

Dispatches

Paleontology: ducks all the way down?

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A new fossil from the Cretaceous of Antarctica reveals the appearance of the skull of the enigmatic bird *Vegavis*. Unraveling the broader implications of this find for our understanding of early bird evolution will inspire further comparative work.

Today, ducks, geese, and swans comprise one of the most distinctive groups of living birds. Collectively known as Anseriformes (or colloquially as waterfowl), even the most novice birdwatchers will know a duck when they see one. What might come as a surprise to those unfamiliar with bird systematics is that waterfowl occupy a pivotal branch on the avian tree of life: along with their terrestrial cousins, the Galliformes (landfowl; that is, chickens and kin), waterfowl comprise one of the three very deepest branches within avian phylogeny. The branch leading to present-day waterfowl and landfowl is so deep, in fact, that it is one of the very few lineages that virtually all experts agree extends back into the Cretaceous Period, during the latter stages of the Age of Dinosaurs. However, direct fossil evidence from the Cretaceous of the early forerunners of today's ducks and chickens is scanty at best, meaning that any new find bearing on the origin of this iconic group of living birds would rank among the most sought-after discoveries for any bird paleontologist. An exciting new study by Torres and colleagues ¹ may present one such paleontological prize.

The new fossil is attributed to the species *Vegavis iaai*, which was first described in 1995 ² and named in 2005 ³. In addition to having a specific epithet entirely lacking in consonants, *Vegavis* is known for being, by far, the most completely known candidate for a modern bird from the Cretaceous Period, with multiple partial skeletons reported to date ^{2,4-6}. But if *Vegavis* has been known for thirty years, what makes the new fossil discovery so notable? While much of the anatomy of *Vegavis* is well known (even its syrinx—the avian vocal organ—has been described! ⁵), it is fair to say that two major questions have hung over *Vegavis* since its initial description. The first regards its appearance: even though several specimens of *Vegavis* have previously been unearthed, these have been composed of only postcranial (non-skull) remains, apart from the backend of one jaw and one bone from the roof of the mouth. The second regards its phylogenetic position: although the 2005 paper that named *Vegavis* strongly inferred its position to be within the waterfowl clade ³, several subsequent studies have called its affinities with waterfowl, and even its phylogenetic position within the modern bird radiation, into doubt ^{7,8}.

The new fossil (almost) undoubtedly resolves the first of the major questions surrounding *Vegavis*. The specimen, an isolated fossil skull assigned to *Vegavis*, is preserved within a concretion from the ~68.7-million-year-old Lopez de Bertodano Formation of Vega Island, off the Antarctic Peninsula. The skull is, by and large, extraordinary—it is largely complete and greatly clarifies our understanding of what the

head of *Vegavis* looked like. The only potential factor limiting its impact on our understanding of *Vegavis* regards its very assignment to *Vegavis* itself: since previous specimens lacked skulls and the new specimen lacks a body, there is limited overlap of the new material with previously known specimens. The only portion of the new material overlapping with a previously known specimen is the back of the lower jaw, and that match is not perfectly spot-on. Nonetheless, the authors make a convincing case that the balance of probabilities favours assignment of the new skull to *Vegavis*. So, with any uncertainties regarding its referral notwithstanding, we can, at long last, assess the nuances of cranial form in this important fossil bird.

And what an interesting skull it is! Unlike living anseriforms, the skull exhibits an elongated, pointed beak—not dissimilar to those of living pursuit-diving birds such as loons or large grebes. Like these living birds, the skull also exhibits deep embayments for powerful jaw musculature—adding to previous evidence from postcranial morphology that *Vegavis* was a foot-propelled diving bird that fed on aquatic prey. Notably, the skull is so well preserved that the authors were able to extract a largely complete model of its brain—something very unusual for birds from the Mesozoic Era⁹⁻¹¹—showing that it resembled the brains of many living birds in the discernible aspects of both its volume and form. Thus, the new specimen provides more than what even the most optimistic students of avian paleontology could have hoped for: a clear picture of both the skull *and* brain of *Vegavis*.

