptional partial skeleton has been recovered with a syrinx and referred to Anseriformes (Tambussi et al., 2019) from the early Paleocene of Seymour Island. This specimen, the holotype of a new species *Conflicto antarcticus*, was also identified as part of at least stem Anseriformes (Tambussi et al., 2019) using a recent phylogenetic dataset. It shows several similarities with *Vegavis* not seen in most other Anseriformes. Clearly these new remains will be key to further phylogenetic analyses of Galloanseres. Although Eocene footprints from King George Island (South Shetland Islands) have been tentatively identified as anseriform (Mansilla et al., 2012), no remains from the Eocene of the James Ross Basin, including the late Eocene fossiliferous deposits on Seymour

Island, have so far been referred to the clade.

3.2 "Ratites"

Defined by their plesiomorphic palatal morphology, the palaeognathous birds comprise the flightless "ratites" and the volant, Neotropical tinamous (Tinamiformes), and are the sister taxon to the neognaths, all other living birds. The "ratites" are composed largely of giant terrestrial herbivores and include the African ostriches (Struthioniformes), the South American rheas (Rheiformes), the New Zealand kiwis (Apterygiformes), and the Australasian cassowaries and emus (Casuariiformes), as well as the recently extinct Madagascan elephant birds (Aepyornithiformes) and the New Zealand moa (Dinornithiformes). The origin of Palaeognathae and their interrelationships have been long controversial. Morphology-based phylogenetic analyses supported a sister group relationship between tinamous and "ratites" (e.g., Livezey and Zusi, 2007; Bourdon et al., 2009; Worthy and Scofield, 2012), but recent molecular analyses found that "ratites" are paraphyletic with respect to tinamous (e.g., Smith et al., 2013; Grealy et al., 2017). Results of ancient DNA analysis show that moa are the sister taxon of tinamous (Phillips et al., 2010; Haddrath and Baker, 2012; Baker et al., 2014) and elephant birds are the closest relatives of kiwis (Mitchell et al., 2014; Grealy et al., 2017).

The Antarctic record of alleged "ratites" is limited to only two extremely fragmentary remains, both of which come from levels of the Submeseta Formation (middle Eocene/early Oligocene). The first is a fragmentary cranial element, a rostrum or beak tip (*corpus ossis premaxillaris*; UCR 22175, Figures 3a–3c) recovered from the RV-8405 locality (TELM 6–7; see Case et al., 1987). Without clear justification, this specimen was considered for many years as the first "terror bird" (i.e., Phorusrhacidae) known from Antarctica (e.g., Case et al., 1987; Chavez, 2007; Tambussi and Acosta Hospitaleche, 2007; Alvarenga et al., 2011), but more recently an affinity with Palaeognathae has been indicated (Cenizo, 2012).

The second specimen consists of the highly eroded distal end of a tarsometatarsus (MLP 94-III-15-1, Figures 3d–3f) found at locality Zone Plate Array Lithography 4 (ZPAL 4) (TELM 7; see Tambussi et al., 1994). The material was identified as belonging to a "giant flightless ground-dwelling ratite" (Tambussi et al., 1994: 17). However, the absence of comparative descriptions renders its affinities with extant or extinct lineages unknown.

Other remains initially assigned to supposed large

Figure 3 Putative "ratite" birds from the middle Eocene–early Oligocene of Seymour Island. **a–c**, UCR 22175 (cast of fragmentary corpus ossis premaxillaris), "Ratitae" indet. in **a**, lateral; **b**, dorsal; and **c**, ventral views; **d–f**, MLP 94-III-15-1 (fragmentary distal end of right tarsometatarsus), "Ratitae" indet. in **d**, dorsal; **e**, plantar; and **f**, distal views. Scale bar is 10 mm.

cursorial birds (Case et al., 2006), also found in the Eocene Submeseta Formation of Seymour Island and the Cretaceous López de Bertodano Formation (lower Maastrichtian) of Vega Island, have been re-identified as belonging to large penguins and pelagornithids, and an indeterminate foot-propelled diving bird, respectively

(Cenizo, 2012; Cenizo et al., 2015). Outside of the James Ross Basin, large tridactyl footprints allocated to a large ground-dwelling bird were reported from early-middle Eocene outcrops of the Fossil Hill Formation (Covacevich and Rich, 1982) of the Fildes Peninsula of King George Island (South Shetland Islands). These ichnites are smaller than the prints produced by adult emus, although they could correspond to juvenile "ratites" or perhaps a different avian taxon. This trace fossil evidence does not provide conclusive data regarding the taxonomic identity of the track producers.

Despite the poor records available, it is probable that large flightless birds inhabited in West Antarctica during the middle-late Eocene. The fragmentary beak (UCR 22175) preserves the presence of conspicuous, dorsolaterally-placed nasolabial grooves that converge with the *apertura nasi ossea*, which was noted as a synapomorphy of palaeognathous birds, including many extant and extinct flightless species (Cenizo, 2012). However, the postulated "ratite" affinities of the eroded distal fragment of tarsometatarsus (MLP 94-III-15-1) should be tested in a broad phylogenetic context. The size and morphology of trochlea metatarsi II differs from that observed in all "ratites" (see also Mayr, 2009). Taking as reference homologous elements in known "ratites", the proportions preserved in both specimens seem to support their referral to different taxa. While the size of UCR 22175 is larger than that observed in the homologous section of the largest moa, MLP 94-III-15-1 is more similar in size to the tarsometatarsus of an ostrich-sized bird.

The novel topologies for the Palaeognathae tree resulting from recent molecular analyses imply that flightlessness and large body size have evolved repeatedly in different lineages of "ratites", and that the current geographic distribution of these birds has been the product of overseas dispersal by a volant ancestor (e.g., Yonezawa et al., 2017). As an evolutionary model for this bird group, classic vicariant speciation driven by the successive breakup of the supercontinent Gondwana (e.g., Cracraft, 1973; Haddrath and Baker, 2001) is in serious conflict (Harshman et al., 2008; Maderspacher, 2017). In this context, future discoveries of more complete specimens may provide decisive evidence regarding the time and lineages involved in these early dispersal events, as well as in the evolution of flightlessness and gigantism in palaeognathous birds in the southern landmasses during the Paleogene.

3.3 Falconiformes

Traditionally, the order Falconiformes grouped the falconid raptors (Falconidae) with the remaining diurnal birds of prey (Cathartidae, Sagittariidae, Pandionidae, and Accipitridae). However, recent molecular phylogenies (e.g., Ericson et al., 2006; Hackett et al., 2008; McCormack et al., 2013; Yuri et al., 2013) agreed with previous morphological studies (Jollie, 1977) in that traditional Falconiformes is paraphyletic and that the similarities between diurnal birds of prey are due mainly to convergence.

