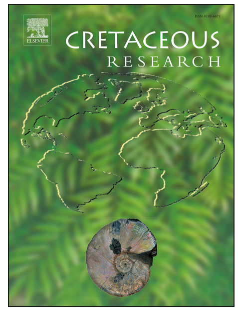

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On the taxonomic composition and phylogenetic affinities of the recently proposed clade Vegaviidae Agnolín et al., 2017 – neornithine birds from the Upper Cretaceous of the Southern Hemisphere

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Abstract

Polarornis and *Vegavis* from the Upper Cretaceous of Antarctica are among the few Mesozoic birds from the Southern Hemisphere. In the original descriptions, they were assigned to two widely disparate avian clades, that is, Gaviiformes and crown group Anseriformes, respectively. In a recent publication, however, specimens referred to both taxa were classified into a new higher-level taxon, Vegaviidae, to which various other late Mesozoic and early Cenozoic avian taxa were also assigned. Here, we detail that classification into Vegaviidae is poorly supported for most of these latter fossils, which is particularly true for *Australornis lovei* and an unnamed phaethontiform fossil from the Waipara Greensand in New Zealand. Plesiomorphic traits of the pterygoid and the mandible clearly show that *Vegavis* is not a representative of crown group Anseriformes, and we furthermore point out that even anseriform or galloanserine affinities of Vegaviidae have not been firmly established.

*Keywords***:** Aves; fossil birds; Mesozoic; phylogeny; taxonomy

Highlights

- The recently proposed taxon Vegaviidae includes two of the best-represented neornithine taxa from the Upper Cretaceous of the Southern Hemisphere, *Vegavis* and *Polarornis*

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- *Australornis* and an unnamed phaethontiform from the lower Paleocene of New Zealand, as well as other fossils from the Upper Cretaceous and lower Cenozoic of the Southern Hemisphere were incorrectly referred to Vegaviidae
- The repeated use of *Vegavis* for the calibration of molecular data notwithstanding, neither anseriform nor galloanserine affinities of Vegaviidae have been firmly established

1. Introduction

Little is known about the earliest evolution of neornithine (crown clade) birds, and most Mesozoic fossils are very fragmentary (Mayr, 2017). In the past decades, however, Upper Cretaceous marine strata of Seymour and Vega Island in Antarctica yielded several partial avian skeletons that were assigned to extant neornithine higher-level taxa.

The report of a putative representative of Gaviiformes (loons) from the Upper Cretaceous López de Bertodano Formation of Seymour Island kept running through the literature for several years (Chatterjee, 1989; Olson, 1992) until this fossil, a partial and poorly preserved skeleton, was formally described as *Polarornis gregorii* by Chatterjee (2002). Further material from the López de Bertodano Formation was assigned to *Polarornis* by Acosta Hospitaleche and Gelfo (2015), who also reported fragmentary limb bones of putative Gaviiformes from Vega Island.

The first description of an avian fossil from Vega Island, however, was given by Noriega and Tambussi (1995), who assigned a partial skeleton to the extinct anseriform taxon Presbyornithidae. The specimen was subsequently described as *Vegavis iaai* by Clarke et al. (2005), and more recently a second, well preserved partial skeleton of this species from Vega Island was reported by Clarke et al. (2016). A phylogenetic analysis performed by Clarke et al. (2005) recovered a clade including *Vegavis*, *Presbyornis*, and Anatidae (ducks, geese, and relatives). This analysis therefore supported a deeply nested position of *Vegavis* within crown group Anseriformes, which are composed of three extant higher-level taxa: the Neotropic Anhimidae (screamers), the Australian Anseranatidae (Magpie Goose), and the globally distributed Anatidae. Presbyornithids are now, however, recovered in a more basal phylogenetic position within Anseriformes (De Pietri et al., 2016; Worthy et al., 2017), and although *Vegavis* was regarded as a "phylogenetically vetted" fossil calibration by Ksepka and Clarke (2015), close affinities to Anatidae had already been questioned (Mayr, 2013;

Feduccia, 2014) and the fossil was deliberately omitted as a calibration point from some studies (Ericson et al., 2006; Prum et al., 2015).

Within extant Anseriformes, the distinctive Anhimidae are the sister taxon of Anatoidea, that is, the clade including the goose- or duck-like Anseranatidae and Anatidae. Externally, Anhimidae exhibit an overall resemblance to Galliformes (landfowl), which are the extant sister group of Anseriformes, with which they form the taxon Galloanseres. Galloanseres, in turn, are one of the two major clades of neognathous birds, the other being Neoaves, which includes most extant avian taxa.

A recent study by Worthy et al. (2017), who analyzed a comprehensive sampling of fossil and extant galloanserine birds under various analytical settings supported a position of *Vegavis* outside crown group Anseriformes but did not conclusively resolve its position within Galloanseres. In some analyses *Vegavis* was recovered as the weakly supported sister taxon of a clade including the large flightless Cenozoic Gastornithidae and Dromornithidae, in others it resulted as an equally weakly supported sister taxon of crown group Anseriformes.

