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Early Pliocene hominids from Gona, Ethiopia

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Comparative biomolecular studies suggest that the last common ancestor of humans and chimpanzees, our closest living relatives, lived during the Late Miocene–Early Pliocene^{1,2}. Fossil evidence of Late Miocene–Early Pliocene hominid evolution is rare and limited to a few sites in Ethiopia^{3,4,5}, Kenya⁶ and Chad⁷. Here we report new Early Pliocene hominid discoveries and their palaeoenvironmental context from the fossiliferous deposits of As Duma, Gona Western Margin (GWM), Afar, Ethiopia. The hominid dental anatomy (occlusal enamel thickness, absolute and relative size of the first and second lower molar crowns, and premolar crown and radicular anatomy) indicates attribution to Ardipithecus ramidus. The combined radioisotopic and palaeomagnetic data suggest an age of between 4.51 and 4.32 million

years for the hominid finds at As Duma. Diverse sources of data (sedimentology, faunal composition, ecomorphological variables and stable carbon isotopic evidence from the palaeosols and fossil tooth enamel) indicate that the Early Pliocene As Duma sediments sample a moderate rainfall woodland and woodland/grassland.

The Early Pliocene fossiliferous sediments at As Duma in the Gona Palaeoanthropological Research Project (GPRP) area are located in the Busidima and Gawis drainages at the base of the Gona western escarpment in the Afar portion of the Ethiopian rift (Fig. 1). During four field seasons between 1999 and 2003, over 1,500 fossils have been recovered from 40 palaeontological sites, seven of which included hominid remains (Table 1 and Supplementary Table 1). These fossil-rich deposits are divided from the younger Hadar and Busidima Formations (3.4 million years (Myr) ago to <0.5 Myr ago) to the east by a major normal fault (Fig. 1). Most of the As Duma sites are distributed across two distinct fault blocks separated by an apparently minor normal fault. The west-dipping orientation of the minor fault implies that all of the GWM-3 block (containing sites GWM-3/3w, and -16) is stratigraphically lower than the GWM-5 block (sites GWM-1, -5m, -5sw and -9), although the lack of stratigraphic repetition between blocks makes the time separation between sites and blocks unclear. Given their many sedimentologic similarities, we interpret these blocks as a part of a single depositional sequence. Similarities

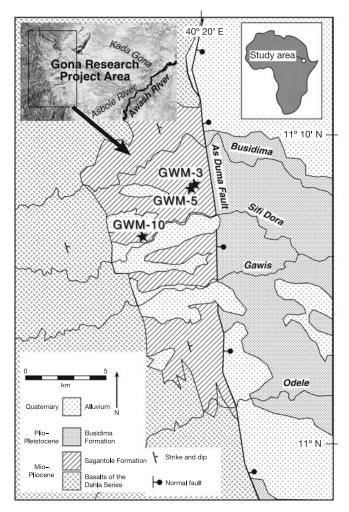


Figure 1 A geological map and thematic mapper (TM) image insert depicting the location of the hominid sites at As Duma in the Gona Western Margin, GPRP study area, Afar, Ethiopia. The north—south trending As Duma fault offsets the younger (≤3.4 Myr ago) Hadar and Busidima Formations against the newly identified Early Pliocene deposits of the Sagantole Formation.

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that distinguish the GWM-3 and GWM-5 deposits from the underlying Dahla Series basalts and overlying Hadar Formation include: the same mix of small-scale fluvial, lacustrine and locally volcaniclastic deposition; similar colour and induration; and the similar petrographic character of the fluvial sands. The GWM-3 site stratigraphic section (Fig. 2a) is capped by a laterally extensive tufa of spring origin containing gastropods, fossilized wood fragments, *Celtis cf. africana* seeds and vertebrate fossils, including hominids. At the base of the GWM-5 stratigraphic block are dark-grey mudstones resting directly on a minor basalt flow (Fig. 2b). The fossiliferous mudstone, which has yielded hominids, contains abundant tuffaceous and volcaniclastic material interpreted to represent ongoing volcanic eruptions into a shallow marsh that lapped onto the basalt flow.