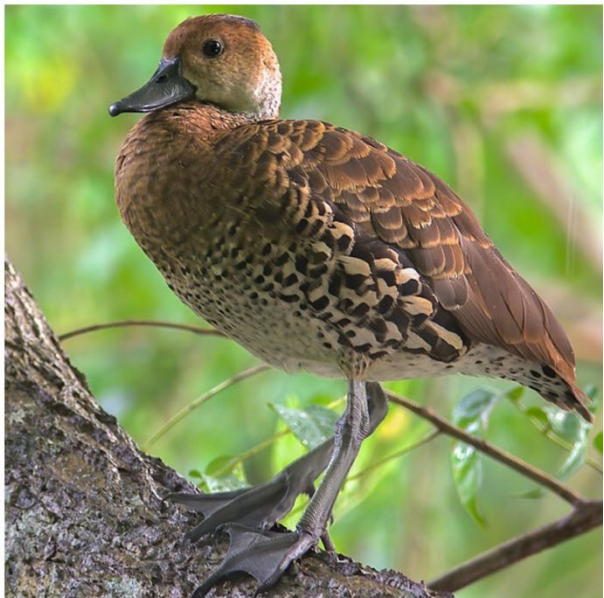
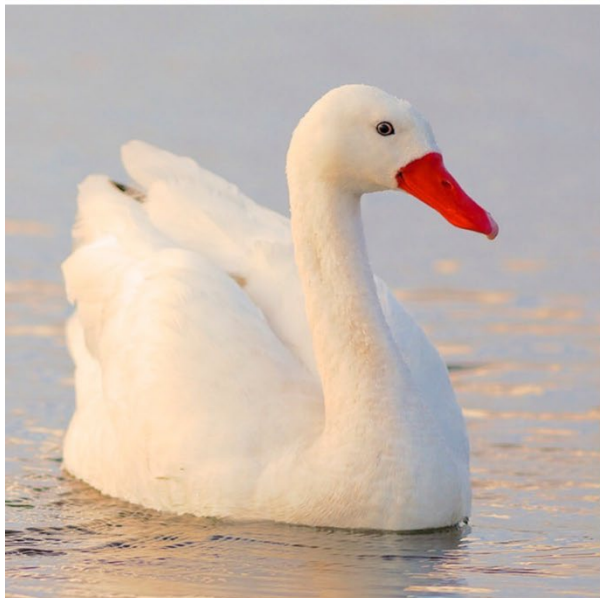
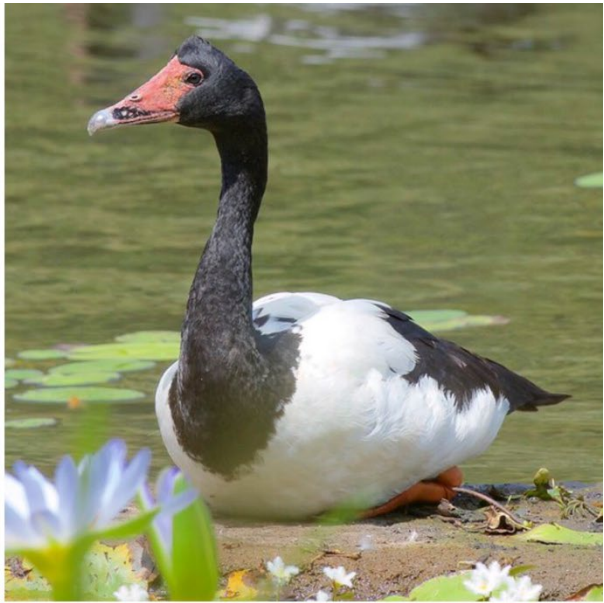
While the new skull greatly clarifies our understanding of its appearance, determining whether the same can be said for the phylogenetic position of *Vegavis*—the second major question surrounding this important fossil bird—is more challenging. As with all previous studies describing significant novel material from *Vegavis*^{2,3,5}, Torres et al. strongly infer *Vegavis* as a member of crown group Anseriformes. So, what makes this controversial? To begin with, some features of the new skull diverge markedly from what would be expected in an early relative of ducks. For example, the mandible lacks elongate projections from its back end, the ‘retroarticular processes’, that are unambiguous diagnostic features of the jaws of all known living anseriforms and galliforms¹². The absence of these structures in *Vegavis* would imply that it, perhaps uniquely in the evolutionary history of this clade, lost these diagnostic structures. The lack of a postorbital process on the skull of *Vegavis*, and the presence of its dagger-like bill, are also surprising features for an early anseriform. Unlike *Vegavis*, other early anseriforms inferred to be close relatives of *Vegavis* by Torres et al., like *Conflicto* and *Presbyornis*, exhibit characteristically wide, duck-like bills.