The analysis of Worthy et al. (2017) temporally coincided with a study by Agnolín et al. (2017), which likewise supported a position of Vegaviidae as the sister taxon of crown group Anseriformes. Agnolín et al. (2017) classified *Vegavis* and *Polarornis* into a new clade, Vegaviidae, to which they also assigned various other fossils from the Upper Cretaceous and lower Cenozoic of the Southern Hemisphere. Here we point out that this convenient placement of all described Southern Hemisphere Mesozoic neognaths in a single clade is neither justifiable nor useful. We furthermore address the phylogenetic affinities of Vegaviidae, although it is not the aim of the present study to perform another formal analysis, which – in addition to a large sampling of extant taxa – would also require the inclusion of numerous fossil taxa (see below).

The figured fossils are deposited in the Canterbury Museum, Christchurch, New Zealand (CM) and in the Museo Argentino de Ciencias Naturales "Bernadino Rivadavia", Buenos Aires, Argentina (MACN).

2. Taxonomic composition of Vegaviidae

We concur with Agnolín et al. (2017) that *Vegavis* and *Polarornis* share characteristic derived traits that may support a sister group relationship between these two taxa. The *Vegavis* and *Polarornis* material comes from geographically and stratigraphically close localities and those bones that are known from both taxa are so similar that we consider classification of *Vegavis* and *Polarornis* in the same clade to be reasonably probable.

However, contra Agnolín et al. (2017), there is no overlap of these taxa in humeral features as no humerus is known for *Polarornis*, so that all humeral features these authors listed as diagnostic for Vegaviidae are unknown from *Polarornis*. Characters that can be considered synapomorphies of *Vegavis* and *Polarornis* are restricted to the femur and tibiotarsus and include a strongly craniocaudally curved shaft of the femur and proximally projected cnemial crests of the tibiotarsus. Both, however, are features widely distributed in foot-propelled diving birds including Gaviiformes, Podicipediformes, and some diving Anatidae.

Clarke et al. (2016) detailed that the femur of *Vegavis* differed from that of *Polarornis* by having a deep “capital ligament scar”. This characteristic form of the impressiones obturatoriae is an apparent autapomophy of *Vegavis* not seen in *Polarornis* or any other bird. For *Vegavis*, Clarke et al. (2016) furthermore noted the presence of “a prominent muscular ridge” (= tuberculum musculus gastrocnemialis lateralis) that is absent in *Polarornis*. This tuberculum is elongate and prominent in all foot-propelled diving birds. We have not assessed this feature in *Polarornis gregorii*, but the poorly prepared holotype specimen makes it difficult to assess whether the lack of a prominence relates to poor preparation or the form of the actual insertion scar. In one specimen referred to *Polarornis* by Acosta Hospitaleche and Gelfo (2015: fig 2b), an elongate and prominent tuberculum is clear and obvious. However, while we therefore concur that a sister group relationship between *Vegavis* and *Polarornis* is a reasonable assumption, we disagree concerning the referral of other species and specimens to Vegaviidae by Agnolín et al. (2017), and these fossils will be discussed below.

2.1. Australornis *from the Paleoecene of New Zealand*

One of the putative Paleocene species of Vegaviidae that played a central role in the study of Agnolín et al. (2017) is *Australornis lovei* from the Waipara Greensand in New Zealand. This species is represented by fragmentary wing and pectoral bird girdle bones of a single individual. It was described by Mayr and Scofield (2014), who considered its phylogenetic affinities to be uncertain.

Agnolín et al. (2017) noted that Mayr and Scofield (2014) compared the humerus of *Australornis* with that of *Vegavis*, but they did not mention that these authors listed some distinct differences between both taxa. As detailed by Mayr and Scofield (2014), the crista bicipitalis of *Australornis* is shorter and meets the humerus shaft at a steeper angle, the tuberculum dorsale of *Australornis* is proportionally larger (Fig. 1A, B), and the humerus shaft of *Australornis* is craniocaudally much more flattened than that of *Vegavis* (Fig. 1C, D). The humerus of *Australornis* furthermore differs from that of *Vegavis* in lacking a distinct fossa between the crus fossa dorsalis and the caput. As discussed by Mayr and Scofield (2014), the humerus traits shared by *Vegavis* and *Australornis* are not restricted to these taxa but are also found in, e.g., Phoenicopteriformes and Podicipediformes.

In addition to the above differences in humerus morphology, *Australornis* is distinguished from *Vegavis* in the shape of the omal extremity of the coracoid, with the facies articularis clavicularis being distinctly projected and overhanging the sulcus supracoracoideus in *Australornis* but being essentially coplanar with the sulcus supracoracoideus in *Vegavis* (Fig. 1E-G). The os carpi radiale of *Australornis* likewise differs from that of *Vegavis* in that it forms a more distinct distoventral projection (Fig. 1H, I).

Agnolín et al. (2017) stated that the laterally facing facies articularis humeralis of the coracoid is a feature shared by *Australornis* and *Vegavis*. However, a similarly-oriented facies also occurs in other taxa, such as penguins (Sphenisciformes), and Mayr and Scofield (2014) actually speculated about the possibility that *Australornis* represents a very archaic stem group representative of the Sphenisciformes. In any case, *Australornis* and *Vegavis* appear to have been birds with different locomotory characteristics of the forelimbs, and a classification of *Australornis* into Vegaviidae is not well supported.