At present, the order Falconiformes includes only Falconidae. This avian family constitutes a group of small to medium-sized diurnal raptors whose monophyly is strongly supported, including three extant clades (e.g., Griffiths et al., 2004; Fuchs et al., 2015): Herpetotherinae (forest falcons and the laughing falcon; i.e., *Micrastur* and *Herpetotheres*), Polyborinae (caracaras and the spot-winged falconet; i.e., *Caracara*, *Phalcoboenus*, *Ibycter*, *Daptrius*, *Milvago*, and *Spiziapteryx*), and Falconinae (falconets and true falcons; i.e., *Microhierax*, *Polihierax*, and *Falco*). The fact that falconid diversity is mainly concentrated in the Neotropics (Olson, 1976; Fuchs et al., 2015) has led many authors to consider that most of their evolutionary history occurred in South America (Olson, 1976; Ericson, 2012). Moreover, sequence-based analyses support an unexpected new clade, the Australaves (Ericson, 2012; Jarvis et al., 2014; Prum et al., 2015), which includes falconid raptors together with seriemas (Cariamiformes), parrots (Psittaciformes), and passerine birds (Passeriformes). From a biogeographical perspective, it is relevant to note that Australaves is composed by birds mainly distributed in the Southern Hemisphere continents.

The only clearly referable neoavian "land-bird" from Antarctica and the only Paleogene falconid-like taxon known in the entire Southern Hemisphere is *Antarctoboenus carlinii* (Cenizo et al., 2016), based on a distal end of tarsometatarsus (MLP 95-I-10-8, Figures 4a–4b) found in the *Cucullaea* I Allomember of the La Meseta Formation at the IAA 2/95 locality (early Eocene). This specimen was originally related to crown-group Falconidae and its allocation into Polyborinae (Tambussi et al., 1995) was uncritically accepted for more than two decades (e.g., Tambussi and Acosta Hospitaleche, 2007; Reguero et al., 2013a; Tambussi and Degrange, 2013). Certainly, the morphology of *A. carlinii* is more similar to that of caracaras than to any other falconid (see Figure 4); however, derived characters of crown-group Falconidae are absent in the Antarctic taxon. The postulated similarities between *A. carlinii* and Polyborinae are based on plesiomorphic characters retained in the tarsometatarsus of the latter clade (Cenizo et al., 2016). This is consistent with the previous assumption that the tarsometatarsal morphology of Polyborinae is close to the ancestral condition for Falconidae (Olson, 1976; Jollie, 1977; Becker, 1987) and a later (late Paleogene) estimated divergence for crown Falconidae (Fuchs et al., 2015). Recent field work has led to the recovery of a probable new specimen of *Antarctoboenus* represented by a fragmentary tarsometatarsus (MLP 15-I-10-2, Figures 4c–4d) found at same type level in the IAA 3/95 locality. Although this specimen lacks the distal end, the observed characters seem to confirm the status of *A. carlinii* as a member of stem-group Falconidae. In this sense, the discovery of a basal falconiform raptor in the early Eocene of Antarctica reinforces the hypothesis of a South American (or Antarctic) origin of Falconidae supported by molecular phylogenies.

Figure 4 Comparative tarsometatarsal morphology of the basal falconiform bird *Antarctoboenus carlinii* from the early Eocene of Seymour Island and the extant falconid Polyborinae *Caracara plancus*. **a–b**, MLP 95-I-10-8 (distal end of left tarsometatarsus), holotype of *Antarctoboenus carlinii* in **a**, dorsal; and **b**, plantar views; **c–d**, MLP 15-I-10-2 (fragmentary left tarsometatarsus), new specimen possibly referable to *Antarctoboenus* in **c**, dorsal; and **d**, plantar views; **e–f**, MMC 265 (complete left tarsometatarsus); *Caracara plancus* in **e**, dorsal; and **f**, plantar views. Scale bar is 10 mm.

3.4 Pelagornithidae

The pseudo-toothed birds or pelagornithids (Pelagornithidae) are a peculiar group of large volant seabirds characterized by osseous tooth-like processes of the beak and highly specialized bones adapted for pelagic soaring (Olson, 1985). They were cosmopolitan birds with a wide Cenozoic timespan between the late Paleocene and the latest Pliocene (e.g., Olson, 1985; Mourer-Chauviré and Geraards, 2008; Mayr, 2009, 2011; Bourdon et al., 2010). Phylogenetic analyses suggest a sister group relationship of pseudo-toothed birds and Anseriformes (Bourdon, 2010, 2005), or a more basal position outside crown-group Galloanseres (Mayr, 2011).

Within Pelagornithidae, two evolutionary types (presumable clades, Bourdon et al., 2010; Mayr et al., 2013; Mayr, 2016) with different body size ranges (based on estimated wingspan ranges, see Cenizo et al., 2015) can be relatively well distinguished. On one hand are the early and basal *Dasornis* species, that have small to large body sizes (1.5–1.7 to 3.5–4.5 m wingspan ranges) and are restricted to the late Paleocene/early Eocene of Morocco and England (e.g., Harrison and Walker, 1976; Mayr, 2008; Bourdon et al., 2010). The second type corresponds to the younger, more derived, and gigantic (5–6 m wingspan ranges) *Pelagornis*-like species (Mayr et al., 2013) with an apparent cosmopolitan distribution during the late Oligocene to late Pliocene (Olson, 1985; Mourer-Chauviré and Geraads, 2008; Mayr et al., 2013; Ksepka, 2014). Notably, the middle Eocene to early Oligocene record (including the timespan between the latest occurrences of *Dasornis* and the first occurrences of *Pelagornis*-like birds) shows a series of taxa whose systematic allocation is very poorly resolved but that exhibit a morphology "intermediate" between the *Dasornis* and *Pelagornis* types, with medium to giant body sizes (2–3 to 5–6 m wingspan ranges).

A recent revision of the affinities of Antarctic pelagornithids (Cenizo et al., 2015) concluded that all remains correspond to the above mentioned "intermediate" grade. They share presumable plesiomorphic characters with late Paleocene/early Eocene *Dasornis* but resemble the derived condition of the Neogene *Pelagornis*-related taxa in other features.

Regarding their inferred body size, the Antarctic pseudo-toothed birds can be segregated into two well-defined morphotypes with different stratigraphic provenance (Cenizo et al., 2015). The specimens allocated to "morphotype 1" (*sensu*, Cenizo et al., 2015) are large-sized (3.5–4.5 m wingspan ranges) and come from the *Cucullaea* I Allomember (level 35) of the La Meseta Formation (early Eocene). To date, only one specimen from the La Meseta

Formation had been referred to this morphotype, represented by a distal humerus (MLP 12-I-20-4, Figures 5a–5c) recovered at locality IAA 1/95. Here we add a rostral-most fragment of dentary (IAA-PV 175, Figures 5d–5f) recently found at locality IAA 1/90. From East Antarctica, outside the James Ross Basin, a portion of humeral shaft found in early-middle Eocene deposits of Mount Discovery in McMurdo Sound (Jones, 2000) was also allocated to this morphotype (Cenizo et al., 2015).