Dates from two different crystal-rich tuffs (GONASH-51 and GONASH-52) found in the middle of the lower lacustrine interval $\sim\!14\,\mathrm{m}$ below GWM-3 and from the stratigraphically higher basalt flow under GWM-5sw indicate that the deposits are Early Pliocene in age (Fig. 2a, b). The two tuffs were dated by laser fusion $^{40}\mathrm{Ar}/^{39}\mathrm{Ar}$ analysis of single plagioclase crystals using methods described previously 8 (Supplementary Figs 1 and 2). Excluding the obvious xenocrysts, 23 of 23 (GONASH-51) and 16 of 18 (GONASH-52) plagioclase crystals yielded statistically homogeneous populations with weighted mean ages $(\pm 2\sigma)$ of 4.56 \pm 0.23 Myr and 4.59 \pm 0.45 Myr, respectively. Although the individual crystal ages

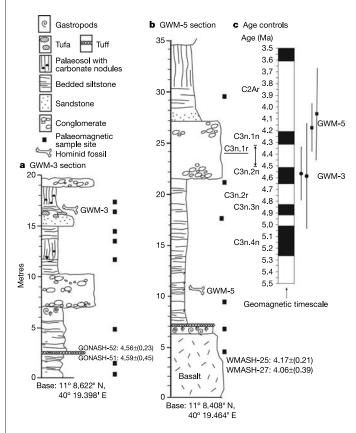


Figure 2 Stratigraphy of the GWM-3 (a) and GWM-5 (b) sites. All of the GWM-3 block in a lies stratigraphically below the minor basalt at the base of the GWM-5 block in b. GPS coordinates based on WGS84 datum. c, Palaeomagnetic timescale (solid, normal polarity; open, reversed polarity) in millions of years but recalculated for conformity with the standard age used in $^{40}\text{Ar}/^{39}\text{Ar}$ dating herein) and $^{40}\text{Ar}/^{39}\text{Ar}$ ages with 2σ uncertainties (solid circles, tuffs from the GWM-3 fault block; solid squares, from basalt at the base of the GWM-5 block). All sediments in both fault blocks are reversely magnetized. C3n.1r (4.32–4.51 Myr) is the only reversed interval where both $^{40}\text{Ar}/^{39}\text{Ar}$ ages also overlap at 2σ uncertainty.

are relatively scattered (unweighted population means and standard deviations of 4.45 ± 0.53 Myr (n=23) and 4.31 ± 0.91 Myr (n=15) for G-51 and G-52, respectively) their intra-sample homogeneity and variable precision justify the weighted mean as the best estimate for the ages (Supplementary Figs 1 and 2; Supplementary Table 2).

Two samples of groundmass concentrate (WMASH-25 and -27) from the basalt flow beneath GWM-5 were dated by resistancefurnace incremental heating yielding plateau ages of 4.17 ± 0.21 Myr and 4.06 ± 0.39 Myr, with a weighted mean of $4.15 \pm 0.18\,\mathrm{Myr}$ (Supplementary Figs 3 and 4; Supplementary Table 3). Palaeomagnetic data (referred to the timescale in ref. 9, recalculated for conformity with the standard age used in 40Ar/39Ar dating herein) provide additional constraints on the age of the deposits. The reversed polarity sediments and flows at all sites within these densely sampled stratigraphic sections may have been deposited during a single interval of reversed geomagnetic polarity, given the strong sedimentologic similarities between the GWM-3 and GWM-5 deposits. If this proves correct, the polarity interval that simultaneously satisfies all palaeomagnetic and radioisotopic data is chron C3n.1r with age limits 4.51-4.32 Myr (Fig. 2c). An alternative—but in our view geologically less plausible—interpretation is that GWM-5 is much younger than GWM-3. In this case, the magnetically reversed sediments of GWM-3 belong to chron C3.2r (4.83–4.65 Myr) or chron C3.1r (4.51–4.32 Myr), whereas the magnetically reversed sediments of GWM-5 could conceivably belong to chron C2Ar (4.21-3.61 Myr). In this model, palaeomagnetic constraints would place the GWM-3 block between 4.83 and 4.32 Myr ago, and combined radioisotopic results would place the GWM-5 block between 4.21 and 3.61 Myr ago. Further sampling may clarify the chronological position of GWM-5. The Early Pliocene age for all of these localities is supported by the presence of biochronologically useful species recovered from the hominid sites (for example, Nyanzachoerus jaegeri¹⁰, Kolpochoerus deheinzelini¹¹, Anancus cf. kenyensis, Pliopapio alemui¹² and Kuseracolobus aramisi12. Another fossil hominid site, GWM-10, although not yet dated geochronologically, is biochronologically indistinguishable from other As Duma localities.