2.2. Unnamed phaethontiform from the Paleoecene of New Zealand

Agnolín et al.'s (2017) assignment to Vegaviidae of an unnamed phaethontiform from the Paleocene Waipara Greensand in New Zealand is particularly unexpected to us. The fossil in question consists of the fragmentary proximal portion of a humerus and the proximal end of a carpometacarpus. It was described by Mayr and Scofield (2015), who explicitly differentiated this bird from *Australornis*, noting that the humerus of the phaethontiform fossil is distinguished from that of *Australornis* in the rounded shaft (flattened in *Australornis*), the better-developed crus dorsale fossae, the proportionally much shorter crista deltopectoralis (Fig. 2A, B), and the fact, that – unlike in *Australornis* – the bone walls of the humerus shaft are not thickened. The much shorter crista deltopectoralis also distinguishes the phaethontiform fossil from *Vegavis* (indeed, Agnolín et al., 2017 considered a long crista deltopectoralis diagnostic for Vegaviidae). The extensor process of the carpometacarpus of the New Zealand phaethontiform is much more prominent than that of *Vegavis* (Fig. 2C-E).

Furthermore, it is also relatively shorter than in *Vegavis*, where it is 2.5 times as long as its craniocaudal width and extends distally to overlap the spatium intermetacarpale.

Agnolín et al. (2017: 5) did not discuss the evidence presented by Mayr and Scofield (2015) for an assignment of the New Zealand fossil to Phaethontiformes. Instead, the authors stated that the phaethontiform fossil shares with *Vegavis* "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." All of these features occur, however, in a wide range of avian taxa (e.g., some Anseriformes, Podicipediformes, and Phoenicopteriformes) and are of little phylogenetic significance. Although the fossil from New Zealand differs from extant Phaethontiformes in the large pneumotricipital fossa, such a fossa is present in the early Cenozoic stem group phaethontiform *Lithoptila* and is therefore likely to be plesiomorphic for tropicbirds.

2.3. Neogaeornis *from the Upper Cretaceous of Chile*

Neogaeornis wetzeli is based on a tarsometatarsus from the Upper Cretaceous Quiriquina Formation in Chile. The specimen was first described by Lambrecht (1929), who compared *Neogaeornis* with the non-neornithine hesperornithiform taxon *Enaliornis*. Olson (1992) restudied the holotype and assigned *Neogaeornis* to the Gaviiformes, but Mayr et al. (2013) detailed that the tarsometatarsus of *Neogaeornis* is very different from that of unambiguously identified Gaviiformes from the Paleogene of Europe.

A possible synonymy of *Polarornis* and *Neogaeornis* was indicated by Mayr (2004a). At that time, however, no tarsometatarsus of *Polarornis* had been reported, as the holotype lacks this element, although tarsometatarsi referred to Gaviiformes by Acosta Hospitaleche and Gelfo (2015) probably pertain to *Polarornis* and differ from *Neogaeornis* in that the shaft widens markedly towards its proximal end. The holotype of *Vegavis* includes fragmentary portions of the distal and proximal end of the tarsometatarsus (Noriega and Tambussi, 1995; Clarke et al., 2005). These bone fragments show that *Neogaeornis* differs from *Vegavis* in that the hypotarsus, while very poorly preserved, has only two obvious crests, whereas – as described by Noriega and Tambussi (1995) and according to the reconstruction of the bone by Clarke et al. (2005) – there are four hypotarsal crests in *Vegavis*, delimiting three sulci. *Vegavis* may share with *Neogaeornis* a "posteroproximal thrust of the trochlea for digit II" (Noriega and Tambussi, 1995: 60), described as extending "distally to approximately the base of metatarsal IV" by Clarke et al. (2005: 306), but such a feature characterizes many diving taxa in Anseriformes, Procellariiformes, Gaviiformes, and Podicipediformes.

Agnolín et al. (2017: 4) referred *Neogaeornis* to the Vegaviidae but identified no shared traits between these taxa that would support this referral. Instead, they reported two putatively anseriform traits of *Neogaeornis,* that is, the "presence of a deep concavity above the center of the middle trochlea and dorsomedial to the distal vascular foramen […] and a distally located distal vascular foramen". However, these features have been misinterpreted and do not constitute anseriform apomorphies (we cannot find their mention as anseriform characteristics in Cenizo, 2012, the supporting reference cited by Agnolín et al., 2017). Both traits also occur in distantly related clades, e.g., in some galliforms, anhingids, and phalacrocoracids. That the trochlea metatarsi IV extends distad of the trochlea metatarsi III in *Neogaeornis* is a trait not seen in any anseriform taxon and, similarly, the extremely proximally located and plantarly retracted trochlea metatarsi II is unlike in any anseriform bird; both, however, are podicipediform and gaviiform traits.

2.4. Tarsometatarsus of an unnamed bird from the lower Paleocene of New Zealand

Agnolín et al. (2017) also referred to Vegaviidae a tarsometatarsus of an unnamed bird from lower Paleocene strata near the K/Pg boundary exposed at Waimakariri River in New Zealand, which was described by Ksepka and Cracraft (2008). According to Agnolín et al. (2017: 6), the fossil shares "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." However, neither details of the shaft nor the presence of deep concavity above the center of the middle trochlea has been described in the holotype of *Vegavis*, wherein the shaft of the tarsometatarsus is not preserved, and a similarity to *Neogaeornis* does not corroborate referral of the Paleocene fossil from New Zealand to the Vegaviidae. Regardless, one of the above points is moot as *Neogaeornis* lacks any depression at the base of trochlea metatarsi III (Olson, 1992: fig. 1).