All pelagornithid specimens included in "morphotype 2" (*sensu*, Cenizo et al., 2015) are giant birds (5–6 m estimated wingspan) and come from the Submeseta II Allomember (level 38) of the Submeseta Formation (middle Eocene). They are represented by the distal end of a tarsometatarsus (UCR 22176, Figures 5g–5i) from locality RV 8702 (Case et al., 2006; Cenizo, 2012), two rostral fragments (MLP 08-XI-30-42, Figures 5j–5k; MLP 78-X-26-1, Figures 5l–5n) recovered from locality DPV 13/84 (Tonni, 1980), and an almost complete unpublished humerus (SGO.PV 22001; Rubilar-Rogers et al., 2011) currently under study by Chilean researchers. Remarkably, the preserved bone proportions indicate that these remains belong to birds larger than most of the huge Neogene *Pelagornis*-like taxa, probably constituting one of the largest pelagornithids known so far (comparable in size only to the North American late Oligocene *Pelagornis sandersi*).

Figure 5 Pelagornithid birds from the early-middle Eocene of Seymour Island. **a–c**, MLP 12-I-20-4 (distal end of right humerus), Pelagornithidae indet. morphotype 1 in **a**, cranial; **b**, caudal; and **c**, dorsal views. **d–f**, IAA-PV 175 (rostral fragment of left dentary), new specimen possibly referable to Pelagornithidae indet. morphotype 1 in **d**, medial; **e**, lateral; and **f**, dorsal views. **g–i**, UCR 22176 (cast of distal end of right tarsometatarsus) Pelagornithidae indet. morphotype 2 in **g**, dorsal; **h**, plantar; and **i**, distal views. **j–k**, MLP 08-XI-30-42 (rostral end of rostrum maxillare), Pelagornithidae indet. morphotype 2 in **j**, lateral; and **k**, dorsal views. **l–n**, MLP 78-X-26-1 (most rostral narial region of rostrum maxillare), Pelagornithidae indet. morphotype 2 in **l**, lateral; **m**, ventral; and **n**, cranial views. Scale bar is 20 mm.

Two additional specimens found in the Submeseta Formation and originally described as those of pelagornithid birds (Tonni and Tambussi, 1985), an articular portion of mandible (MLP 83-V-30-1) and a fragmentary dentary with two conical teeth (MLP 83-V-30-2), are now considered as belonging to giant penguins (*Palaeeudyptes* or *Anthropornis* spp.) and the cod-icefish *Mesetaichthys jerzmanskae*, respectively (Cenizo et al., 2015).

Antarctic pelagornithids provide valuable information about several topics related to the early evolution of this avian group that dominated global marine ecosystems for more than 50 Ma. Both recognized morphotypes are advanced than the late Paleocene/early Eocene *Dasornis*. Moreover, the middle Ypresian "morphotype 1" constitutes the oldest non-*Dasornis* pelagornithid and therefore presumably, represents the earliest member of the radiation that led to the first appearance of giant forms in the middle Eocene (represented in Antarctica by the specimens included in "morphotype 2") and that later would reach its maximum specialization with the evolution of *Pelagornis*-like species during late Oligocene–Neogene times. Paleoecological topics concerning the marine avian communities of Antarctica are still pending revision, including the recognition of the bioclimatic factors that determined the apparently synchronous diversification of giant forms of penguins and pseudo-toothed birds.

3.5 Sphenisciformes

Penguins (Aves, Sphenisciformes) are highly specialized flightless diving seabirds of undisputed monophyly. Their present-day representatives have been grouped into 16–19 species in six genera constituting a single family, Spheniscidae, a taxon that is confined to the Southern Hemisphere (e.g., Jadwiszczak, 2009; Ksepka and Clarke, 2010; and sources cited therein). Clarke et al. (2003) restricted this family name to crown-group Sphenisciformes. Penguins descended from flying ancestors, and their closest living relatives are Procellariiformes (e.g., Hackett et al., 2008; Jarvis et al., 2014). These two orders are sometimes grouped as a single superorder Procellariimorphae (e.g., Jarvis et al., 2014).

Sphenisciformes have an ancient history whose known fossil record extends to the Paleocene, and its earliest portion comes from New Zealand and Seymour Island, James Ross Basin, Antarctic Peninsula (Tambussi et al., 2005; Slack et al., 2006; Ksepka and Clarke, 2010; Jadwiszczak et al., 2013; Mayr et al., 2017a, 2017b, 2018b). However, the most extensive collections of early penguin bones, representing a vast array of taxa, were gathered during exploration of Eocene strata, especially those exposed within Seymour Island (Figure 6; Wiman, 1905;
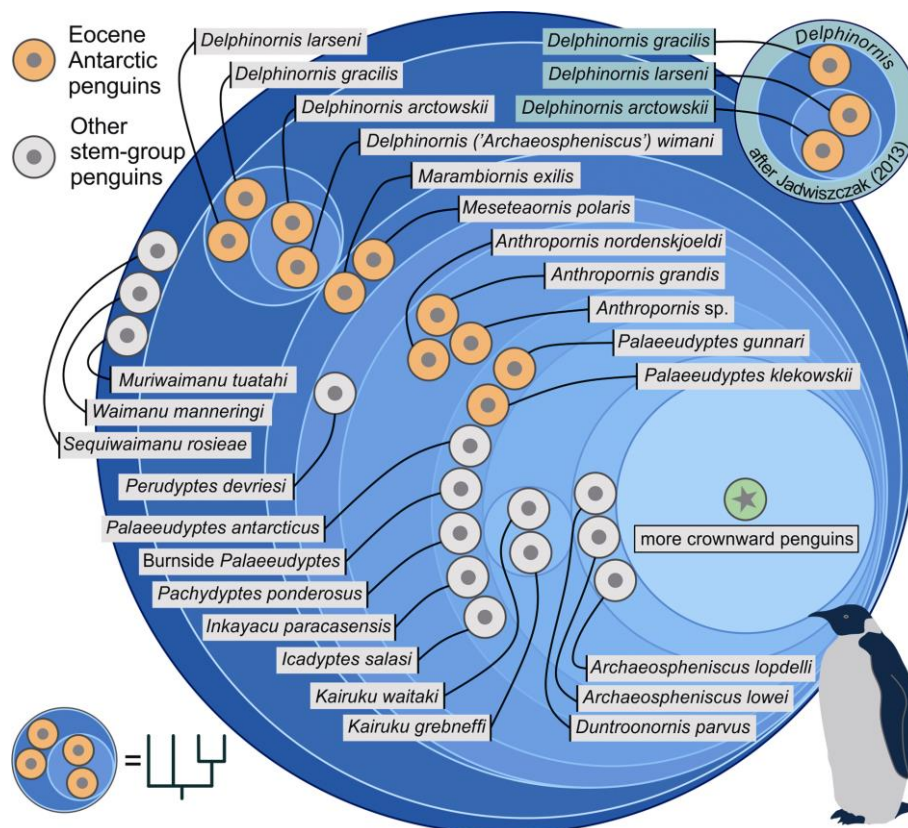
Figure 6 Circular treemap showing a simplified phylogeny of stem penguins based on topology of the strict consensus tree by Mayr et al. (2018b). Each node of the tree is visualized as a circle with its respective subnodes represented as inner circles.