Fossils from at least nine hominid individuals were recovered from the As Duma deposits (Fig. 3 and Table 1). No hominid fossil shows evidence of transport. Primarily jaws and teeth fossils, the collection includes three variably complete manual phalanges and a

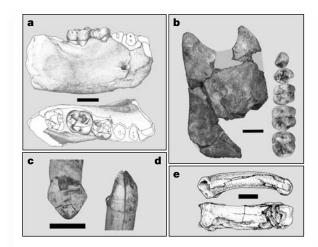


Figure 3 Early Pliocene hominid fossils from As Duma, Gona Western Margin. **a**, GWM3/P1, lateral and occlusal view of right mandibular corpus. **b**, GWM5sw/P56, mesial view of left mandibular ramus and occlusal views of right P_3 — M_3 . Grey shaded area of ramus is area of reconstruction. **c**, GWM9n/P51, labial view of maxillary left canine. **d**, GWM9n/P50, labial view of mandibular right canine. **e**, GWM10/P1, lateral and palmar view of manual proximal phalanx. Solid bar, 1 cm. Drawings by L. Gudz.

Specimen	Element	Finder	Date	GPS-N*	GPS-E*	Measurements (mm)†
GWM1/P37	Proximal pedal phalanx fragment	S. W. Simpson	16 Feb 2001	11° 08.386′	40° 19.597′	Base: DV = 7.8; ML = 9.2
GWM3/P1	Right mandible corpus fragment	Abdu Mohamed Ali	6 Mar 1999	11° 08.613′	40° 19.492′	RM_1 : MD = 10.2; BL_{MAX} =(10.0); RM_2 : MD = 12.7; BL_{MAX} =11.6
GWM3/P2	Proximal manual phalanx fragment	Excavation	7 Mar 1999	11° 08.613′	40° 19.492′	Base: DV = 11.6; ML = 15.2
GWM3W/P185	Mandibular left M ₁	Asahmad Humet	24 Feb 2003	11° 08.640′	40° 19.449′	LM_1 : $MD = (10.5)$; $BL_{MAX} = 10.25$
GWM5M/P55	Maxillary left P4	Asahmad Humet	28 Feb 2001	11° 08.657′	40° 19.238′	LP^4 : MD = 7.25; BL = 10.65
GWM5SW/P56	Partial dentition	Asahmad Humet	17 Feb 2001	11° 08.547′	40° 19.238′	Ll ₂ : MD = 6.65; LL= -; Rl ₂ : MD = 6.60; LL= -; L ₀ & R ₀ : -; L ₀ & R ₀ : -; RP ₃ : MD = (8.0), BL = -; LP ₃ : MD = 7.8, BL = 8.8; RP ₄ : MD = 7.6, BL = 9.3; LP ₄ : MD = 7.6, BL = 9.3; RM ₁ : MD = 10.6, BL _{MAX} = 10.7; LM ₁ : MD = 10.8; BL _{MAX} = 11.0; RM ₂ : MD = 12.7; BL _{MAX} = 11.7; LM ₂ : MD = 12.7; BL _{MAX} = 11.7; RM ₃ : MD = 12.8, BL _{MAX} = 11.3; LM ₃ : MD = -, BL _{MAX} = 11.4; U ^C : -; LP ³ : MD = -, BL = 9.2; LM ¹ : MD = 9.7, BL = -
GWM5SW/P58	Intermediate manual phalanx fragment	Excavation	21 Feb 2001	11° 08.547′	40° 19.238′	
GWM9N/P50	Mandibular dentition	Asahmad Humet	11 Feb 2003	11° 08.449′	40° 19.427′	$\begin{array}{l} R_{c}\text{: MD} = 8.5, BL = 9.7; \\ RP_{4}\text{: MD} = (7.3), BL = 8.7; \\ RM_{1}\text{: MD} = 10.7, BL_{MAX} = 10.0; \\ LM_{1}\text{: MD} = 10.6; BL_{MAX} = (9.7); \\ LM_{2}\text{: MD} = (12.4); BL_{MAX} = 11.3 \end{array}$
GWM9N/P51	Maxillary dentition	Kampiro Qairento	11 Feb 2003	11° 08.449′	40° 19.427′	RI ² : MD = 7.2; LL = 6.8; L ^c : MD = 11.1; LL = 10.6; RP ³ : MD = 7.5, BL = 11.0; RP ⁴ : MD = 7.4, BL = 11.0; RM ¹ : MD = 10.5, BL _{MAX} =12.3; RM ³ : MD = 1, BL _{MAX} =-; LM ³ : MD = 11.4, BL _{MAX} =14.2
GWM10/P1	Proximal manual phalanx	Abdu Mohamed Ali	22 Feb 2000	11° 07.489′	40° 18.112′	Length = 49.9; Base: DV = 11.7; ML = (1
GWM16/P10	Mandibular right M ₃	Asahmad Humet	18 Feb 2003	11° 08.783′	40° 19.058′	RM_3 : MD = 12.55, BL_{MAX} =(11.9)