In its overall proportions, the tarsometatarsus reported by Ksepka and Cracraft (2008) indeed resembles the tarsometatarsi assigned to Gaviiformes by Acosta Hospitaleche and Gelfo (2015), which we consider likely to stem from *Polarornis*. Clearly, however, the Paleocene tarsometatarsus from the Waimakariri River is markedly different from that of *Neogaeornis* in its proportions, and whereas the tarsometatarsus of the latter has an equal width over most of its length, it becomes markedly wider towards the proximal end in the Waimakariri bird (compare Ksepka and Cracraft, 2008: fig. 1 with Olson, 1992: fig. 1).

2.5. Eocene fossils referred to Vegaviidae by Agnolín et al. (2017)

A coracoid of a putative gaviiform bird from the Eocene of Seymour Island, which was reported by Acosta Hospitaleche and Gelfo (2015), was also compared with Vegaviidae by Agnolín et al. (2017: 6). As noted by Mayr and Goedert (2017), the specimen is more likely to be from a procellariiform bird (compare Acosta Hospitaleche and Gelfo, 2015: fig. 3A with Mayr and Smith, 2012: fig. 1J, K). The broad shaft of the Antarctic coracoid, which is aligned at a wide angle to the sternal facet, and the shape of the facies articularis humeralis, which is aligned at a distinct angle to the shaft axis, differ markedly from the coracoid of *Vegavis*. In the latter, the shaft is at right angles to the sternal facet, the transverse shaft-width is relatively narrow, and the planar surface of the facies articularis humeralis is roughly parallel to the shaft axis. We consider it probable that the coracoid belongs to one of the procellariiform species from the Eocene of Seymour Island described by Acosta Hospitaleche and Gelfo (2016). The same is possibly true for tibiotarsi from the Eocene of Seymour Island that were described by Acosta Hospitaleche and Gelfo (2015) and that were also likened with Vegaviidae by Agnolín et al. (2017: 6).

3. Phylogenetic affinities of Vegaviidae

So far, either gaviiform or galloanserine affinities have been proposed for members of Vegaviidae, that is, *Polarornis* and *Vegavis*. Gaviiform affinities were suggested for *Polarornis* and are essentially based on derived features of the hindlimbs (Chatterjee, 2002; Acosta Hospitaleche and Gelfo, 2015). That great caution has to be exercised in the interpretation of similarities in the hind limb bones of foot-propelled diving birds is exemplified by the fact that Gaviiformes and Podicipediformes formed a clade in the analysis of Acosta Hospitaleche and Gelfo (2015) – a result sharply contrasting with all analyses based on molecular data, which strongly support a clade including Podicipediformes and Phoenicopteriformes (e.g., Ericson et al., 2006; Prum et al., 2015; see also Mayr, 2004b). Acosta Hospitaleche and Gelfo (2015) only compared in detail the fossils they described with Gaviiformes. The differences they later raised to distinguish loons from other taxa are not assessable in most of the fragmentary fossils described, such as key features of the hypotarsus and the trochleae, and so are irrelevant to the referral of the fossil specimens to gaviiforms. Moreover, detailed comparisons still have to be performed between *Polarornis* and early Cenozoic stem group representatives of the Gaviiformes, such as *Colymbiculus* or *Colymboides*, which markedly differ from extant loons in skeletal morphology (Mayr, 2017).

Analyses that resulted in galloanserine affinities of Vegaviidae found these birds to be either within crown group Anseriformes (Clarke et al., 2005), or as the sister taxon of Anseriformes (Agnolín et al., 2017; Worthy et al., 2017 [in some of the analyses, with weak support]). The initial referral of *Vegavis* to the extinct anseriform taxon Presbyornithidae by Noriega and Tambussi (1995) was based on rather unspecific characters that occur in a number of only distantly related avian taxa. The main synapomorphy of *Vegavis* and Anatidae identified by Clarke et al. (2005) is a derived morphology of the hypotarsus, which in *Vegavis* and Anatidae exhibits three sulci for the pedal tendons. This hypotarsus morphology, especially the presence of a separate sulcus for the tendon of musculus flexor perforans digiti 2, distinguishes Anatidae and Anseranatidae from Anhimidae (Mayr, 2016), but a similar hypotarsus morphology to that of the Anatidae occurs in various only distantly avian taxa, including stem group Gaviiformes (Mayr et al., 2013: fig. 1E, I), stem group Phoenicopteriformes (Mayr, 2014: fig. 5H), and many Charadriiformes (Mayr, 2011a: fig. 6). Moreover, stem group representatives of Anatidae have a more plesiomorphic, Anhimidae-like hypotarsus shape, which lacks a sulcus for the tendon of sulcus flexor perforans digiti 2 (Mayr and Smith, 2017).

Most derived postcranial characteristics of the Anseriformes have a wider distribution within neornithine birds and osteological apomorphies of the superordinate clade Galloanseres likewise mainly pertain to the skull (e.g., Livezey and Zusi, 2007). Extant Galloanseres exhibit a derived morphology of the basipterygoid articulation, in which the pterygoid exhibits a large and ovate articulation facet for a sessile basipterygoid process (e.g., Mayr and Clarke, 2003). In addition, galloanserine birds are characterized by an apomorphic structure of the articulation between the quadrate and the mandible, with the quadrate having only two mandibular condyles (Weber and Hesse, 1995; Ericson, 1997), and the mandible of galloanserine birds furthermore bears very long, blade-like retroarticular processes.

