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Vegaviidae, a new clade of southern diving birds that survived the K/T boundary

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Abstract The fossil record of Late Cretaceous–Paleogene modern birds in the Southern Hemisphere includes the Maastrichtian *Neogaeornis wetzeli* from Chile, *Polarornis gregorii* and *Vegavis iaai* from Antarctica, and *Australornis lovei* from the Paleogene of New Zealand. The recent finding of a new and nearly complete *Vegavis* skeleton constitutes the most informative source for anatomical comparisons among *Australornis*, *Polarornis*, and *Vegavis*. The present contribution includes, for the first time, *Vegavis*, *Polarornis*, and *Australornis* in a comprehensive phylogenetic analysis. This analysis resulted in the recognition of these taxa as a clade of basal Anseriformes that we call Vegaviidae. Vegaviids share a combination of characters related to diving adaptations, including compact and thickened cortex of hindlimb bones, femur with anteroposteriorly compressed and bowed shaft, deep and wide popliteal fossa delimited by a medial ridge, tibiotarsus showing notably proximally expanded cnemial crests, expanded fibular crest, anteroposterior compression of the tibial shaft, and a tarsometatarsus with a strong transverse compression of the shaft. Isolated bones coming from the Cretaceous and Paleogene of South America, Antarctica, and New Zealand are also referred to here to Vegaviidae and support the view that these basal anseriforms were abundant and diverse at high southern latitudes. Moreover, vegaviids represent the first avian lineage to have definitely crossed the K–Pg boundary, supporting the idea that some avian clades were not affected by the end Mesozoic mass extinction event, countering previous interpretations. Recognition of Vegaviidae indicates that modern birds were diversified in southern continents by the Cretaceous and reinforces the hypothesis indicating the important role of Gondwana for the evolutionary history of Anseriformes and Neornithes as a whole.

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Introduction

The fossil record of Late Cretaceous–Paleogene modern birds in the Southern Hemisphere is patchy and highly fragmentary (Chiappe 2016). It includes *Neogaeornis wetzeli* from Maastrichtian beds of Chile, *Polarornis gregorii* and *Vegavis iaai* from the Maastrichtian of Antarctica, and *Australornis lovei* from the Paleogene of New Zealand (Chatterjee 2002; Clarke et al. 2005, 2016; Mayr 2009; Mayr and Scofield 2014). The phylogenetic relationships of these taxa as well as various isolated specimens from Paleogene and Cretaceous of Antarctica have been variously interpreted by different authors (e.g., Olson 1992; Chiappe 1996; Chatterjee 2002; Clarke et al. 2005; Acosta Hospitaleche and Gelfo 2015). The best supported taxonomic referral is that of *Vegavis*, represented by two

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partially articulated skeletons that exhibit several features in common with living anseriforms (Clarke et al. 2005, 2016). Mayr and Scofield (2014) compared *Australornis* with *Vegavis*, indicating shared anatomical details of the humerus.

A recently published (Clarke et al. 2016; ESM) *Vegavis* skeleton [MACN-PV (Vertebrate Paleontology Collection, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina) 19.748] constitutes the most informative source for anatomical comparisons among *Australornis*, *Polarornis*, *Vegavis* as well as other southern avian specimens. In the present contribution, we offer evidence that these Late Cretaceous and Paleogene birds are closely related constituting a new clade of basal anseriforms. Isolated bones from Cretaceous and Paleogene beds of South America, Antarctica, and New Zealand may be also referable to this new clade of anseriforms. Moreover, it represents the first avian lineage to have definitely crossed the K–Pg boundary, supporting that some avian clades were not affected by the end Mesozoic mass extinction event, countering previous interpretations.

Results

Comparative study of *Vegavis*, *Polarornis*, and *Australornis*

Vegavis is represented by two articulated partial skeletons (Clarke et al. 2005, 2016). It overlaps with *Australornis* (Mayr and Scofield 2014) in the proximal portion of the humerus, proximal part of the coracoid, scapula, and ulna. Besides, the new specimen of *Vegavis* overlaps with that of *Polarornis* [Chatterjee 2002; TTU P (Texas Tech University, Lubbock, USA) 9265] in the humerus, femur, and proximal end of the tibia, and with *Neogaeornis* in the tarsometatarsus. This set of taxa allows comparison with fragmentary Paleogene Antarctic and New Zealand specimens represented by isolated coracoid, femur, tibiotarsus, and tarsometatarsus (e.g., Case and Tambussi 1999; Case et al. 2006; Acosta Hospitaleche and Gelfo 2015).