Marples, 1953; Simpson, 1971; Myrcha et al., 2002; Tambussi et al., 2006; Jadwiszczak, 2006a, 2009). The largest sets of said remains are housed at the Museo de La Plata (Argentina), the University of Bialystok (Poland), the Naturhistoriska riksmuseet (Sweden) and the Natural History Museum (United Kingdom), with smaller collections at the American Museum of Natural History, the Museo Nacional de Historia Natural (Chile), and the University of Texas. The purpose of this contribution is to give a concise review of early (stem) Antarctic penguins.

The oldest bones assignable to Antarctic penguins come from the upper Cross Valley Formation (upper Paleocene). They were collected within the easternmost exposure of the Cross Valley C (CV C) Allomember, close to its base, in 2000. The discovery comprises four anatomically identifiable elements, all poorly preserved,

including a humerus (Figure 7c), femur (Figure 7a), tibiotarsus, and thoracic vertebra, as well as 28 other fragments (MLP 00-I-10-1; Tambussi et al., 2005; Jadwiszczak et al., 2013). These remains, which belong to a single, large-bodied individual, were designated as the holotype of *Crossvallia unienwillia* (Tambussi et al., 2005).

Recently, another fossil penguin bone, an isolated limb bone shaft (MLP 00-I-1-16; Figure 7b), from the CV C Allomember has been reported (Acosta Hospitaleche et al., 2016). According to Acosta Hospitaleche et al. (2016), the specimen is large and badly preserved, and its taxonomic identification other than Spheniscidae indet. is not possible. The sedimentary environment of the allomember is interpreted as low energy, very shallow marine, possibly deltaic (Elliot and Trautman, 1982; Tambussi et al., 2005; Marenssi et al., 2012; Acosta Hospitaleche et al., 2016; and sources cited therein).

Figure 7 Non-tarsometatarsal holotypes and other key specimens attributable to Paleocene **a–c** and Eocene **d–h** Antarctic penguins from Seymour Island, Antarctic Peninsula, supplemented with comparative material from the Natural History Museum at Tring, UK, abbreviated NHM(T)UK (**i**, **j**); **a**, and **c**, MLP 00-I-10-1, femur (cranial and caudal view) and humerus (dorsal and ventral view)–the best-preserved elements of the holotype partial skeleton of *Crossvallia unienwillia*; **b**, MLP 00-I-1-16, isolated (supposedly) femoral shaft (two aspects) of an unknown Paleocene penguin; **d**, NRM-PZ A.23 (synsacrum), a type specimen of *Orthopteryx gigas* (ventral view); **e**, MLP 93-I-6-3 (humerus), a type specimen of *Tonniornis minimum* (dorsal and ventral view); **f**, NHMUK A3367 (humerus), a type specimen of *Wimanornis seymourensis* (dorsal and ventral view); **g**, MLP 00-I-1-19 (humerus), a type specimen of *Aprosdokitos mikrotero* (dorsal and ventral view); **h**, MLP 93-X-1-145 (humerus), a type specimen of *Tonniornis mesetaensis* (dorsal and ventral view); **i**, NHM(T)UK 1905.12.30.419, humerus of the largest present-day penguin *Aptenodytes forsteri* (dorsal view); **j**, NHM(T)UK s/2002.2.1, humerus of the smallest present-day penguin *Eudyptula minor*. Some specimens were mirrored to facilitate comparisons. Scale bar is 50 mm.

Contrary to the scarce Paleocene record of Antarctic Sphenisciformes, their fossil bones recovered from Eocene strata are immensely numerous. Since the onset of the 20th century, thousands of specimens have been collected, predominantly represented by isolated bones (Wiman, 1905; Marples, 1953; Simpson, 1971; Myrcha et al., 2002; Tambussi et al., 2006; Jadwiszczak, 2006a, 2009; Acosta Hospitaleche et al., 2013). They are distributed unevenly through the Eocene (or Eocene–?earliest Oligocene, e.g., Montes et al., 2013) La Meseta Formation, but with the most abundant fossils (representing all known species) being within its upper part (Myrcha et al., 2002; Tambussi et al., 2006; Jadwiszczak, 2006a, 2006b, 2010; Acosta Hospitaleche et al., 2013). This geologically youngest section, roughly corresponding to units TELM 6–7 of Sadler (1988) or the Submeseta Allomember of Marenssi et al. (1998), was separated by Montes et al. (2013) as the Submeseta Formation. Its lowermost part is regarded as either middle Eocene (e.g., Montes et al., 2013) or late Eocene (e.g., Buono et al., 2016) in age. Detailed considerations on the age of subunits that make up both formations are beyond the scope of this paper. The depositional environment of the La Meseta Formation (*sensu* Sadler, 1988) has been interpreted as deltaic, estuarine and shallow marine (Porębski, 1995, 2000; Marenssi et al., 1998).

The earliest Eocene Antarctic penguin fossils were collected within the lowest levels of the La Meseta Formation (TELM 1/Valle de las Focas Allomember) in 1994. The oldest bones claimed to be *in situ* come from TELM 2s/Acantilados Allomember and were found, in the same year, close to the Polish locality ZPAL 8 (Jadwiszczak, 2006b).

Eocene strata on Seymour Island yielded a fair number of type specimens of fossil penguin species. However, not all of these taxa have stood the test of time (e.g., Jadwiszczak, 2009). The vast majority of holotypes are tarsometatarsi (Figure 8), hind limb bones formed as a result of fusion of the metatarsals and the distal row of tarsals (Baumel and Witmer, 1993). The first five tarsometatarsus-based species were erected by Wiman (1905) after analyzing the fossil material recovered from locality no. 11 of the Swedish South Polar Expedition (1901–1903), a part of the current Argentine locality DPV 13/84 (Andersson, 1906; Acosta Hospitaleche et al., 2017a), which is situated within the TELM 7/Submeseta Allomember/Submeseta II units. Two of these species, *Anthropornis nordenskjoeldi* and *Delphinornis larseni* (type specimens NRM-PZ A.45 and NRM-PZ A.21 respectively; Figures 8a, 8d), have retained their original taxonomic positions to the present. However, *Pachypteryx grandis* was included by Brodkorb (1963) in the genus *Anthropornis*, *Eosphaeniscus gunnari* Wiman, 1905 was transferred by Simpson (1971) to *Palaeeudyptes* Huxley, 1859, and *Ichtyopteryx gracilis* Wiman, 1905 was reassigned by Jadwiszczak and Mörs (2011) to *Delphinornis* (holotypes:

NRM-PZ A.22, NRM-PZ A.7, and NRM-PZ A.20 respectively; Figures 8b, 8h, 8i).

Another isolated incomplete tarsometatarsus designated as a holotype (NHMUK A3331; Figure 8k) of a new penguin species, *Notodyptes wimani* Marples, 1953, had been collected by members of the Falkland Island Dependencies Survey from the same Swedish locality in 1946 (Marples, 1953). The taxon was reassigned to the genus *Archaeospheniscus* Marples, 1952 by Simpson (1971). This nomenclatural act, published with a revision of the genus *Eosphaeniscus*, ended the period in which the fossil record, at the generic level, of all Antarctic penguins was not known outside the region. Ksepka and Clarke (2010), based on phylogenetic analyses, had reassigned *A. wimani* to the genus *Delphinornis*, but Jadwiszczak (2013) showed that such an act appeared to be premature (see Figure 6).