The anatomical information available to Clarke et al. (2005) was limited to the poorly preserved *Vegavis iaai* holotype, which does not allow an assessment of skull features. Clarke et al. (2016) reported a new specimen of *Vegavis* (MACN-PV 19.748), in which the caudal portion of the mandible and the pterygoid are preserved (Fig. 3A, B, I). Clarke et al. (2016: Supplementary Material) noted that the pterygoid shows “a large, projected basipterygoid articulation, a plesiomorphic condition not present in Neoaves. In Neoaves these processes are absent or minute and vestigial”. However, this statement is erroneous and a basipterygoid process similar to that of Vegaviidae occurs in several only distantly related neoavian taxa, such as Charadriiformes (Fig. 3F), Strigiformes (Fig. 3G), and Columbiformes (Fig. 3H). Overall, the pterygoid of *Vegavis* actually shows a closer resemblance to that of *Philomachus pugnax* (Charadriiformes; Fig. 3F) than to the pterygoid of any galloanserine bird.

If compared with extant Galloanseres, the pterygoid of *Vegavis* is most similar to the pterygoid of the Anhimidae (Fig. 3C), in which the articulation facet of the basipterygoid process is less rostrally situated and has a less ovate outline than in Anseranatidae (Fig. 3D) and Anatidae (Fig. 3E). The basipterygoid articulation facet of *Vegavis* is located in the rostral half of the bone, as in most Galloanseres, thereby differing from non galloanserine taxa, where it is at mid-length or more caudal (Fig. 3). The facet, while robust, is however proportionally shorter than in all extant Anseriformes, in which it measures more than one third of the entire length of the pterygoid, whereas the facet reaches only one fourth of the pterygoid length in *Vegavis*, thereby supporting the position of *Vegavis* outside of Anseriformes (Worthy et al., 2017; Agnolín et al., 2017).

Chatterjee (2002) reported a partial quadrate in the *Polarornis gregorii* holotype, but identification of this bone was questioned by Clarke et al. (2016). Whereas Chatterjee (2015: 156) stated that the mandible of the then still undescribed new *Vegavis* specimen (MACN-PV 19.748) exhibits cotylae “for the articulation with the three articular facets of the quadrate”, Clarke et al. (2016: Supplementary Material) noted that the articulation was bicondylar, stating “[n]o distinct caudal cotyla is present. This conformation is similar to that of Anseriformes”. Taken alone, however, the presence of only two mandibular condyles of the quadrate and of two corresponding mandibular cotylae, respectively, does not represent an unambiguous apomorphy of Galloanseres, because a caudal condyle is also absent in the non-neornithine *Ichthyornis* (Clarke, 2004) and in a few neoavian taxa, that is, the gruiform taxon *Aptornis* (Weber and Hesse, 1995) and Columbidae. Clarke et al. (2016: Supplementary Material) further wrote that while “the articular/retroarticular region exhibits breakage (i.e., nearly the medial one-half of this region is missing), a retroarticular process appears to have been absent or short (…). The morphology of the articular and retroarticular region are both similar to pelagornithids, the soaring pseudotoothed birds that have also been identified as basal Anseriformes”. The narrow beak of *Polarornis* (Chatterjee, 2002) shows that, if this taxon is the sister taxon of *Vegavis*, then Vegaviidae had a bill dissimilar to all galliforms and anseriforms.

Agnolín et al. (2017: 4) discussed several characters that were identified as anseriform or galloanserine apomorphies by previous authors. However, as just detailed, the "well-developed and transversely compressed retroarticular process" cannot be confirmed for *Vegavis* and actually appears to be absent: at the very least breakage obliterates its form. Further features of the caudal end of the mandible are difficult to evaluate in the published photographs and the X-ray computed tomographic model shown by Clarke et al. (2017) (i.e., "an extended fossa for the attachment of M. adductor mandibulae externus", a "pronounced coronoid inflection", and "mandibular cotylae anteroposteriorly elongate, separated by a low longitudinal crest"). Most other characters discussed by Agnolín et al. (2017: 4f.) are not specific for Anseriformes or even Galloanseres and have a wider distribution among Neoaves, which is true for a "lacrimal lacking contact with the jugal bar", "a well-developed craniofacial flexor zone", and further characters listed by the authors. Of the 14 characters that were optimized as synapomorphies of Anseriformes and Vegaviidae in the analysis of Agnolín et al. (2017: ESM), at least three are not observable in the fossils (chs. 40, 62, 185). One character pertains to the quadrate (ch. 58), whose identification in *Polarornis* is questionable (Clarke et al., 2016). Another character, which concerns a fossa on the dorsal surface of the pterygoid, has a state that is not defined in the character description (ch. 42-2). Three of the remaining nine characters refer to the humerus and are found in a number of unrelated neornithine higher-level taxa (chs. 125, 134, 138), and this is also true for six further characters that refer to features of the axis, pelvis, and hindlimb bones (chs. 75, 179, 202, 204, 226, 257).