The humerus is probably the most diagnostic element among anseriforms (Woolfenden 1961). This bone shows a large number of features that are shared between *Vegavis* and *Australornis* (Fig. 1). In the latter two taxa, the humerus is notably narrow and medially tilted on its proximal half. It shows an unusually proximodistally elongate deltopectoral crest that quadruplicates the length of the bicipital crest. In the case of *Vegavis* and *Australornis*, the deltopectoral crest extends for more than one third of the humeral length. The dorsal tubercle is notably robust and proximally projected, as in presbyornithids (De Pietri et al. 2016). Both features were previously considered autapomorphic for *Australornis* by Mayr and Scofield (2014), but their presence in *Vegavis* indicates that both are diagnostic of a clade including these two

taxa. The capital ridge is strongly marked, and the ventral pneumotricipital fossa is wide, deep, and non-pneumatic. The dorsal pneumotricipital fossa is relatively wide, well defined, and subcircular in outline. The ventral tubercle is notably expanded and proximally projected.

Vegavis, *Australornis*, and presbyornithids share a well-marked and elongate scar for insertion of *M. scapulohumeralis* and *M. latissimus dorsi caudalis* (De Pietri et al. 2016). The coracobrachialis impression is notably deep and well defined, and the transverse ligament groove is notably undercut and proximally extended.

The coracoid of *Vegavis* is well known, but it is incompletely preserved in *Australornis*. However, both taxa share a humerus with an expanded articular surface for the furcula (a feature recovered diagnostic for Anseriformes in recent analyses; Clarke et al. 2016), and the main plane for the articular humeral facet is laterally oriented, thus meeting the ventral surface of the humerus at an angle close to 90° (a feature originally considered autapomorphic for *Australornis* by Mayr and Scofield 2014). As in other anseriforms, *Vegavis* exhibits the sternocoracoid impression with transverse linear ridges (De Pietri et al. 2016). In *Vegavis*, the sternal end of the coracoid is transversely expanded, being subequal to total coracoidal length. The scapula is narrow and elongate with subparallel margins in both *Vegavis* and *Australornis*.

The femur is well known both in *Vegavis* and *Polarornis* (Fig. 1). They share a combination of characters absent in other Mesozoic or Paleogene birds, including strongly anteriorly bowed and anteroposteriorly compressed shaft (especially near its distal end). This last condition of the distal part of the femur produces an ovoid-shape cross-section, a popliteal fossa wide and deep, an intercondylar distal groove wide and shallow, a medial distal condyle smaller than the lateral one, a trochlea fibularis wide and strongly laterally projected, and a medial supracondylar crest proximodistally extended.

The tibiotarsi of *Vegavis* and *Polarornis* share a pair of proximally expanded cnemial crests (Fig. 1). The cranial cnemial crest is proximally and anteriorly expanded and extends distally down the tibiotarsal shaft. The lateral cnemial crest is thickened in both *Vegavis* and *Polarornis* (this feature was originally considered autapomorphic for *Polarornis* by Chatterjee 2002). It flares distally and is separated from the cranial cnemial crest by a deep intercnemial groove. A patellar crest is absent. In both taxa, the fibular crest is located far from the proximal end of the bone, and the shaft is strongly anteroposteriorly flattened.

The tarsometatarsus is only incompletely known in *Vegavis*, and the nearly complete tarsometatarsus of *Neogaeornis* is known. The shaft is notably transversely compressed with sharp lateral and medial edges. In *Vegavis*, the intercotylar prominence is low and rounded, and the hypotarsus shows four small ridges of which the medial one is larger and more distally extended than the remaining crests. The distal end of the bone resembles

