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Definitive fossil evidence for the extant avian radiation in the Cretaceous

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Long-standing controversy[1–9] surrounds the question of whether living bird lineages emerged after non-avian dinosaur extinction at the Cretaceous/Tertiary (K/T) boundary[1,6] or whether these lineages coexisted with other dinosaurs and passed through this mass extinction event[2–5,7–9]. Inferences from biogeography[4,8] and molecular sequence data[2,3,5,9] (but see ref. 10) project major avian lineages deep into the Cretaceous period, implying their 'mass survival'[3] at the K/T boundary. By contrast, it has been argued that the fossil record refutes this hypothesis, placing a 'big bang' of avian radiation only after the end of the Cretaceous[1,6]. However, other fossil data—fragmentary bones referred to extant bird lineages[11–13]—have been considered inconclusive[1,6,14]. These data have never been subjected to phylogenetic analysis. Here we identify a rare, partial skeleton from the Maastrichtian of Antarctica[15] as the first Cretaceous fossil definitively placed within the extant bird radiation. Several phylogenetic analyses supported by independent histological data indicate that a new species, *Vegavis iaai*, is a part of Anseriformes (waterfowl) and is most closely related to Anatidae, which includes true ducks. A minimum of five divergences within Aves before the K/T boundary are inferred from the placement of *Vegavis*; at least duck, chicken and ratite bird relatives were coextant with non-avian dinosaurs.

The *Vegavis iaai* holotype specimen from Vega Island, western Antarctica, was discovered in 1992 and received rudimentary preparation that, in fact, degraded delicate bones that were originally exposed. It was reported[15] as a possible 'transitional' form close to extant lineages[15]. For a decade since, the specimen's exact systematic position and possible crown clade avian status have been debated[6,14,16,17]. Significant new preparation, X-ray computed tomography (CT)[18] and recovery of latex peels of the specimen before its original preparation reveal numerous, previously unknown bones and anatomical details. These new data, when included serially in three of the largest cladistic data sets considering Avialae[19], Aves[20] and Anseriformes[16], establish hierarchically nested character support for the placement of *Vegavis*.

Aves Linnaeus, 1758 (*sensu* Gauthier, 1986)
Neognathae Pycraft, 1900
Anseriformes Wagler, 1831
Anatoidea Leach, 1820 (*sensu* Livezey, 1997)
Vegavis iaai sp. nov.

Etymology. 'Vegavis' is for the holotype specimen's Vega Island provenance; 'avis' is from the Latin for bird; and 'iaai' is for the Instituto Antártico Argentino (IAA) expedition that collected the specimen.

Holotype. MLP 93-I-3-1 (Museo de La Plata, Argentina), a disarticulated partial postcranial skeleton preserved in two halves of a concretion (Figs 1 and 2; see Supplementary Information for additional CT scan images, photographs, character data and measurements). Newly uncovered elements include five thoracic vertebrae, two cervical vertebrae, left scapula, right ulna, all pelvic bones, right and left fibulae and left? tarsometatarsal shaft. Previously reported elements[15] include the complete right humerus, proximal left humerus, right coracoid, femora, left tibiotarsus, distal right radius, sacrum, distal left (right of ref. 15) tarsometatarsus, proximal right (left of ref. 15) tarsometatarsus and more than six dorsal ribs.

Locality. Cape Lamb, Vega Island, locality VEG9303 of the 1992/1993 IAA expedition[15]. Deposits are near-shore marine fine-grain sandstones[21] from the Middle? to Upper Maastrichtian (~66–68 million years ago (Myr)) lithostratigraphic unit K3 of ref. 21 (see Supplementary Information for locality, horizon and dating details).

Diagnosis. *Vegavis* is unique among the surveyed taxa (Fig. 3) in that it has a low ridge on the medial edge of the proximal tibiotarsus that is proposed to be an autapomorphy of the new species (Fig. 2). The additional unique combination of characters from the phylogenetic analyses that differentiate *Vegavis* are given in the Methods.