Of course, the authors also note several features of the skull that *do* match the condition in anseriforms, but some of these may reveal little about the phylogenetic affinities of *Vegavis*. For instance, the authors tout the articulation between the quadrate bone and mandible of *Vegavis* (an articulation via two points of contact rather than the typical three) as probable evidence of its anseriform affinities, as this feature is present in extant galliforms and anseriforms, and absent in most other groups of living birds^{13,14}. However, toothed fossil birds outside the living bird radiation also have two points of contact between the mandible and quadrate, implying that the last common ancestor of all modern birds likely exhibited the same condition^{7,8,15,16}. Thus, the condition shared by living anseriforms and *Vegavis* may reflect retention of this ancestral avian feature, rather than representing a shared, derived characteristic uniting *Vegavis* with ducks.

If the phylogenetic affinities of *Vegavis* are less than clear-cut, what can explain the recurring propensity for *Vegavis* to nest within the waterfowl group in phylogenetic analyses like some kind of Cretaceous ugly duckling? Here, it is important to note that *Vegavis* is not alone. Numerous enigmatic fossils from early stages of the modern bird radiation have traditionally been inferred as relatives of anseriforms, including the bizarre pseudotoothed birds and the giant gastornithids, despite these groups exhibiting few, if any, features unambiguously tying them to waterfowl¹⁷. Rather than providing evidence of close evolutionary kinship, the tendency for these enigmatic early bird fossils to resolve near anseriforms may instead suggest that living waterfowl retain a greater number of skeletal features present in the last common ancestor of living birds than do other major bird groups. The process of distinguishing between ancestral and derived character states lies at the heart of the phylogenetic method¹⁸, and recent evidence suggests that the field of avian paleontology may need to reassess assumptions regarding the suite of features characterizing the last common ancestor of all living birds^{10,17}. Similar realizations have challenged longstanding hypotheses surrounding the distribution of phenotypic features near the origins of other major vertebrate clades. Among lizards, for example, the clade Iguania also appears to retain a disproportionate number of plesiomorphic features relative to other major squamate clades, complicating phylogenetic inference¹⁹.

A famous example of abductive reasoning is the ‘duck test’, usually expressed as some variant of the adage: ‘if it looks like a duck and sounds like a duck, it probably *is* a duck’. While useful in some contexts, the duck test’s originator may have inadvertently oversimplified the challenge of distinguishing between apomorphic and plesiomorphic character states in phylogenetic datasets. Recent work is beginning to reevaluate the distribution and polarity of avian morphological character states near the origin of the modern bird radiation²⁰. Until the challenge of disentangling character state optimisation at the origin of crown birds has been more thoroughly explored, though, it will be challenging to confidently determine the phylogenetic affinities of *Vegavis*, and those of several other early fossil birds. Whether practitioners of fossil bird systematics truly have their ducks in a row, or have mistakenly aligned birds of a different feather, thus remains to be seen.

Fig. 1: Living representatives of the major subdivisions of Anseriformes. Clockwise from upper left: Southern Screamer (*Chauna torquata*), representing Anhimidae, the sister group to all other anseriforms. Magpie-Goose (*Anseranas semipalmata*), the monotypic sister taxon to all other ducks, geese, and swans. West Indian Whistling-Duck (*Dendrocygna arborea*), sister taxon to the typical ducks, geese and swans. Coscoroba Swan (*Coscoroba coscoroba*), representing the typical ducks, geese and swans. Photos by the author. Torres et al. [1] estimate a position for *Vegavis* within Anseriformes, nearer to ducks, geese and swans than to screamers.



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