We conclude that the affinities of Vegaviidae remain poorly constrained. The plesiomorphic morphology of the pterygoid of *Vegavis* and the bill shape of *Polarornis* support a position outside the clade formed by Anseranatidae and Anatidae, and the absence of a greatly elongated retroarticular process indicates a position outside crown group Anseriformes. While we therefore support a position for *Vegavis* outside of Anseriformes, as found by Agnolín et al. (2017) and Worthy et al. (2017), we reiterate that morphological evidence for Galloanseres is sparse as noted by Ericson (1997). The strongest and most often quoted apomorphy, a bicondylar quadrate-mandible articulation is found in the neoavian taxon Columbiformes and in the ornithuromorph non-neornithine *Ichthyornis*, raising issues of its character polarity (i.e., whether it is plesiomorphic for Neornithes or apomorphic for Galloanseres). Similarly, the nature of the basipterygoid facet on the pterygoid needs further investigation, as similar structures occur among Charadriiformes and Columbiformes (actually, Ericson, 1997: 441

stated that the "basipterygoid articulation of the Anhimidae is in fact almost identical with that in, for example, the Scolopacidae").

4. Conclusions

As we have detailed above, there exists no strong evidence for an assignment of fossil taxa other than *Vegavis* and *Polarornis* to Vegaviidae, and some Paleocene specimens undoubtedly were erroneously assigned to the clade by Agnolín et al. (2017). Contrary to the conclusion of the latter authors, current data therefore do not support a survival of Vegaviidae across the K/Pg boundary and into the Cenozoic. Likewise, Agnolín et al.'s (2017: 7) assumption of a flightlessness of *Polarornis* is essentially speculative, because wing elements of this taxon are unknown. The well-developed wing and pectoral girdle bones of *Vegavis* argues against a loss of flight capabilities of this taxon even though it had similar diving capabilities to *Polarornis*, as shown by the morphology of its femora and tibiotarsi.

We furthermore note that attempts to squeeze all late Mesozoic and early Cenozoic birds from the Southern Hemisphere into a single clade contrasts with the fact that detailed comparisons between members of Vegaviidae and Late Cretaceous bird fossils from the Northern Hemisphere still have to be carried out. A femur from the North American Lance Formation that was referred to Phalacrocoracidae by Hope (2002: fig. 15.9A), for example, shows an overall resemblance to the femora of *Vegavis* and *Polarornis*, and the distal tarsometatarsus that formed the holotype of the alleged gaviiform *Lonchodytes estesi*, which was described by Brodkorb (1963), likewise needs to be compared with the distal tarsometatarsus preserved in the holotype of *Vegavis iaai*.

The new (second) specimen of *Vegavis* (Clarke et al., 2016) provides conclusive evidence that Vegaviidae are not closely related to the Anatidae or Anatoidea. However, the exact affinities of these birds remain poorly resolved and all current analyses including *Vegavis* and/or *Polarornis* have their limitations. Only the study of Agnolín et al. (2017) included both *Polarornis* and *Vegavis*, but although this study and the analyses of Worthy et al. (2017) sampled a large number of extant and fossil galloanserines, Gaviiformes or any other foot-propelled extant neornithine birds were not included. Representatives of both Galloanseres and foot-propelled diving Neoaves were considered in an analysis of Clarke et al. (2005), but this was based on the data set of Mayr and Clarke (2003), which has only extant taxa in the ingroup sampling; the anatomical data from the new *Vegavis* fossil (MACN-PV 19.748) and from *Polarornis* were furthermore not available to Clarke et al. (2005).

Indeed, several critical fossil taxa were not included in any of the previous studies. Such is, for example, true for the early Eocene *Anatalavis oxfordi*, which is the earliest well-represented modern-type anseriform bird (Olson, 1999; Mayr, 2017). Even more importantly, none of the existing analyses included Pelagornithidae in the ingroup sample. These marine soaring birds exhibit the same key features that are used to support galloanserine affinities for vegaviids (Bourdon, 2005, 2011; Mayr, 2011b), and the mandibular articulation of *Vegavis* was likened to that of Pelagornithidae and Anatidae by Clarke et al. (2016: Supplementary information).

It is very difficult, if not altogether impossible, to support some of the novel phylogenetic findings of sequence-based analyses with morphological apomorphies. If such difficulties already arise in the study of extant birds, it would be surprising if an assignment of the earliest neornithine birds – for which the available anatomical data is much more limited – was straightforward. Vegaviidae may be a stem lineage representative of Anseriformes, but current data do not convincingly refuse alternative placements within Galloanseres or even a position outside the latter clade.