Description. *Vegavis* has heterocoelous cervical and thoracic vertebrae and 14–15 fused sacral vertebrae (Fig. 1). The apneumatic coracoid is penetrated by a supracoracoideus nerve foramen (Fig. 1). The blade of the scapula is slightly curved and narrow (Fig. 1). Its

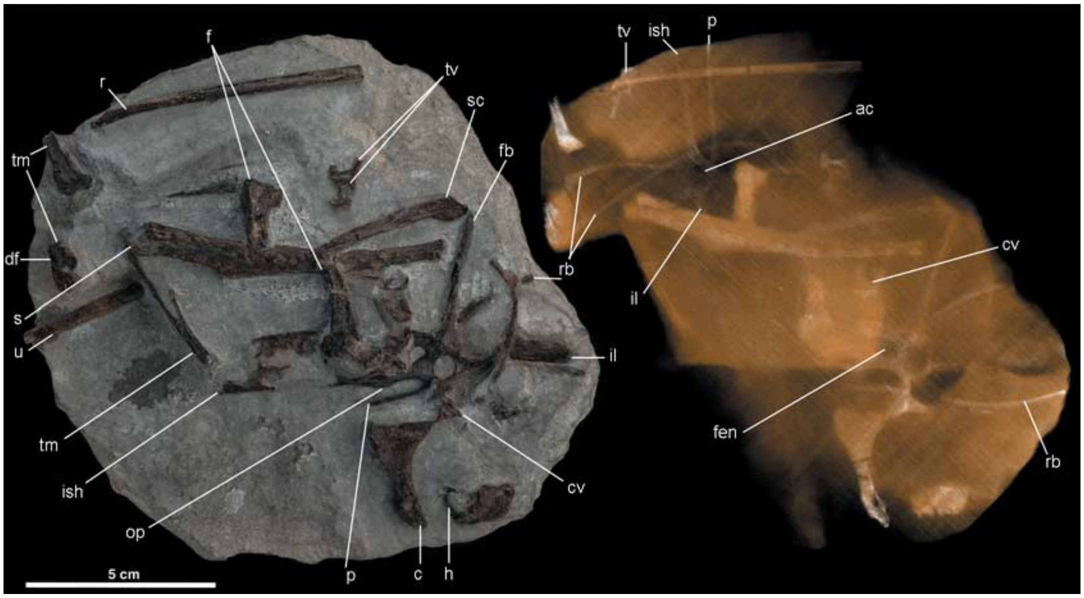

Figure 1 The half of the *Vegavis iaai* concretion that preserves most of MLP 93-I-3-1. Photograph (left) and volume renderings using CT data, highlighting the bone and rendering the matrix semi-transparent to elements preserved within the block (right). ac, acetabulum; c, coracoid; cv, cervical vertebra; df, distal vascular foramen; f, femora; fb, fibula; fen, ilioischiadic fenestra; h, humerus; il, ilium; ish, ischium; op, obturator process; p, pubis; r, radius; rb, rib(s); tm, tarsometatarsus; tv, thoracic vertebrae; s, sacrum; sc, scapula; u, ulna.

coracoid tubercle is well projected and hemispherical. The humerus is slightly longer than the sacrum and about the length of a tibiotarsus (Fig. 2). Its deltopectoral crest is anteriorly deflected, less than shaft width and extends for approximately one-third of the shaft length (Fig. 2). A faint scar is developed in the location of the scapulohumeralis cranialis muscle insertion in Aves[15,22] (Fig. 2). The capital ridge of the humeral shaft is strongly marked and the pneumotricipitalis fossa is shallow. The brachial scar angles obliquely, deepening ventrodistally into a fossa. The dorsodistal radius preserves one narrow ligamental groove.