The first distinct species of early Sphenisciformes from Seymour Island with explicitly designated paratypes was *Palaeeudyptes klekowskii* (Myrcha et al., 1990). The holotype (IB/P/B-0065; Figure 8g) as well as five paratypes (IB/P/B-0061, IB/P/B-0081, IB/P/B-0093, IB/P/B-0101, and IB/P/B-0142), were isolated incomplete tarsometatarsi found by the Argentine-Polish Field Party in 1985 (Myrcha et al., 1990). According to Myrcha et al. (1990), bones had been collected on the northern slope of the La Meseta Formation, along a horizon (Myrcha et al., 2002: Figure 6) "with an especially large number of penguin bones" (Myrcha et al., 1990: 197). In a later paper, co-authored by these researchers (among others) (Myrcha et al., 2002), the collecting site was declared to be within TELM 7 of the La Meseta Formation (and hence the Submeseta Allomember/ Submeseta Formation as well). Importantly, there is an ongoing debate on the legitimacy of maintaining the same genus-level position for all species of *Palaeeudyptes*, and such an uncertainty also applies to *Archaeospheniscus* (e.g., Acosta Hospitaleche and Reguero, 2010; Ksepka et al., 2012; Jadwiszczak, 2013, but see also Tambussi et al., 2006). The representatives from New Zealand have nomenclatural priority.

The 21st century has brought two new genera and four new species of Eocene penguins based on tarsometatarsi from the unit TELM 7/Submeseta Allomember of the La Meseta Formation (=Submeseta Formation), collected during the 1990s (Myrcha et al., 2002). Their holotypes, which are better preserved than other type tarsometatarsi discussed so far, are as follows (Myrcha et al., 2002): IB/P/B-0484 (*Delphinornis arctowskii* collected from Polish locality ZPAL 4; Figure 8f), IB/P/B-0279a (*D. gracilis* collected from scree; Figure 8e), IB/P/B-0490 (*Marambiornis exilis* collected from ZPAL 4; Figure 8l), and IB/P/B-0278 (*Mesetaornis polaris* collected from scree; Figure 8m). The first three taxa also have single designated paratypes (MLP 93-X-1-92, IB/P/B-0492 and MLP 93-X-1-111), which come from localities DPV 14/84, ZPAL 4, and DPV 13/84, respectively. Interestingly, in connection

Figure 8 Tarsometatarsi of Eocene Antarctic penguins from Seymour Island (**a–n**) designated as actual or potential holotypes, supplemented with comparative material from the Natural History Musem at Tring, UK, abbreviated NHM(T)UK (**o**, **p**). **a**, NRM-PZ A.45, a type specimen of *Anthropornis nordenskjoeldi*; **b**, NRM-PZ A.22, a type specimen of *Anthropornis grandis*; **c**, NRM-PZ A.856, a new morphotype of *Anthropornis*; **d**, NRM-PZ A.21, a type specimen of *Delphinornis larseni*; **e**, IB/P/B-0279a, a type specimen of *Delphinornis gracilis*; **f**, IB/P/B-0484, a type specimen of *Delphinornis arctowskii*; **g**, IB/P/B-0065, a type specimen of *Palaeeudyptes klekowskii*; **h**, NRM-PZ A.7, a type specimen of *Palaeeudyptes gunnari*; **i**, NRM-PZ A.20, a type specimen of *Ichtyopteryx gracilis*; **j**, IB/P/B-0541c, an enigmatic small tarsometatarsus; **k**, NHMUK A.3331, a type specimen of *Archaeospheniscus wimani*; **l**, IB/P/B-0490, a type specimen of *Marambiornis exilis*; **m**, IB/P/B-0278, a type specimen of *Mesetaornis polaris*; **n**, IB/P/B-0279b, *Mesetaornis* sp.; **o**, NHM(T)UK s/2002.2.1, tarsometatarsus of the smallest present-day penguin *Eudyptula minor*; **p**, NHM(T)UK 1905.12.30.419, tarsometatarsus of the largest present-day penguin *Aptenodytes forsteri*. Bones are in dorsal and plantar view (**a–n**) or solely dorsal view (**o**, **p**). Some specimens were mirrored to facilitate comparisons. Scale bar is 50 mm.

with the later synonymization of *Delphinornis gracilis* with *Ichtyopteryx gracilis* by Jadwiszczak and Mörs (2011), their specific epithets became secondary homonyms. Anyhow, this nomenclatural act resulted in the following new combination (comb. nov.): *Delphinornis gracilis* (Wiman, 1905; Jadwiszczak and Mörs, 2011; but see Acosta Hospitaleche and Reguero, 2011).

A number of other (incomplete) Eocene tarsometatarsi from Seymour Island most likely also represent new species of early penguins. The most suggestive in this respect appear to be the following (but see also Jadwiszczak, 2013): IB/P/B-0279b (Figure 8n) from the scree of TELM 7 (a smaller *Mesetaornis*; Myrcha et al., 2002), NRM-PZ A.856 (Figure 8c) from the Swedish locality NRM 5, TELM 7 (a

new morphotype of *Anthropornis*; Jadwiszczak and Mörs, 2017), and IB/P/B-0541c (Figure 8j) from the locality ZPAL 4, TELM 7 (considered a new genus and species of small penguin; Jadwiszczak, 2008).

The first Antarctic fossil penguin holotype representing a different part of the skeleton was a large partial synsacrum NRM-PZ A.23 (Figure 7d), from the aforementioned Swedish locality no. 11, that can be aptly termed a foundation stone (pun intended) of *Orthopteryx gigas*. Wiman (1905) was not, however, fully convinced that the specimen actually belonged to a penguin. According to Simpson (1971), *O. gigas* (like *Ichtyopteryx gracilis*) was a dubious taxon (of "little or no present significance"), whereas Acosta Hospitaleche and Reguero (2011) considered these taxa nomenclaturally valid but also as *nomina dubia*. Jadwiszczak and Mörs (2011) synonymized *O. gigas* with *A. nordenskjoeldi*.

All four remaining holotypes from the fossil record of Eocene Antarctic penguins are humeri. Simpson (1971) claimed that "humeri are generally taxonomically significant bones for penguins" and decided that two such bones reported by Marples (1953) and assigned by that author to *Eosphaeniscus gunnari*, and possibly also some of Wiman's specimens, represented a new genus and species, *Wimanornis seymourensis* Simpson, 1971. The holotype is a nearly complete bone, NHMUK A3367 (Figure 7f), and the second part of the hypodigm is a proximal half of the humerus, NHMUK A3325. Both had been collected in 1946, albeit from different localities– the British sampling station D.521 within the Swedish locality no. 11 (TELM 7) and the British locality D.499 (supposedly TELM 5/Cucullaea I Allomember), respectively. Jadwiszczak (2006a) postulated that *W. seymourensis* was not a distinct species (i.e., rather a junior synonym of *P. gunnari*).