Fig. 1 **a**, **b** Proximal end of right humerus of *Vegavis iaai* in **a** medial and **b** lateral views. **c**, **d** *Australornis isoni*; **e** *Vegavis iaai* left coracoid in dorsal view; **f** *Vegavis iaai* right ulnare in proximal view; **g–i** right femur of *Vegavis iaai* in **g** anterior, **h** medial, and **i** posterior views; **j**, **k** proximal left tibiotarsus of *Vegavis iaai* in **j** lateral and **k** anterior views; **l** *Vegavis iaai* right hand in dorsal view; **m–o** left femur of *Polarornis gregorii* in **m** anterior, **n** medial, and **o** posterior views; **p**, **q** proximal left tibiotarsus of *Polarornis gregorii* in **p** lateral and **q** anterior views; **r** left scapula of *Vegavis iaai* in medial view; **s** rostrum of *Polarornis gregorii* in left lateral view; **t** articular portion of the left mandible of *Vegavis iaai* in lateral view; **u** left pterygoid of *Vegavis iaai* in ventral view. Abbreviations: al, alular digit; bptf, basipterygoid articular surface; cas, facies articularis clavicularis; cbc, crista bicipitalis; ccc, cranial cnemial crest; csr, capital ridge; dpc, deltopectoral crest; ep, extensor process; fib, fibula; fns, foramen nervi supracoracoidei; fo, pneumotricipital fossa; gl, glenoid; ig, intercondylar groove; isc, impressio *M. sternocoracoidei*; lc, lateral crest; lcc, lateral cnemial crest; lr, transverse linear ridge; mc, medial condyle; proc., procoracoidal process; pvf, proximoventral fossa; rad, radiale; rp, retroarticular process; rs, raised scar; shc, scar for *M. scapulohumeralis cranialis*; tbd, dorsal tubercle; tbv, ventral tubercle; tfc, tibiofibular crest; ul, ulnare. (**c**) and (**d**) modified from Mayr and Scofield (2014). Scale bar equals 1 cm for (**a**), (**b**), (**c**), (**d**), (**g**), (**h**), (**i**), (**j**), (**k**), (**l**), (**m**), (**n**), (**o**), (**r**), (**s**), (**t**), and (**u**) and 0.5 cm for (**f**), (**p**), and (**q**)

that of diving birds (e.g., gaviiforms, podicipediforms) and anseriforms (Ericson 1997) in having a posteriorly tilted trochlea of metatarsal II. Interestingly, the tarsometatarsus of *Neogaeornis* exhibits two anseriform traits: presence of a deep concavity above the center of the middle trochlea and dorsomedial to the distal vascular foramen (Cenizo 2012), and a distally located distal vascular foramen (Bourdon 2005). This anatomical evidence allows recognizing *Neogaeornis* as an anseriform, but also as related to *Vegavis* and its kin, dismissing previous hypotheses proposing this taxon as a hesperornithiform or a gaviiform (see Olson 1992).

Increase of osteosclerosis in the femur has been reported previously for *Polarornis* (Chinsamy et al. 1998; De Mendoza and Tambussi 2015). The humerus and femur of *Vegavis* also exhibit a notably thickened cortex, composed of a highly vascularized (semi-reticular pattern), woven-fibered matrix that grades into an avascular matrix subperiosteally and endosteally (Fig. 2). Lines of arrested growth are absent. Cross-sections of the shafts are characterized by osteosclerosis. The relative bone thickness (RBT) (sensu Smith and Clarke 2014) in the femur is ~ 21.6, a value that is closely similar to that of the diving ducks *Tachyeres* and *Aythya*, while in the case of the humerus the RBT is ~ 20, a value similar to that of *Tachyeres*. Osteosclerosis of limb bones in *Vegavis* and *Polarornis* may constitute an additional derived trait sustaining the close phylogenetic relationship between these genera.

Phylogenetic relationships

A comprehensive phylogenetic analysis of Anseriformes is here conducted including, for the first time, *Vegavis*,

Polarornis, and *Australornis* (ESM). As a result, a monophyletic clade gathering these taxa emerges at the base of Anseriformes. This new clade is here termed as Vegaviidae nov., and it is sustained by 12 unambiguous synapomorphies and is supported by strong statistical values (ESM; Fig. 3).