^{*}GPS coordinates based on WGS84 datum.

†All measurements are in millimetres. Parentheses indicate that values in measurements are estimates. MD, mesio-distal length; BL_{MAX}, maximum bucco-lingual breadth. DV, dorso-ventral; ML, medio-lateral; LL, labio-lingual; -, no data; subscripts indicate lower teeth, supercripts upper teeth; R, right; L, left; C, canine; I, incisor; M, molar; P, premolar.

pedal phalanx fragment. In labial view, the maxillary canine crown is diamond shaped, with the mesial and distal shoulders about equidistant from the cervix and cusp. The third upper molar (M³) is relatively transversely broad with low relief and complex occlusal anatomy. The lower canine is tall with an asymmetric labial profile. The mesial shoulder is about mid-height on the crown with a steep apical mesial margin (Fig. 3d). A distal marginal tubercle is present and prominent. The major axis of the narrow oval mandibular canine root is more anteriorly oriented rather than more obliquely directed to the tooth row as in later hominids. The unicuspid third lower premolars (P₃s) have an unbifurcated root with two pulp canals (Tome's root). The P4 crown is mesiodistally compressed with an oval plan, a simple cusp pattern and a single root matching the Aramis (Ethiopia) specimens of Ardipithecus ramidus⁵ and distinct from the triangular/quadrangular cervical cross-section of Australopithecus multi-rooted P₄s.

The small lower first molars are bunodont with a simple cuspal pattern. The molar buccal margins vary in their degree of occlusal slope from near vertical to oblique. The naturally fractured GWM3/P1 M1 has entoconid occlusal enamel similar in thickness (1.1 mm) to Aramis *Ar. ramidus*. The rectangular M3s are distally rounded with complex occlusal topography (additional cuspids and accessory occlusal folding) and only moderate cuspal relief. The wear gradient across the molar row is minor, which, along with a molar microwear pattern of numerous long bucco-lingual (BL) oriented striae with few pits, indicates a low abrasion diet.

The M_3 crown is separated from the low ramus by a narrow paramolar sulcus. The mandibular corpora are low and broad. The anterio-superiorly opening mental foramen is located midcorpus between the premolars. The M_3 –C tooth row in GWM-3/P1 is

sigmoidal with the M_3 lateral to the M_1 – M_2 axis and the canine medial to it. Reconstruction of this small, perhaps female, mandible indicates that it is 'V'-shaped, common in smaller hominid mandibles (for example, AL 288-1) and different from the parallel tooth rows characteristic of *Australopithecus anamensis*¹³. The large, diamond shaped maxillary canines, small first molar crowns, thickness of occlusal enamel and morphology of the premolar crown and roots indicate assignment to *Ar. ramidus*.