The pelvic elements are firmly ankylosed to each other but may not have been fused to the sacrum. That the ilioischiadic fenestra was closed posteriorly is inferred from a flat sheet of bone (Fig. 1) preserved in both parts of the concretion. The postacetabular ilium is approximately twice the length of the preacetabular portion. A small pectineal process is present. The obturator foramen is elongate and posteriorly demarcated. The pubis is robust, straight, posteriorly directed and subparallel with the ischium (Fig. 1). The femur has a low trochanteric crest proximally (Fig. 1) and a patellar groove distally (Fig. 2). The proximal tibiotarsus preserves proximal portions of anterior and lateral cnemial crests (Fig. 2). The distal condyles are approximately the same width, and an ossified supratendinal bridge is developed over the extensor groove (Fig. 2). The diameter of the intercondylar groove is approximately one-third of the total distal tibiotarsal width. Metatarsals II–IV are fused throughout their length to enclose the distal vascular foramen (Fig. 1). Metatarsal II extends distally to approximately the base of metatarsal IV. There are four crests bounding three distinct hypotarsal sulci (Fig. 3c, insets). The medial hypotarsal crest is plantarly projected slightly farther than the other approximately equally projected crests.

The morphology of the *Vegavis* hypotarsus, with multiple, similarly proportioned canals, shares its derived structure with Anatidae (true ducks, geese and swans; Fig. 3c, insets). This feature, however, is only one of 20 unambiguously optimized synapomorphies preserved in *Vegavis* that support its placement as part of the interested clades Ornithurae, Aves, Neognathae, Anseriformes and Anatoidea, and finally, in an unresolved trichotomy with

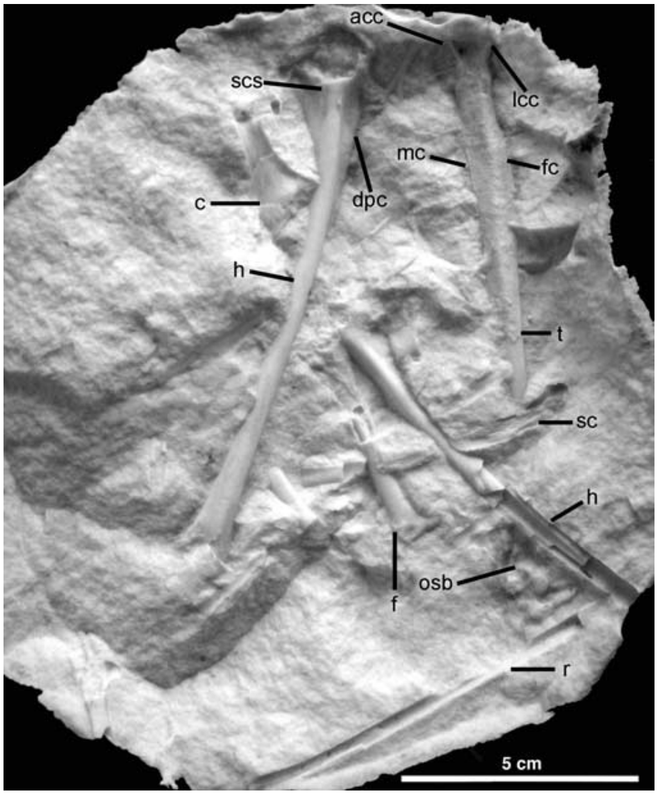

Figure 2 Recovered latex peel of the other half of the *Vegavis iaai* holotype block before original preparation. The coracoid, humerus and tibia were severely damaged when prepared out of this block. acc, anterior cnemial crest; c, coracoid; dpc, deltopectoral crest; f, femur; fc, fibular crest; h, humerus; lcc, lateral cnemial crest; mc, medial crest; osb, ossified supratendinal bridge; r, radius; t, tibiotarsus; sc, scapula; scs, scar of m. scapulohumeralis cranialis.

Presbyornis and Anatidae (Fig. 3). This placement of *Vegavis* implies a minimum of five cladogenetic events within Aves by the Upper Maastrichtian. The anseriform crown clade must be present (including three anseriform lineages with extant descendants) as well as parts of minimally stem-lineage neoavian neognaths, palaeognaths and galliforms.

Histological analysis of the *Vegavis* radius (using polarized microscopy) and examination of the humeral and femoral diaphyses (using dissecting microscopy) revealed most of the cortices to be composed of a highly vascularized (semi-reticular pattern) fibrolamellar matrix that grades into an avascular matrix periosteally[23]. Lines of arrested growth (LAG or growth lines; Fig. 4) are absent in all specimens. Portions of the medullar cavities are lined by lamellar endosteal bone (Fig. 4). These characteristics suggest that the *Vegavis* holotype specimen was a somatically (skeletally) mature adult at the time of death[23]. This suite of features is phylogenetically inconsistent with more common basal Mesozoic birds such as enantiornithines but supports placement of *Vegavis* within Ornithurae, a clade inclusive of extant bird lineages[24,25] (Fig. 3). This conclusion is consistent with the independent phylogenetic results.