In agreement with previous interpretations (Noriega and Tambussi 1995; Clarke et al. 2005), *Vegavis* is here recovered as belonging to Anseriformes. The combination of skull and postcranial characters exhibited by *Polarornis* sustains that it belongs to Anseriformes, contrary to its original interpretation as a member of Gaviidae (Chatterjee 2002). *Vegavis* shares with Galloanseres a well-developed and transversely compressed retroarticular process (Mayr and Clarke 2003), an extended fossa for the attachment of *M. adductor mandibulae externus* (Dzerzhinsky 1995), a pronounced coronoid inflection, and mandibular cotylae anteroposteriorly elongate, separated by a low longitudinal crest (Weber and Hesse 1995; Ericson 1997; Clarke et al. 2016; Fig. 1). Furthermore, analysis of skull material of *Polarornis* indicates that this taxon shares with Galloanserae a lacrimal lacking contact with the jugal bar (Mayr 2011) and a well-developed craniofacial flexor zone marked by a transverse groove between nasals and frontal process (Worthy et al. 2016). Clarke et al. (2016) reported for the pterygoid of *Vegavis* a large and prominent, anteriorly located and dorsoventrally facing basipterygoid articulation, a condition diagnostic for Galloanserae (see also Cracraft and Clarke 2001). *Vegavis* differs from Galliformes, but resembles Anseriformes, in that the basipterygoid articular surface is not located at the anterior margin of the bone (Olson and Feduccia 1980; Fig. 1).

Furthermore, vegaviids share with Anseriformes a carpometacarpus with processus pisiformis at the level of the