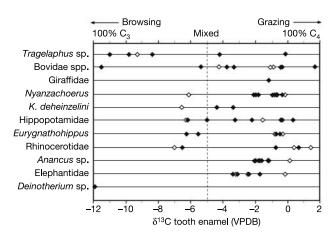


Figure 4 δ ¹³C values (GWM-5 block fauna, closed symbols; GWM-3 block fauna, open symbols) of fossil tooth enamel grouped by taxon. *Tragelaphus* sp. = *Tragelaphus* cf. *kyaloae*; Bovidae spp. include multiple species (*Ugandax* sp., Bovini, Reduncini and Bovidae gen. et sp. indet.); *Nyanzachoerus jaegeri=Nyanzachoerus* cf. *jaegeri* and *Nyanzachoerus* sp.; *K. deheinzelini=Kolpochoerus deheinzelini.*

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GWM-10/P1 is a nearly complete manual left proximal phalanx probably from ray IV. The GWM-3/P2 manual proximal phalanx, represented by the proximal ~40% of the bone, is large. These phalanges are similar in overall morphology to those from Hadar, with two differences: a more transversely broad proximal articular surface and longer absolute length¹⁴. The pedal proximal phalanx fragment retains the proximal third of the bone. The transversely broad oval proximal facet is oriented dorsally, a character diagnostic of bipedality and a trait also seen in the latest Miocene hominid *Ardipithecus kadabba*^{3,4}.

Faunal composition, bovid tooth mesowear and stable carbon isotopic composition of tooth enamel and soil carbonate provide palaeoenvironmental indicators for As Duma. N. jaegeri, a grazer considered to be ancestral to the more hyposodont Notochoerus suids^{10,15}, is the most common suid whereas Nyanzachoerus kanamensis and the mixed feeding K. deheinzelini are either rare or absent at individual hominid sites. The papionine monkey Pliopapio alemui is more common (~65%) than the colobine Kuseracolobus aramisi (\sim 35%). Observations of the bovid maxillary molar mesowear¹⁶ shows that the tragelaphines (\sim 38% of all bovid individuals) have the characteristic wear pattern of browse or mixed (browse and graze) feeders. The predominance of low, rounded cusps in the remaining bovids indicates a grazing diet, agreeing with the isotopic composition of their teeth (see below). Fossils of the mole rat (Tachyoryctes sp.), currently found in montane grasslands, perhaps provide evidence of higher elevation in the past.

Most palaeosols at As Duma are calcareous vertisols that form in seasonal, low-rainfall ($<\sim$ 1,000 mm yr $^{-1}$) tropical environments^{17,18}. Fifteen carbonate nodules were sampled from ten palaeosols at and around (2 km radius) GWM-3. Sixty-eight total analyses yielded a range of δ^{13} C values (VPDB; Vienna Pee Dee belemnite standard) from -3.9% to -12.0%, for an average of -7.5% indicating an environment of woodlands and grassy woodlands reflecting a mixture dominated by C_3 (trees and shrubs) and fewer C_4 grasses (warm-season grasses), assuming pure endmember carbonate δ^{13} C values of -12% and +2%, respectively (Supplementary Table 4). Only locally, particularly in the vicinity of GWM-3, do analyses indicate the presence of up to 50% grasses, where values range between -3.9% to -7.9% and average -6.0% (n=4).

Stable carbon isotope values in enamel were obtained for most of the macrofauna (except primates) found at the hominid sites (Fig. 4 and Supplementary Table 5). δ^{13} C values fall between -11.9% and +1.7% (n=73), reflecting a range of diet composed of C_3 ($\delta^{13}C=-12\%$) and C_4 plants ($\delta^{13}C=+2\%$). The diets of most of these large mammals indicate a significant reliance on C_4 grasses ($\delta^{13}C_{\rm enamel}>-5\%$, n=57). Taxa with diets dominated by C_4 plants (grazers) include N. jaegeri, Hexaprotodon harvardi, most rhinocerotidae, Anancus sp., most bovids, all Elephantidae, most Eurygnathohippus sp., and a sivathere, which all returned $\delta^{13}C$ values >-5.0%. K. deheinzelini, some rhinocerotidae and some Eurygnathohippus produced intermediate values. A Deinotherium and most tragelaphines yielded $\delta^{13}C$ values typical of a primarily C_3 (browsing) diet.

The As Duma Early Pliocene deposits sample a low-relief, internally draining basin with lakes, swamps, springs and streams amid local volcanic centres. The carbonate-rich palaeosols formed in a sub-humid and seasonally dry climate in a landscape covered by C_3 -dominated woodland and grassy woodland. At As Duma, *Ardipithecus* was exposed to this mosaic of environments. Only further evidence that more tightly associates the hominids (and other fauna) with the varied local environments will reveal the habitat preferences of these early hominids.