The placement of *Vegavis* confirms the origin of Aves and the presence of several basal lineages by the latest Cretaceous. This result is compatible with either limited deep avian divergences by this time and, thus, limited survivorship at the K/T boundary[9,10], or the presence of most major lineages in the Cretaceous[2–5,8] and 'mass survival'[3] at this boundary. It contradicts a proposed early Tertiary crown clade origin[1,6]; basal avian lineages were present with non-avian dinosaurs. Hypotheses implying a causal relationship between the extinction of non-avian dinosaurs and diversification of basal avian lineages[9,26] must address these new data. *Vegavis* is the most complete Cretaceous specimen to be identified as part of the extant avian radiation and the first so identified through cladistic analyses; therefore, it provides the first reliable Cretaceous internal calibration point for 'molecular clock' approaches to dating the emergence of all living birds. It is strikingly close in age to some (for example, 66 Myr[9]) estimates of crown anseriform divergences made using these techniques[9,10]. However, these estimates place most other major avian divergences earlier than or approximately contemporaneous with the Cretaceous[2–5,9], a proposal still unsupported by the fossil record in the Cretaceous. Only the lineage leading to the presently most speciose extant clade of birds, Neoaves, can be inferred present by the Maastrichtian from *Vegavis*' placement.

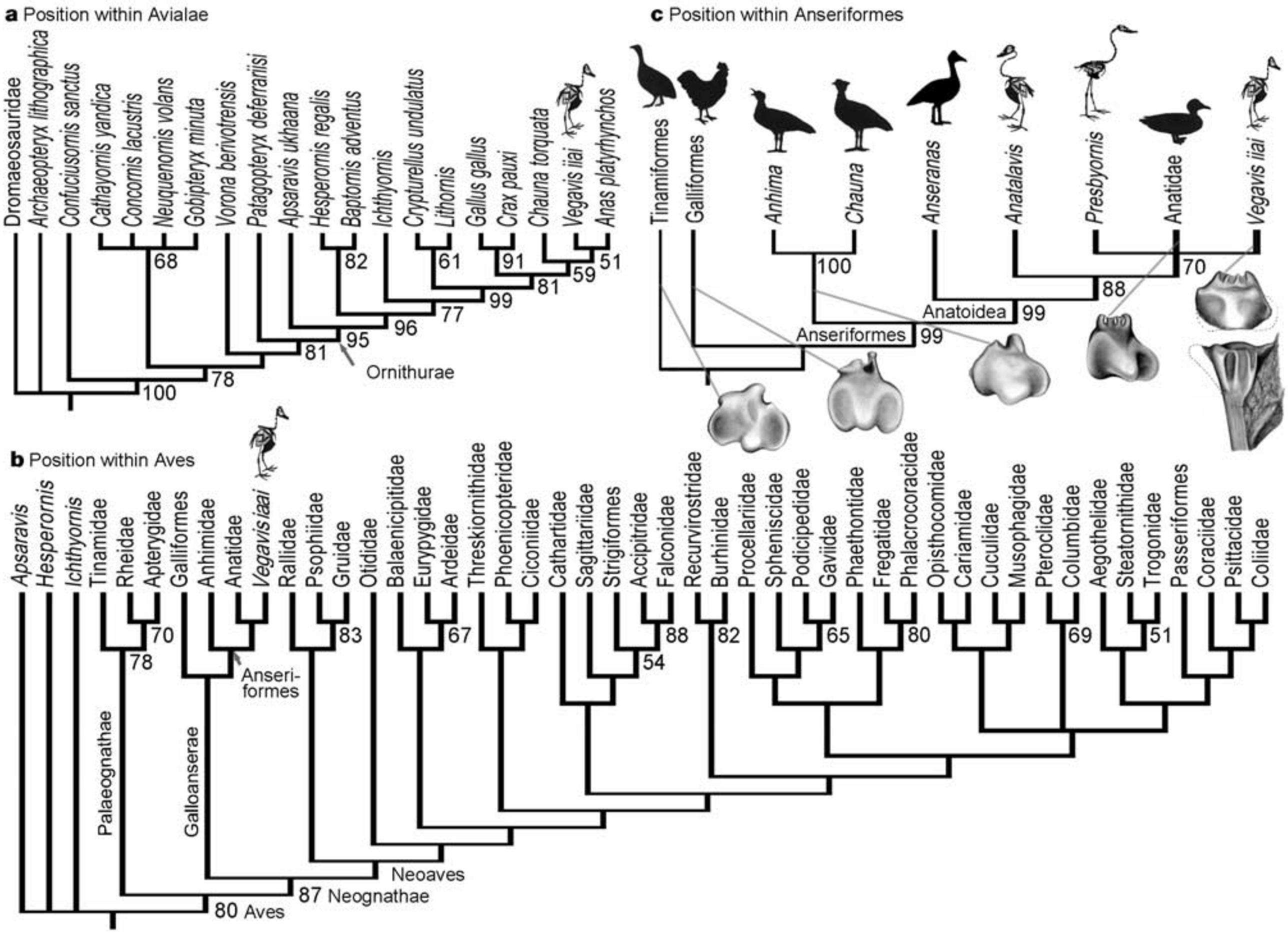

Figure 3 Phylogenetic placement of *Vegavis* in three successive cladistic analyses progressing from Avialae to Anseriformes (see Methods). **a**, Placement within Avialae in the strict consensus cladogram of two most parsimonious trees (MPTs): length, 385; consistency index (CI), 0.67; retention index (RI), 0.81; rescaled consistency index (RC), 0.54. **b**, Placement within