Fig. 2 Histological sections of *Vegavis iaai* (MACN-PV 19.748) humerus (**a**), femur (**b**), and polarized detail of humerus (**c**). Scale bar equals 10 mm for (**a**), (**b**) and 5 mm for (**c**)
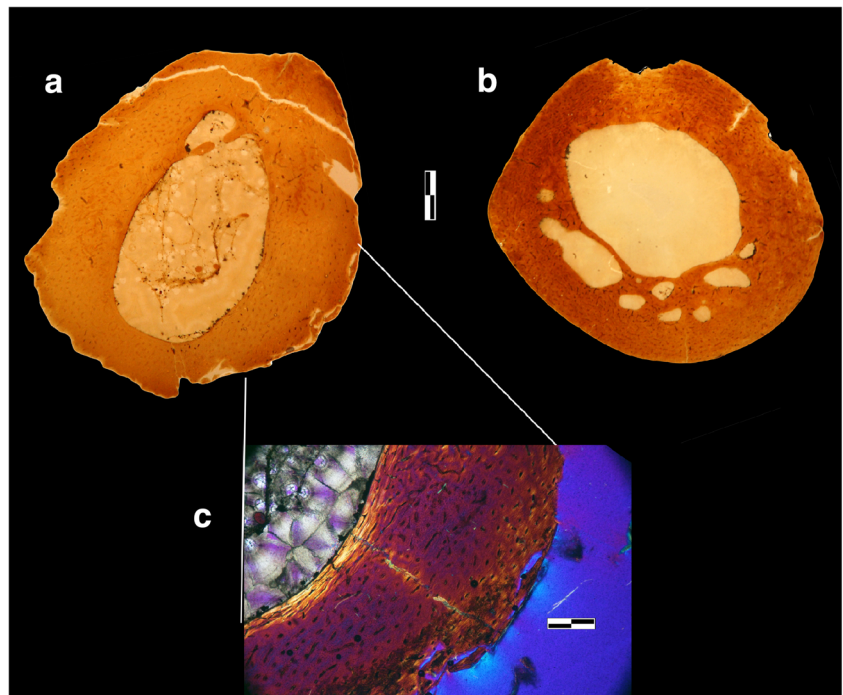
Fig. 3 Phylogeny with geographical distribution of Vegaviidae (**a**) and fossiliferous localities that yielded vegaviid genera (**b**). Schematic skeletal reconstruction of *Vegavis iaai* based on specimens MLP 93-I-3-1 and MACN-PV 19.748 (**c**). Skull based on preserved remains of *Polarornis gregorii* (Chatterjee 2002)
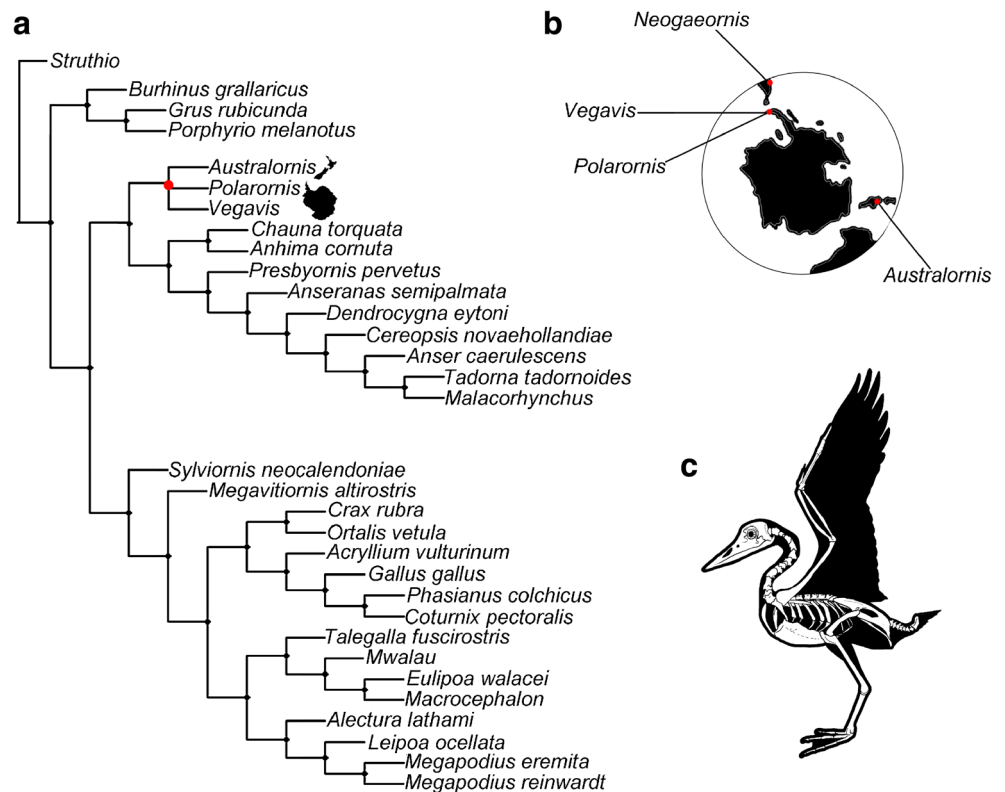
carpal trochlea (Bourdon 2005), a deep fossa within the supracoracoidal sulcus in the coracoid (Mayr 2008), well-developed haemal arches in distal caudal vertebrae (as evidenced by the well-developed haemal facets on the ventral surface of the vertebral centra; Mayr and Clarke 2003), a prominent tubercle on the caudal end of the dorsal ramus of the ulnare (Ericson 1997; Clarke et al. 2016), a tibiotarsus with proximally extended cranial cnemial crest, and a tarsometatarsus with four or more hypotarsal crests (Worthy et al. 2016). The retention in *Vegavis* of a well-developed foramen nervi supracoracoidei in the body of the coracoid, a transversely expanded sternal end of coracoid, and a small distal metacarpal symphysis constitute plesiomorphies present in vegaviids that sustain them as stem-Anseriformes (Fig. 1).

Polarornis and *Neogaeornis* were considered as related to modern loons (i.e., Gaviiformes; Olson 1992; Chiappe 1996; Cooper and Penny 1997; Padian and Chiappe 1998; Hope 2002; Chatterjee 2002; Van Tuinen and Hedges 2004; Acosta Hospitaleche and Gelfo 2015). However, the gaviiform affinities of these taxa have been questioned by several authors (e.g., Mayr 2009; Mayr and Poschmann 2009; Smith 2010; Mayr et al. 2013; Feduccia 2014), and Mayr et al. (2013) noted the strong morphological discrepancy in morphology between putative Late Cretaceous gaviiform taxa and those from the early Paleogene. In fact, most features that were originally interpreted to include *Polarornis* and *Neogaeornis* within Gaviiformes are mostly related to the proportions and general morphology of the femur, proximal

tibiotarsus, and distal metatarsal trochleae (Fig. 1). As noted above, all these traits are present in the anseriform *Vegavis*, and most of them are recovered as synapomorphies of Vegaviidae. These features of the hindlimb are related to diving habits and were probably convergently acquired by loons and vegaviids (see "Discussion" section below).