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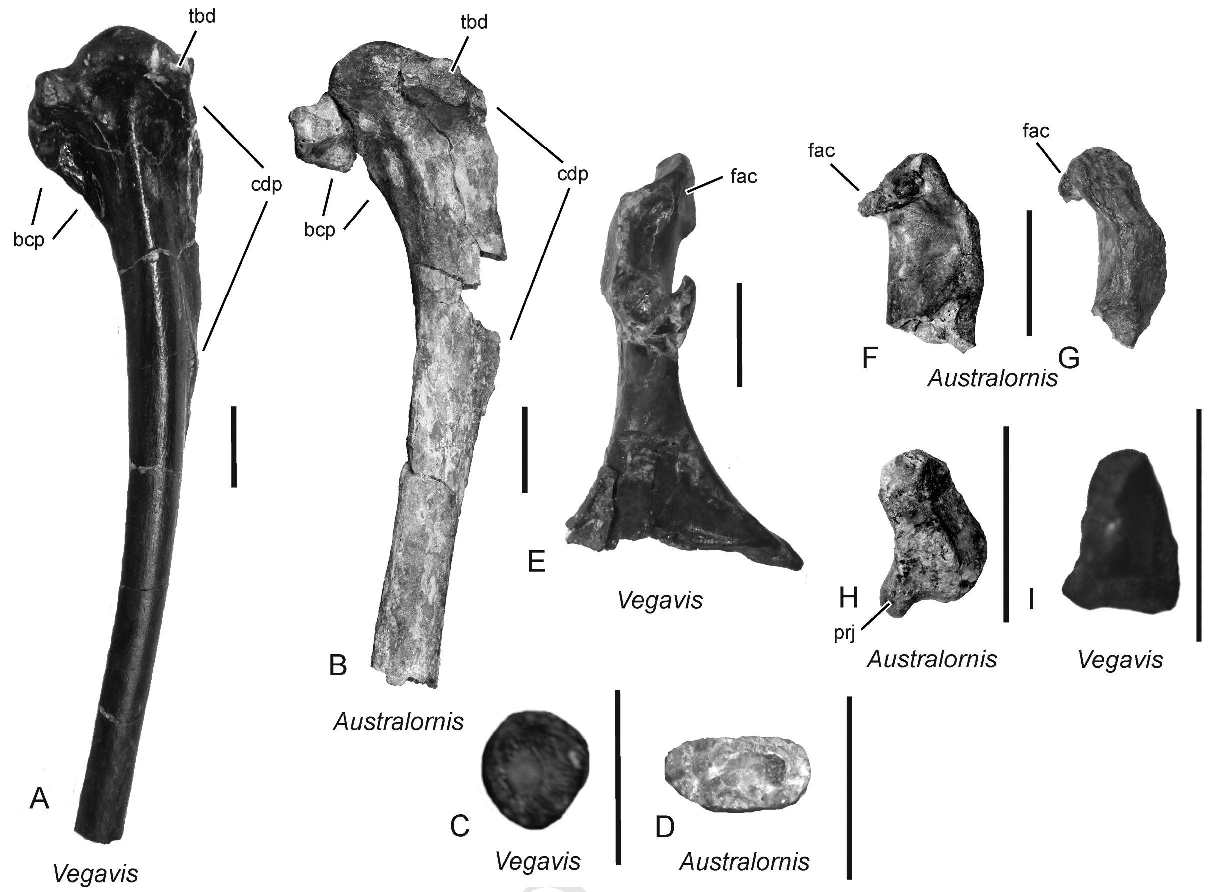
Figure captions

Fig. 1. A-D, Humerus, **E-G**, coracoid, and **H**, **I**, os carpi ulnare of *Vegavis iaai* from the Upper Cretaceous of Vega Island, Antarctica (MACN-PV 19.748) and *Australornis lovei* from the Paleocene Waipara Greensand in New Zealand (holotype, CM 2010.108.2). **A**, **B**, Right humerus in caudal view. **C**, **D**, broken humerus shaft in distal view to show the cross section of the bone. **E**, Left coracoid in dorsal view. **F**, **G**, Extremitas omalis of right coracoid in **F**, dorsomedial and **G**, dorsal view. **H**, **I**, Right os carpi radiale (note, that, for *Australornis*, the bone was erroneously considered to be from the left side by Mayr and Scofield, 2014); Abbreviations: bcp, crista bicipitalis; cdp, crista deltopectoralis; fac, facies articularis clavicularis; prj, distoventral projection; tbd, tuberculum dorsale. Scale bars equal 10 mm.

Fig. 2. A, **B**, Humerus and **C-E**, carpometacarpus of *Vegavis iaai* from the Upper Cretaceous of Vega Island, Antarctica (MACN-PV 19.748) and the unnamed phaethontiform bird from the Waipara Greensand (CM 2010.108.4). **A**, **B**, Humerus in caudal view (specimen in **A** mirrored to ease comparisons). **C**, **D**, Proximal end of left carpometacarpus in **C**, ventral and **D**, dorsal view. **E**, Right carpometacarpus in dorsal view. The dotted lines in **A** and **B** indicate reconstructed bone portions; the arrows denote the distal terminus of the crista deltopectoralis. Abbreviations: ext, processus extensorius. Scale bars equal 10 mm.