Aves in the strict consensus of three MPTs: length, 822; CI, 0.33; RI, 0.48; RC, 0.16. **c**, Placement in Anseriformes in one MPT: length, 148; CI, 0.91; RI, 0.88; RC, 0.81. Bootstrap support values >50% from 2,000 replicates (10 random addition sequences/replicate; random start trees; tree bisection reconnection) are reported below and to the right of corresponding nodes. Insets in **c** compare the right hypotarsus (see also character 90:0, ref. 16) of exemplars for Tinamiformes (*Eudromia elegans*), Galliformes (*Ortalis canicollis*), Anhimidae (*Chauna torquata*) and Anatidae (*Anas platalea*). All analyses used PAUP* 4.0b10 (ref. 28) and branches were collapsed if minimum length was 0. Character scoring of *Vegavis* in all data sets is given in the Supplementary Information.

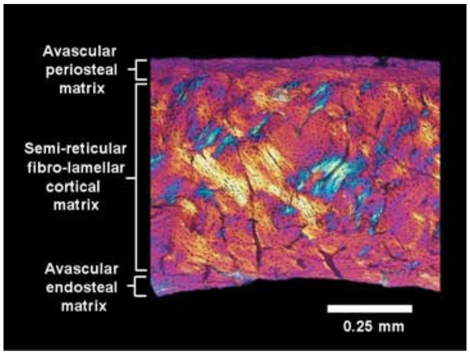

Figure 4 Histological section from the MLP 92-I-3-1 radius viewed with polarizing microscopy. The innermost seven-eighths of the cortex show a moderately vascularized, semi-reticular pattern, fibrolamellar matrix that is uninterrupted by lines of arrested growth. These data suggest that the animal showed relatively rapid, uninterrupted growth as in most living birds, including Anatoidea[24,25]. The outermost cortices (top) are avascular indicating that a slowing of growth occurred, presumably as adulthood was approached. The presence of endosteal, avascular lamellar bone that partially lines the medullar cavity supports this developmental status interpretation. The primitive avialan long bone histological condition consists of moderately vascularized cortices with most vascular canals oriented longitudinally. The cortices in these birds are interrupted by lines of arrested growth (LAGs)[24,25]. The vascular pattern and absence of LAGs in MLP 92-I-3-1 is consistent with its placement within Ornithurae[25] from the independent morphological character evidence.