In spite of the fact that *Vegavis* and *Polarornis* appear roughly contemporaneous in age, both come from the same geographical region (NE Antarctic Peninsula), and few comparable bones share the same general morphology. Clarke et al. (2016) indicated some anatomical differences between both genera. *Vegavis* is slightly over approximately one half the size of *Polarornis* (Clarke et al. 2016), and details in femoral anatomy (see ESM) suggest they represent two separate, albeit closely related, taxa.

In addition to *Polarornis*, *Vegavis*, *Australornis*, and *Neogaeornis*, there are several additional specimens that may belong to Vegaviidae. Mayr and Scofield (2014) described from the Paleocene of New Zealand an incomplete proximal humerus that was referred to Phaethontiformes. However, this element shares with *Vegavis* and *Australornis* a notably wide and deep dorsal pneumotricipital fossa that is subcircular in outline (Mayr and Scofield 2015), a distally thin shaft, and well-developed ventral and dorsal tubercles. On this basis, we tentatively interpret this specimen as an indetermined vegaviid (ESM).

Case et al. (2006) and Acosta Hospitaleche and Gelfo (2015) described two incomplete distal femora from the Late

Cretaceous of Antarctica, referred by these authors to Cariamiformes and Gaviiformes, respectively (ESM). Further, Yury-Yáñez et al. (2012) described the distal end of a femur of an indeterminate bird from the Eocene beds of Southern Chile (ESM). These three femora show a combination of features shared with vegaviids, including anteriorly bowed shaft, medial distal condyle smaller than the lateral one, and trochlea fibularis transversely wide and laterally projected.

Acosta Hospitaleche and Gelfo (2015) described an isolated coracoid from the Eocene of Antarctica as belonging to Gaviiformes (Tambussi and Degrange 2013; Acosta Hospitaleche and Gelfo 2015). However, this element shares with *Vegavis* several features, suggestive of vegaviid affinities of the specimen (ESM).

Acosta Hospitaleche and Gelfo (2015) described from the Late Cretaceous and Paleogene of Antarctica isolated tibiotarsi that they referred to Gaviiformes. Nevertheless, these specimens share with *Vegavis* and *Polarornis* several features that suggest their inclusion among vegaviids.

Isolated tarsometatarsi from the Late Cretaceous of Antarctica (identified as Gaviiformes by Acosta Hospitaleche and Gelfo 2015) and from the Paleogene of New Zealand (Ksepka and Cracraft 2008) share a combination of features reminiscent to Vegaviidae. These tarsometatarsi share with *Vegavis*, and specially *Neogaeornis* a transversely compressed shaft with sharp lateral and medial edges, asymmetrical distal trochleae, and a deep concavity above the center of the middle trochlea (ESM).

To sum up, we recognize *Polarornis*, *Vegavis*, *Australornis*, and *Neogaeornis* as members of the new clade Vegaviidae, and that a large number of isolated specimens collected from Late Cretaceous and Paleogene beds of Antarctica, South America, and New Zealand may also belong to this group of basal anseriforms. Consequently, previous reports of Late Cretaceous and Paleogene Gaviiformes, Charadriiformes, Cariamiformes, Phaethontiformes, and Hesperornithiformes (Hou in Feduccia 1999; Chatterjee 2002; Clarke et al. 2005; Chatterjee et al. 2006; Cenizo 2012; Cordes 2002; Tambussi and Degrange 2013; Reguero et al. 2013) from the Southern Hemisphere are here dismissed, but interpreted as anseriforms and possible members of Vegaviidae.

Systematic paleontology

Aves Linnaeus, 1758.
    Neornithes Gadow, 1893.
    Galloanserae Sibley, Ahlquist and Monroe, 1988.
    Anseriformes Wagler, 1931.
    Vegaviidae nov.
    Diagnosis. Clade of birds having the following synapomorphies: Humerus with: 1—very long deltopectoral crest that represents more than four times the length of the bicipital crest (Mayr and Scofield 2014; ch. 122-3); 2—presence of a dorsal pneumotricipital fossa that is shallow and relatively wide, being smaller than the ventral pneumotricipital fossa (ch. 118-1; 119-1); 3—incisura capitis conforming a distinct proximal notch (ch. 130-2); 4—humeral shaft becomes narrow toward its distal third (ch. 135-1); Femur with: 5—absent or distinct trochanteric fossa (ch. 186-1); 6—obturator scars represented by two rugose impressions (ch. 194-1); 7—femoral shaft strongly curved in lateral view (ch. 200-2); 8—well-developed, deep, fibular trochlea with a distinct proximal depression (ch. 209-1); 9—patellar groove wide and flat (ch. 213-0); Tibiotarsus with: 10—cranial cnemial crest proximally expanded and straight (ch. 222-2); 11—indistinct cresta patellaris (ch. 227-2); and 12—fibular crest well separated proximally from the cranial cnemial crest (ch. 228-1).