Another genus of early Sphenisciformes was erected by Tambussi et al. (2006) based on three humeri from an unspecified locality within the Submeseta Allomember (supposedly TELM 7). Specimens were assigned to two species, *Tonniornis mesetaensis* and *T. minimum* (Tambussi et al., 2006). The former taxon is represented solely by an almost complete bone, MLP 93-X-1-145 (Figure 7h), and the latter is represented by two incomplete specimens, MLP 93-I-6-3 (holotype; Figure 7e) and MLP 93 X-1-22 ("referred material").

The most recent specimen in the list of holotypes of Eocene Antarctic penguins is a poorly preserved humerus (MLP 00-I-1-19; Figure 7g) collected from the locality DPV 16/84 (Submeseta III of the TELM 7/Submeseta Formation) in 2000 (Acosta Hospitaleche et al., 2017b). This small bone is the only skeletal element attributable to *Aprosdokitos mikrotero* (Acosta Hospitaleche et al., 2017). It should also be noted that, according to Tambussi et al. (2006), a number of humeri from the Submeseta Allomember/Formation are assignable to two penguin species known from the Oligocene of New Zealand, *Palaeeudyptes antarcticus* Huxley, 1859 and *Archaeospheniscus lopdelli* Marples, 1952. However,

this claim appears disputable.

The fossil record of Eocene Sphenisciformes from Seymour Island comprises virtually all types of bones that make up an avian skeleton, although some of them are particularly abundant. Comprehensive studies of this aspect, taking into account a number of potential biases, have not yet been carried out. Nevertheless, a very preliminary assessment made by Jadwiszczak (2006a; 784 bones from the IB/P/B) indicated that six categories of specimens exceeded the 10% threshold. The most numerous were tibiotarsi, with their long shafts being prone to break into fragments, followed by humeri, pedal phalanges, femora, tarsometatarsi, and coracoids. Attempts to assign isolated bones to known taxa were based largely on their dimensions (e.g., Wiman, 1905; Jadwiszczak, 2006b) and needless to say that approach has limitations. There is no doubt that the assemblage of Eocene penguins from Seymour Island was characterized by an extremely wide range of body sizes (Figures 7, 8). Interestingly, representatives of at least four species, namely *Anthropornis nordenskjoeldi*, *A. grandis*, *Palaeeudyptes klekowskii*, and *P. gunnari*, were larger (and heavier) than the largest present-day Sphenisciformes (Figures 7, 8; for details, see Simpson, 1975; Jadwiszczak, 2001; Jadwiszczak and Chapman, 2011; Acosta Hospitaleche, 2014, and references therein).

The partial skeletons of early penguins from Seymour Island are very rare and not all of them can be taxonomically identified. In this respect, two specimens assignable to *Palaeeudyptes* are noteworthy: MLP 96-I-6-13 from the locality DPV 10/84 (*P. gunnari*; Acosta Hospitaleche and Reguero, 2010), and MLP 11-II-20-07 from DPV 13/84 (*P. klekowskii*; Acosta Hospitaleche and Reguero, 2014). Importantly, these skeletons include both the tarsometatarsus and humerus. Other key specimens are mostly limb bones (NHMUK A3348/3355, 3360[I], 3357/3359, 3372) from the locality D.515 (=Swedish locality no. 11) that supposedly belong to a single representative of *Anthropornis* (Marples, 1953; Jadwiszczak, 2012). Other associated specimens include MLP 77-IV-10-1 (very large coracoids, sternum, and partial vertebral column) from the locality DPV 20/84 (Submeseta Allomember; Acosta Hospitaleche and Di Carlo, 2010), a set comprising IB/P/B-0382, 0440, 0444, and 0446 (a small partial wing skeleton) from an unspecified locality within TELM 7 (Jadwiszczak, 2010), IB/P/B-0159 (a large knee joint) from an unknown locality within TELM 7 (Jadwiszczak, 2006b), and IB/P/B-0981 (a series of three articulated cervicodorsal vertebrae) from the so-called 'shelves locality' (southwest of the end of the airstrip at Base Marambio) within TELM 7 (Jadwiszczak, 2014a). The newly published article by Jadwiszczak and Mörs (2019) provides a description of the partial skeleton of *Delphinornis larseni* from TELM 7.

The fossil record of early stem penguins from Seymour Island constitutes an indispensable source of data. It is obviously the most abundant record, in terms of collected specimens and erected taxa, for Sphenisciformes from a

single epoch. Aside from the Paleocene *Crossvallia*, thousands of bones were recovered and partially compartmentalized into at least ten distinct Eocene species, and this figure represents a very conservative view based exclusively on tarsometatarsi (see above). These morphologically diverse birds, which span a remarkable range of body sizes, not unexpectedly also differed in their ecology. According to Haidr and Acosta Hospitaleche (2012), results from analyses of cranial and mandibular remains indicate a variety of trophic habits and food preferences. Haidr and Acosta Hospitaleche (2012) claimed that early Sphenisciformes from Seymour Island could be divided into the following categories: medium-sized piscivorous birds, large-sized crustacean eaters, and medium-sized generalists.

The thin sections of penguin bones studied by Cerda et al. (2015) revealed distinctive microanatomical variation that was interpreted by these authors as related to differential adaptations to aquatic life. Jadwiszczak (2014b) reported on the development of the alleged lumbosacral sense organ for the control of walking in Eocene Antarctic penguins and claimed that it was comparable to that in present-day Sphenisciformes. Tambussi et al. (2015) analyzed virtual endocasts of skulls belonging to three extinct species and found a combination of a large number of primitive and apomorphic features not previously reported in penguins. Ksepka et al. (2015) analyzed the bone structure of modern and extinct penguins and found that Eocene Sphenisciformes from Seymour Island (also those termed 'giant') were apparently able to complete their growth cycle without prolonged fasting during the pre-fledging stage. Jadwiszczak and Mörs (2016) reported on the first quill pits found in early penguins. The studied specimen was a small ulna. Obviously, during their lifetimes, early penguins were exposed to physical traumata and diseases. Acosta Hospitaleche et al. (2012) described a partially healed femoral fracture, and Jadwiszczak and Rothschild (2019) presented evidence of an infectious disease, osteomyelitis, that had complicated the healing of a pedal phalanx fracture.

This is by no means an exhaustive list of recent findings inferred from studies of the fossil record of Paleogene Antarctic penguins. Nevertheless, it is a representative account of current focuses of research regarding these intriguing birds. It appears that paleobiological approaches continue to gain popularity among students of early Sphenisciformes, although there are still many obscure lower-level issues awaiting clarification. Such gaps in our knowledge will hopefully shrink as the quality of the fossil record improves.

3.6 Procellariiformes

The order Procellariiformes includes a group of seabird almost exclusively pelagic that feed in the open seas. They have a cosmopolitan distribution across the oceans, and a wide variety of migration patterns among the different species.