Although the *Vegavis* holotype was originally suggested to be ‘Presbyornithidae indeterminate’[15], there is no evidence that it is part of this extinct taxon of predominately Eocene wading birds, averred by some to be transitional shorebird–duck ‘mosaics’[1,6,22,27]. Presbyornithids were proposed to be bridging taxa to waterfowl, indicating shorebird-like taxa to be the progenitors of all extant bird lineages[1,6,22,27]. *Vegavis* has different proportions from *Presbyornis* that are closer to other extant basal anseriform species. Thus, there is further support[16] that the wader proportions and the ecology used to diagnose Presbyorntihidae[17,22,27] are derived for that particular anseriform lineage and not ancestral avian characteristics. Finally, because of *Vegavis*’ placement and its unknown skull morphology, advanced filter feeding cannot be assumed to be present in the anseriform lineage by the Maastrichtian. The Anseriformes that can be inferred as present by this point are lineages that today include large-bodied terrestrial browsers and occasional omnivores (that is, screamers, Anhimidae and magpie geese, *Anseranas*) as well as the lineage leading to true ducks and geese. □

Methods

Vegavis iaai was placed phylogenetically in three successive cladistic analyses progressing from Avialae to Anseriformes. Placement within Avialae was evaluated using the ref. 19 data set: 200 characters, 19 ingroup taxa; branch and bound search (Fig. 3a). Placement within Aves was evaluated using the ref. 20 data set: 148 characters, 46 ingroup taxa, heuristic search strategies of original publication (Fig. 3b). Placement in Anseriformes was evaluated using the ref. 16 data set: 123 characters, 8 ingroup taxa, branch and bound search (Fig. 3c). Extinct taxa *Anatalavis* and *Presbyornis* are included as the only other well-preserved basal anseriforms. *Anatalavis* is scored in this matrix from ref. 29.

The following unambiguously optimized synapomorphies are preserved in *Vegavis* and support its placement (character numbers in parentheses refer to the data sets referenced).

Ornithurae: at least 10 sacrals (61:4, ref. 19), domed humeral head (106:1, ref. 19), radius shaft with muscular impression (135:1, ref. 19), posterodorsal antitrochanter (158:1, ref. 19), pubis mediolaterally compressed (166:1, ref. 19), patellar groove present (172:1, ref. 19), distal tibiotarsal condyles equal in width (182:1, ref. 19) and proximal metatarsal III plantarly displaced (190:1, ref. 19).

Aves: anteriorly deflected humeral deltopectoral crest (112:1, ref. 19) that is less than shaft width (113:0, ref. 19), at least 15 ankylosed sacral vertebrae (61:6, ref. 19; 91:3, ref. 20) and ossified supratendinal bridge on tibiotarsus (100:1, ref. 20).

Neognathae: closed ilioischiadic fenestra (94:1, ref. 20, 154:1, ref. 19) and humeral m. scapulotriceps groove (127:1, ref. 19; 81:1, ref. 20).

Anseriformes: diminutive pectineal process on pelvis (82:1, ref. 16) and hypotarsus with well developed cristae and sulci (103:12, ref. 20).

Anatoidea: lack of a sternal pneumatic foramen (70:0, ref. 16; apneumatic coracoid 90:0, ref. 19), ovoid m. scapulohumeralis cranialis scar (78:1, ref. 20) and metatarsal II shorter than IV (202:2, ref. 19). Lack of a pneumatic foramen on the proximomedial surface of ribs (59:2, ref. 16) and numerous hypotarsal cristae (90:0, ref. 16) are also synapomorphies of *Vegavis*, *Presbyornis* and Anatidae relative to *Anseranas*, but are ambiguously optimized because they are unknown in the Eocene *Anatalavis*. Loss of the n. supracoracoideus foramen (65:1, ref. 20) and weak to absent thoracic vertebrae lateral excavations (58:0, ref. 19) are unambiguously optimized as synapomorphies of Anatidae relative to *Vegavis* and *Presbyornis*, but it is unresolved if *Vegavis* is the sister taxon of Anatidae, *Presbyornis*, or *Presbyornis* + Anatidae.

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