Type genus. *Vegavis* Clarke et al., 2005.

Included taxa. *Polarornis gregorii* Chatterjee, 2002; *Vegavis iaai* Clarke et al., 2005; *Australornis lovei* Mayr and Scofield, 2014; *Neogaeornis wetzeli* Lambrecht, 1929.

Temporal and geographical distribution. Latest Cretaceous and Paleogene of Antarctica, New Zealand, and Latest Cretaceous and Eocene of Chile (South America) (Fig. 3).

Discussion

Diving adaptations of vegaviids

Vegavis, *Polarornis*, and *Neogaeornis* show the following distinctive features typically present among foot-propelled diving birds (e.g., Hesperornithidae, Baptornithidae, Gaviidae, Podicipedidae, Anhingidae): compact and thickened cortex of hindlimb bones (Fig. 2), femur with anteroposteriorly compressed and bowed shaft, deep fovea ligamentaris capitis, deep and wide popliteal fossa delimited by a medial ridge, wide patellar groove, medial condyle smaller than the lateral one, and expanded fibular condyle; tibiotarsus with notably proximally expanded cnemial crests, expanded fibular crest, anteroposteriorly compressed shaft, and broad distal extensor groove; and tarsometatarsus with strongly transversely compressed shaft and asymmetrical distal end with proximally located distal trochlea II (Chatterjee 2002; Worthy et al. 2007; Ksepka and Cracraft 2008; Noriega et al. 2008; Cenizo 2012; Acosta Hospitaleche and Gelfo 2015; Fig. 1).

Furthermore, in *Vegavis* and *Australornis*, the humerus shows a distally narrowing shaft, strongly marked capital ridge, and pneumotricipital fossa wide, deep, and non-pneumatic, a combination of characters typical of diving anseriforms (Watanabe and Matsuoka 2015). Furthermore, the large dorsal tubercle does not indicate well-developed soaring capabilities (Mayr and Scofield 2014).

Paleohistological analysis (Garcia Marsà et al. 2017) (Fig. 2) indicates that *Vegavis* and *Polarornis* were diving birds and, based on the osteosclerotic condition of the femur and shape of the hindlimb bones, were foot-propelled (Ibañez and Tambussi 2012). Furthermore, the humeral cross-section has RBT values that approach taxa that use their wings for underwater strokes (Humphrey and Livezey 1982), which also may have been the case for *Vegavis*. These interpretations are in agreement with Chinsamy et al. (1998) who on the basis of the high degree of osteosclerosis propose flightless habits for *Polarornis*.

Paleobiogeographical implications

Mayr and Scofield (2014) suggested the possibility that early Paleocene marine avifaunas from New Zealand had a similar composition to those from Antarctica due to their geographical closeness. In this context, they also speculated that *Vegavis* and *Australornis* may be closely related, but comparisons between these taxa were impossible because of the absence of overlapping materials. The new *Vegavis* specimen MACN-PV 19.748 allows comparing each other, bolstering the suspicion of these authors.

The geographical proximity, as well as the land connections among Southern South America and Antarctica, and the latter continent with Oceania, resulted in a shared fauna and flora on these landmasses. Zinsmeister (1982) recognized the Weddellian Bioprovince for the marine invertebrate faunas shared during the Late Cretaceous and Paleogene of Patagonia, Antarctica, Australia, and New Zealand. Novas et al. (2002) indicated that marine reptile faunas for these southern continents were also related to each other and were isolated from Laurasian taxa. The same is true for marine fish faunas (Bogan et al. 2016). On land, the Weddellian realm includes plants, remarkably *Nothofagus*, metatherian mammals (Case et al. 1988), and dinosaurs (Agnolin et al. 2010; Rozadilla et al. 2016). The presence of Vegaviidae in marine sediments of southern South America, Antarctica, and New Zealand during the Cretaceous and Paleogene reinforces such paleobiogeographical scenarios.