Fig. 3. A, **B**, Left pterygoid of *Vegavis iaai* from the Upper Cretaceous of Vega Island, Antarctica (MACN-PV 19.748; in the lower picture the surrounding matrix was digitally removed). **C-H**, Left pterygoids of **C**, *Chauna torquata* (Anhimidae), **D**, *Anseranas semipalmata* (Anseranatidae), **E**, *Bucephala clangula* (Anatidae), **F**, *Philomachus pugnax* (Charadriiformes), **G**, *Tyto alba* (Tytonidae), and **H**, *Caloenas nicobarica* (Columbiformes). **I**, **J**, Caudal end of right mandible (medial view) of **I**, *V. iaai* (MACN-PV 19.748; surrounding matrix digitally brightened) and **J**, *C. torquata*. Abbreviations: fab, basipterygoid articulation facet (facies articularis basipterygoidea); ret, retroarticular process. Scale bars equal 5 mm.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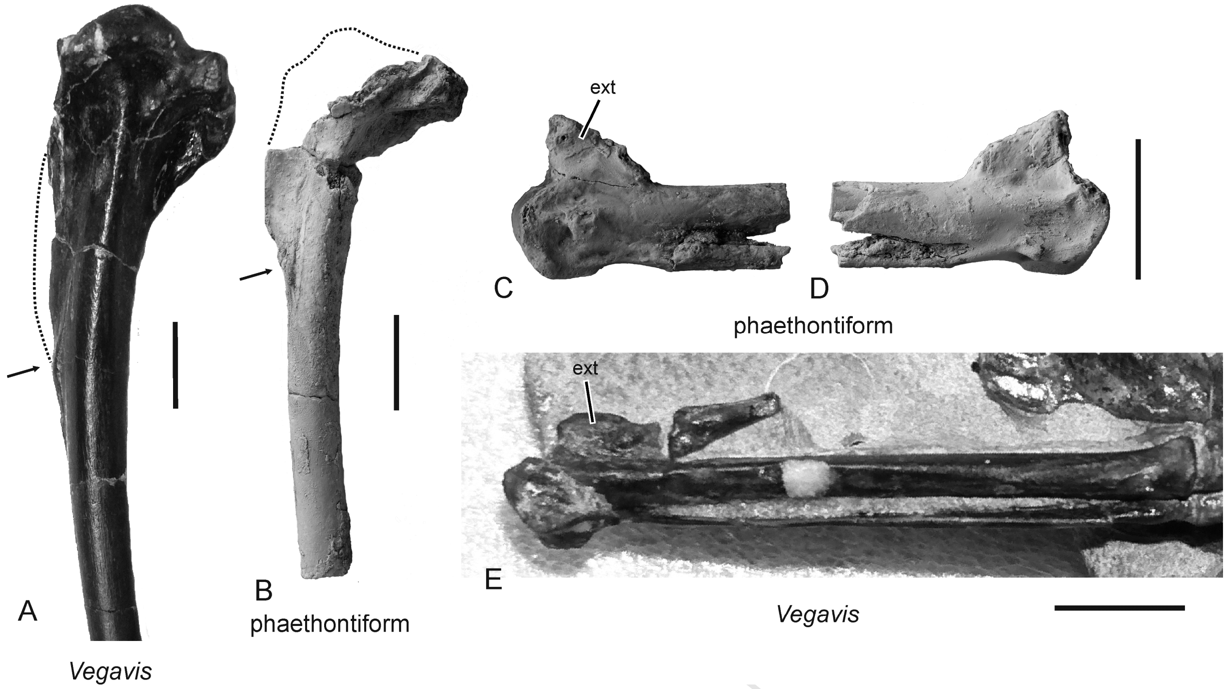
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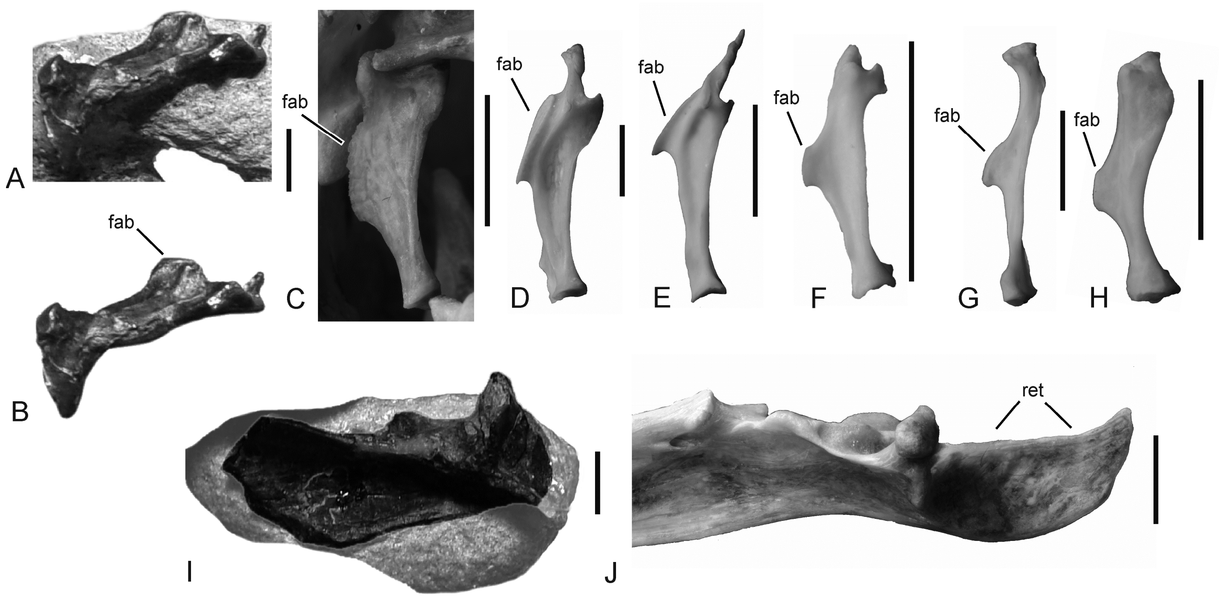

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