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Short communication

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

Gerald Mayr [a, *], Vanesa L. De Pietri [b], R. Paul Scofield [b], Trevor H. Worthy [c]

[a] Senckenberg Research Institute and Natural History Museum Frankfurt, Ornithological Section, Senckenberganlage 25, D-60325 Frankfurt am Main, Germany
[b] Canterbury Museum, Rolleston Avenue, Christchurch 8013, New Zealand
[c] Biological Sciences, College of Science and Engineering, Flinders University, GPO 2100, Adelaide 5001, Australia

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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.

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 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).

* Corresponding author.
E-mail address: Gerald.Mayr@senckenberg.de (G. Mayr).

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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), in which a comprehensive sampling of fossil and extant galloanserine birds was analyzed 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 autapomorphy 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 preservation 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 humeral 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