Furthermore, the recognition of *Polarornis*, *Vegavis*, *Neogaeornis*, *Australornis*, and a wide array of isolated specimens as belonging to Vegaviidae also dismisses previous hypotheses explaining the past distribution of some avian clades. Acosta Hospitaleche and Gelfo (2015) indicated that Gaviiformes were abundant during the Late Cretaceous and Paleogene of Antarctica, but later ecological competition with sphenisciforms geographically displaced gaviiformes to the northern hemisphere. Our present reinterpretation of Antarctic bird remains as possible vegaviid anseriforms, instead of Gaviiformes, contradicts this alternative hypothesis. However, we concur with Acosta Hospitaleche and Gelfo (2015) in that two different faunal stages may be recognized among the Late Cretaceous–Early Tertiary diving birds from southern seas: a first Cretaceous–Paleocene assemblage dominated by vegaviid anseriforms and a second post-Paleocene stage dominated by penguins.

It is worth mentioning that the oldest record of modern diving ducks is from the Oligocene of Kazakhastan (Zelenkov 2012). Vegaviids constitute an early experiment of diving forms that preceded modern ducks for more than 30 million years.

The fossil record of Mesozoic birds from the Southern Hemisphere is still relatively poor. In spite of the paucity of this record, some authors proposed that Southern Hemisphere Cretaceous avifaunas were dominated by archaic birds such as enantiornithes and basal ornithurines, and suggested that modern birds were absent from the Southern Hemisphere (Feduccia 2003; Longrich 2008; O'Connor and Forster, 2010). However, documentation of the neornithines *Vegavis* and *Polarornis* in Cretaceous beds from Antarctica clearly demonstrates that modern birds were already present in southern Gondwana by the Late Cretaceous, at least. Furthermore, recognition that Vegaviidae is a clade deeply nested within Galloanseres indicates that the early radiation of Neornithes in Gondwana was more complex than previously thought. Additionally, the recognition of this group reinforces the hypothesis that southern landmasses constituted a center for neornithine diversification and emphasizes the role of Gondwana for the evolutionary history of Anseriformes and Neornithes as a whole (Ericson et al. 2006; Cracraft 2001).

Vegaviidae, first documentation of an avian clade that survived the K/T boundary

The hypothesis of an avian mass extinction at the K–Pg boundary has been hotly debated. Many studies based on molecular evidence imply mass survival of birds across the K–Pg boundary (Hedges et al. 1996; Cooper and Penny 1997), whereas paleontological studies (see summary in Feduccia 1999, 2003, 2014; Longrich et al. 2011) claim that a large neornithine radiation by the Late Cretaceous is not supported by the present fossil record. The recognition of Vegaviidae in Cretaceous as well as Paleogene beds constitutes the first documented clade that crossed the K/T boundary.

Longrich (2008) and Bono et al. (2016), based on the fossil record from the Northern Hemisphere, considered the possibility that derived ornithurines (including Neornithes) exploited niches which were available at high latitudes, whereas Enantiornithes did not. In support of his hypothesis, Longrich (2008) indicated that Neornithes had remarkably higher growth rates than enantiornithes, a physiological adaptation that may be critical for surviving in seasonal climates at high latitudes. The same argument may be applied to the high latitudes in the Southern Hemisphere: all specimens collected from Antarctica, southern South America, and New Zealand

belong to Neornithine-like birds, whereas Enantiornithes and other basal birds remain unknown from these circumpolar regions of the southern hemisphere. In this regard, paleohistological data from *Vegavis* and *Polarornis* suggests that they exhibited relatively rapid and uninterrupted growth rates as in most living birds (Chinsamy 2002; Padian et al. 2001). High growth rates may have been an advantage in highly seasonal climates (i.e., presence/absence of freezing conditions) because it enabled these birds to acquire adult body size rapidly (see Chinsamy 2002; Bono et al. 2016). This high growth rate, as demonstrated by paleohistological analysis on *Vegavis*, may also constitute the key adaptation that allowed vegaviids to survive the K/T mass extinction event.

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