Methods

40Ar/39Ar dating

 40 Ar/ 39 Ar dating of single plagioclase crystals separated from GONASH-51 and -52 used the facilities at the Berkeley Geochronology Center (California, USA) following

procedures described by ref. 20 (see Supplementary Information). Plagioclases from GONASH-51 and -52 have high Ca/K (24–65 and 6–13, respectively) that consequently yield relatively imprecise single crystal ages. The plagioclase single crystal ages are intrinsically less precise than the basalt ages due to their low K and high Ca concentrations coupled with the imperative need (demonstrated by refs 8, 21) to analyse crystals individually in order to recognize xenocrystic contamination. The low precision of individual plagioclase analyses unfortunately only enables recognition of xenocrysts that are substantially older, whereas xenocrysts as much as 0.5 Myr older might go undetected in the present data. Furthermore, these low-K plagioclases are relatively susceptible to subtle excess argon contamination. These possible sources of geologic error, not reflected in the analytical precision, both would bias the results towards spuriously old ages. The possibility of xenocrystic contamination precludes analysis of multiple crystal aliquots: indeed, two plagioclase crystals (with anomalously low Ca/K) from GONASH-52 yielded ages of 334 \pm 2 Myr and 8.00 \pm 1.06 Myr (1 σ errors), illustrating the necessity of single-crystal analysis.

Groundmass concentrates from basalt samples WMASH-25 and -27 were analysed at New Mexico Geochronology Research Lab (Socorro, New Mexico) following full procedures described in ref. 22. Reported ages are based on 28.02 Myr for the Fish Canyon sanidine standard²⁰, which yields ages approximately 0.7% older than the calibration used in refs 8 and 23, and errors are reported at the 2σ level. Electron microprobe examination of the two basalt samples showed some clay alteration and dissolution of groundmass and phenocryst phases. However, remaining K_2O was concentrated in unaltered plagioclase, and the relatively flat age spectra and moderately high radiogenic yields suggest that alteration phases degassed during low temperature steps, and that the weighted mean ages of higher temperature steps are an accurate record of eruption age of the basalts.

Palaeomagnetism

Four oriented samples for palaeomagnetic analysis were collected from each of 14 sites in the GWM-3 block and eight sites in the GWM-5 block. All samples were thermally demagnetized in ≥12 temperature steps ranging up to 580 °C, and characteristic remnant magnetization (ChRM) directions for each sample were determined by principal component analysis²⁴. Site mean ChRM directions were calculated using Fisher statistics³⁵. All site-mean ChRM directions from continuous sections in both blocks are reverse polarity.

Isotope analysis (see Supplementary Information)

Soil carbonate nodules were roasted under vacuum at 400–430 °C before conversion to CO $_2$ with 100% phosphoric acid. Micro-sampling of individual nodules avoided mmscale secondary calcite veins that cross-cut many nodules. Multiple $\delta^{13}\mathrm{C}$ analyses of single nodules in individual palaeosols tend to cluster $\pm 1.0\%$. Crushed enamel was reacted with 1 M CH $_3\mathrm{COOH}$ and with 2% H $_2\mathrm{O}_2$ for 1 h. Isotopic analyses were performed on a Finnigan Delta-S and a Finnigan MAT 252 gas-source mass spectrometer at the University of Arizona. Results are presented in the usual δ notation as the per mil (%) deviation of the sample CO $_2$ from the PDB standard, where $R=^{13}\mathrm{C}/^{12}\mathrm{C}$ or $^{18}\mathrm{C}/^{16}\mathrm{C}$, and $\delta=(R_{\mathrm{sample}}/R_{\mathrm{standard}}-1)(\times 1,000)$.

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Definitive fossil evidence for the extant avian radiation in the Cretaceous

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Long-standing controversy¹⁻⁹ 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 lineages¹¹⁻¹³—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 Antarctica¹⁵ 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 reported¹⁵ as a possible 'transitional' form close to extant lineages¹⁵. 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 Avialae¹⁹, Aves²⁰ and Anseriformes¹⁶, 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 elements¹⁵ 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 expedition¹⁵. Deposits are near-shore marine fine-grain sandstones²¹ 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

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