Procellariiformes comprises five families, from which four are represented by extant taxa, whereas the fifth one, the Diomedeoididae is only known through a substantial Oligocene–Miocene fossil record (Mayr and Smith, 2012). The living species are ordered in the families Diomedeidae (albatrosses), Procellariidae (petrels, prions, and shearwaters), Pelecanoididae (diving petrels), and Hydrobatidae (storm petrels). Sometimes, however, the storm petrels are classified into two different families: the Hydrobatidae and the Oceanitidae (see Carboneras, 1992; Carboneras and Bonan, 2019).

Fossil record of Procellariiformes is scarce during the Paleogene, which is rare taking into account the current abundance and diversity of the group, the colonial habit of the modern species (and presumably of the fossils), and the divergence time estimation for the group around 60 Ma ago (Jarvis et al., 2014; Li et al., 2014). The Antarctic record is restricted to a few isolated remains coming from two different levels and assigned with certain doubts to Procellariidae and Diomedeidae.

Isolated materials preliminary assigned to Procellariidae and Diomedeidae were collected from Eocene (Ypresian; Cucullaea I Allomember) of the La Meseta Formation. This fossil locality named RV 8200 by Woodburne and Zinsmeister (1984), and DPV 6/84 by Argentine researchers (see next references) is a famous outcrop due to the discovery of a number of bones of volant taxa (Tambussi and Degrange, 2013; Cenizo et al., 2015, 2016; Acosta Hospitaleche and Gelfo, 2015, 2017), and mammal teeth (Woodburne and Zinsmeister, 1984; Reguero et al., 2013a).

Notoleptos giglii, was recently described on the base of a single tarsometatarsus (Figure 9a) collected on the fossil locality DPV 16/84, where upper Bartonian–Priabonian strata assigned to "Submeseta III" (Submeseta Formation) crop out. The affinities between *N. giglii* and the rest of the Procellariiformes are uncertain; this species could be a part of an ancient lineage, or a representative of a stem group procellariiform (Acosta Hospitaleche and Gelfo, 2017).

The fossil record of Procellariiformes is not complete enough to give us a complete picture of the group. However, the number of reported findings in the Eocene of Seymour Island indicates that albatrosses and petrels would have been frequent members of the marina avifauna.

Notoleptos giglii MLP 12-I-20-305 was a seabird known from a left tarsometatarsus (Figures 9a–9b) considerably smaller than other albatrosses (Figures 9a, 9c). Another small Procellariiformes from central Asia, named *Murunkus subitus,* was originally assigned to Diomedeidae (Pantelev and Nessov, 1987), and then to a probable Diomedeididae (Mayr, 2015). However, morphological differences with *Diomedeides* reported more recently, come alive the controversy about its systematic position (de Pietri et al., 2010).

The small size of *N. giglii* is one of the most striking features about this species. It seems that albatrosses shared

Figure 9 Tarsometatarsi of Procellariiformes. **a**, holotype of *Notoleptos giglii* MLP 12-I-20-305; **b**, albatross silhouette indicating the location of the material figured in "**a**"; **c**, tarsometatarsus of the modern Diomedeidae *Thalassarche melanophrys*. Scale bar is 10 mm.

the aerial space with median and giant pseudo-toothed birds (Cenizo et al., 2015), the other group of gliding seabirds that lived in Antarctica during Eocene times (Acosta Hospitaleche and Gelfo, 2017). Unfortunately, a single tarsometatarsus is the only bone known for this species, and it is insufficient for answering the number of questions posed by *N. giggli*.

It is reasonable to think that the successful pelagornithids (Cenizo et al., 2015) developed the hyper-specialized flight earlier than the albatrosses like *N. giglii*. That way, small albatrosses would be relegated to a more generalist niche (Acosta Hospitaleche and Gelfo, 2017).

3.7 Controversial records

3.7.1 Charadriiformes

They constitute a group of cosmopolitan birds that includes small to medium-large forms. Many of these species are pelagic seabirds, but some others occupy exclusively near shore settings or even deserts and forested areas. There are currently three accepted clades within Charadriiformes that are thought to have diverged during the late Cretaceous, the Scolopaci (Scolopacidae, Jacanidae and Rostratulidae), the Lari (Alcidae, Dromadidae, Glareolidae, Laridae, Rhynchopidae, Stercorariidae, Sternidae), and the Charadrii (Charadriidae, Haematopodidae, Ibidorhynchidae, Pluvianidae, Pluvialidae, Recurvirostridae) (Baker et al., 2007).

Cretaceous records from Vega Island have been assigned to this order (Case and Tambussi, 1999; Cordes-Person, 2001, 2002). However, none of these assignments could be confirmed after a careful examination of the fossils and one of these fossils (a partial skeleton the Snow Hill Island formation of appears to lack characters of the avian crown clade; Clarke and Acosta Hospitaleche, pers. ob). The incomplete tarsometatarsus MLP 98-I-10-25 from the Maastrichtian of Vega Island assigned to a charadriiform by Case and Tambussi (1999) was ignored in subsequent contributions until Reguero et al. (2013a) mentioned it again. Nevertheless, this material is not complete enough for any certain systematic assignment. A second tarsometatarsus MLP 88-I-1-262 from La Meseta Formation was also assigned to this order (Tambussi and Degrange, 2013), but it does not seem to correspond to a charadriiform.

Other remains assigned to this group are even more fragmentary. A proximal end of ulna MLP 95-I-10-9 identified by Tambussi and Degrange (2013) could belong to an anseriform. A second incomplete ulna MLP 96-I-5-7 identified as a charadriiform (*in schedis*) was originally reported as a probable Presbyornithidae (Noriega and Tambussi, 1995). A more accurate assignment is not currently possible due to fragmentary state of the material.

3.7.2 Gruiformes

This taxon formally included what is now recognized as a polyphyletic group of birds. Although a monophyletic core Gruiformes is now recognized (see Mayr, 2009, and references cited therein), a number of extinct taxa of uncertain affinities need to be reassessed in light of the removal of many other "traditional Gruiformes" to other parts of Aves (e.g., Cariamidae, Otidae). Core Gruiformes is generally understood to comprise the Ralloidea (Rallidae, Sarothruridae, and Heliornithidae) and Gruoidea (Psophiidae, Aramidae, and Gruidae). Represented by wading and terrestrial birds that live in all continents, except in Antarctica (del Hoyo et al., 1996), the Paleogene

fossil record of this group is wide, although many species are based on fragmentary remains.

A distal fragment of a right tarsometatarsus MLP 90-I-20-9 coming from the upper levels of the La Meseta Formation was mentioned as a possible gruiform (Tambussi and Degrange, 2013: Figure 6.1g). Due the absence of preserved trochleae in this specimen, a reliable identification is not possible. More material will be needed to assess the possible Paleogene presence of this group. In addition, a proposed Cretaceous record of a cariamid (a taxon no longer considered part of Gruiformes) has also been removed and referred to a diving taxon (c.f. *Vegavis*, West et al., 2019).

3.7.3 Phoenicopteriformes

They encompass the flamingos and their fossil relatives. Stem lineage flamingos, and stem relatives of the clade flamingos+grebes, are known in the fossil record since the Eocene (e.g., Mayr, 2009). Extant species are characterized by filter feeding adaptations, whereas the most stem lineage species lack of these derived features of the skull. They are thought to evolve from aquatic and probably more grebe-like ancestors (for a further explanation see Mayr, 2009).

A slender, slightly-curved and incomplete right radius MLP 87-II-1-2 (Tambussi and Degrange, 2013: Figure 6.1h) of a flamingo was reported by Tambussi and Noriega (1996). This referral was reassessed by Tambussi and Degrange (2013: Figure 6.1h), who supported the assignment to a phoenicopteriform. Indeed, some similarities can be found between this fossil and a flamingo radius, but the incompleteness of the material limits confidence in its final systematic assignment. The presence of flamingos in Antarctica would not be unexpected as the Eocene of Seymour Island was interpreted as sampling deltaic, estuarine and shallow-marine environments (Porębski, 1995, 2002; Marenssi et al., 1998) suitable for these birds.

3.7.4 Threskiornithidae

This family includes two subfamilies known as ibises (Threskiornithinae) and spoonbills (Plataleinae), and is classically grouped into the Ciconiiformes together with other long-legged wading birds. However, the family was reallocated after recent molecular analyses to the order Pelecaniformes (Ramirez et al., 2013, and references therein).

Two fragments of the maxillary jaw with portions of rhamphotheca were collected from sediments assigned to TELM 6, or the uppermost Cucullaea II Allomember (La Meseta Formation, Seymour Island; Jadwiszczak et al., 2008). Assuming they are correctly identified, they may constitute the only record of an ibis in Antarctica, including living and fossil specimens, and would also be the oldest record in the Southern Hemisphere. The title given by the authors to their paper (Jadwiszczak et al., 2008) is more

conservative, however, and refers only to an ibis-like bird. Recently, Agnolín et al. (2019) have challenged this view; in their opinion, both fossils supposedly represent the dorsal spine of a chimaeroid chondrichthyan.

3.7.5 Gaviiformes

This order is represented today by the single genus *Gavia* with five species united in Gaviidae. This family also includes proposed fossil species, among which the Cretaceous fossil genus *Polarornis* was included from Antarctica (Chatterjee, 2002).

Polarornis gregorii is a species based on a partial skeleton (TTU P 9265) collected from the Upper Cretaceous (Unit 9) of the López de Bertodano Formation on Seymour Island in the 1980's (Chatterjee, 1989, 2002). Notwithstanding the numerous revisions of the material, *Polarornis* is still a controversial taxon regarding its preserved morphologies, diagnosibility, and phylogenetic affinities (Mayr, 2004; Acosta Hospitaleche and Gelfo, 2015; Clarke et al., 2016, and references cited therein). Unfortunately, the identity of bone fragments such as parts of the basicranium and quadrate were not confirmed in a recent revision, and the partial rostrum and tibia were described after extensive reconstruction including bone fragments that are not identifiable as part of these elements (Clarke et al., 2016). Only one element, the femur, was directly comparable to the holotype of *Vegavis iaai*, although proxima- most end of the tibia and several additional elements can be compared from a second specimen referred to *Vegavis iaai* (Clarke et al., 2016). *Polarornis* is nearly twice the size of *Vegavis*.

Isolated bones of variable sizes, belonging to diving birds very similar to *Polarornis* and *Vegavis* (see Section 3.1 Anseriformes) are very common in late Cretaceous sediments of both Seymour Island and Vega Island in the James Ross Basin (Reguero et al., 2013b; Roberts et al., 2014; Acosta Hospitaleche and Gelfo, 2015). Unfortunately, their incompleteness precludes a confident assignment for many of these materials. They could belong, for example, to described or new species of *Vegavis* or *Polarornis* or a distinct diving taxon. It is noteworthy that while some hind limb elements (femur and tibiotarsus) from Seymour Island of large *Polarornis*-sized individuals appear referable to that taxon, others with thickened bone cortices are diagnosably distinct (Acosta Hospitaleche and Gelfo, 2015; MLP 98-I-10-47) from *Vegavis* with what some would call major, possibly "ordinal level", differences. The tarsometatarsus is not preserved in the *Polarornis* holotype specimen.

Our assessment of the affinities of *Polarornis* has changed since the recovery of a second specimen of *Vegavis* (Clarke et al., 2016), which allows further comparisons between both taxa (Clarke et al., 2016; Agnolin et al., 2017). While shown to be similar to *Vegavis*, the *Polarornis* holotype remains are highly fragmentary; the reported brain case, quadrate are not those elements (Clarke et al., 2016)

but appear to be unidentifiable fragments of other bones. The rostrum of the *Polarornis* specimen appears to have been modified during preparation (Clarke et al., 2016). Only the hind limb can be compared between *Vegavis* and *Polarornis* holotypes, but they both clearly show thickening of the bone cortices seen in most hindlimb propelled diving birds regardless of taxonomic affinity. While similar in overall proportions, the *Polarornis* holotype lacks a conspicuous pit and muscular scar on the femur that are clear in both *Vegavis* specimens (Clarke et al., 2005, 2016). *Polarornis* lacks gaviiform apomorphies and was instead proposed to be a part of Anseriformes, or a basal Galloanseres with *Vegavis*, according to most recent revisions (Clarke et al., 2016; Acosta Hospitaleche and Gelfo, 2017; Agnolin et al., 2018; see also Section 3.1 Anseriformes). Other authors maintain that the affinities of *Polarornis* and *Vegavis* may or may not lie within Galloanseres, and that they are part of an as yet unspecified distinct avian subclade (Mayr et al., 2018a).

4   Conclusions

The James Ross Basin, rich in fossils, comprises one of the most complete Cretaceous–Paleogene sedimentary sequences in the Southern Hemisphere. The fossil records of birds from these largely nearshore marine deposits is particularly rich. However, most of the known remains are from a relatively limited array of aquatic clades and most are comprised of isolated single bones. Penguins are the most abundant birds represented, and Anseriformes are known from the most complete partial skeletons. Preservation of structures such as the syrinx that are quite rare fossil records of birds are comparatively well represented the James Ross Basin. Records for clades of birds with more terrestrial ecologies are sparse, and many have been controversial. However, with increased sampling and collaborative comparative work bringing together fossils housed in many different institutions should enable a more synoptic look at this diversity.

Abbreviations

AMNH–American Museum of Natural History, New York, USA
DPV–División Paleontología de Vertebrados, Museo de La Plata, La Plata, Argentina
IAA–Instituto Antártico Argentino, San Martín, Argentina
IB/P/B– University of Bialystok, Poland
MACN PV–Sección Paleontología Vertebrados, Museo Argentino de Ciencias Naturales, Argentina
MLP–Museo de La Plata, Argentina
MNHN–Museo Nacional de Historia Natural, Santiago, Chile
NRM-PZ–Naturhistoriska riksmuseet, Stockholm, Sweden
NHMUK–Natural History Museum, London, United Kingdom
SGO.PV–Vertebrate Paleontology Collection, Museo Nacional de Historia Natural, Santiago, Chile
TMM-VPL–University of Texas, Austin, USA
UCR–University of California, Riverside, USA

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