

PALEONTOLOGY

Bird neurocranial and body mass evolution across the end-Cretaceous mass extinction: The avian brain shape left other dinosaurs behind

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Birds today are the most diverse clade of terrestrial vertebrates, and understanding why extant birds (Aves) alone among dinosaurs survived the Cretaceous-Paleogene mass extinction is crucial to reconstructing the history of life. Hypotheses proposed to explain this pattern demand identification of traits unique to Aves. However, this identification is complicated by a lack of data from non-avian birds. Here, we interrogate survivorship hypotheses using data from a new, nearly complete skull of Late Cretaceous (~70 million years) bird *Ichthyornis* and reassess shifts in bird body size across the Cretaceous-Paleogene boundary. *Ichthyornis* exhibited a wulst and segmented palate, previously proposed to have arisen within extant birds. The origin of Aves is marked by larger, reshaped brains indicating selection for relatively large telencephala and eyes but not by uniquely small body size. Sensory system differences, potentially linked to these shifts, may help explain avian survivorship relative to other dinosaurs.

INTRODUCTION

Traits hypothesized to explain differential patterns of dinosaur survivorship of the Cretaceous-Paleogene (K-Pg) mass extinction include aspects of neuroanatomy (1, 2) and feeding ecology (3, 4). Extant birds (Aves) have brains with relative volumes (5) and neuronal densities (6) that surpass all other reptiles (5–7). These traits may have provided a selective advantage over other dinosaurs in the face of rapidly changing environmental conditions at the K-Pg boundary. Dietary shifts associated with modification of the jaws and palate have also been proposed as drivers of both this survivorship and highly disparate diversification rates in the Early Paleogene (3, 8). Of the two basal-most avian lineages, Neognathae today comprises more than 10,000 extant species, while Palaeognathae is known from fewer than 100. This disparity in diversification has been hypothesized to have been driven by greater beak adaptability imparted by a mobile palate detached from the cranium, a feature historically considered derived for Neognathae (8). However, a paucity of well-preserved skulls from small-bodied outgroups of living birds has limited estimates of ancestral brain and craniofacial characteristics. This lack of data has confounded identification of unique crown traits demanded by hypotheses explaining K-Pg survivorship. Furthermore, body size and other traits proposed to have influenced dinosaur survivorship are known to scale allometrically (e.g., brain size, flight, growth rate, habitat preference, and metabolism) (4, 9–15). However, investigations of body mass evolution in Aves have rarely included data from the stem, allowing distantly related non-avian theropods and basally diverging ratites, both large-bodied, to disproportionately influence ancestral avian body mass estimates.

Ichthyornis dispar is a toothed stem bird (Avialae) known from the Late Cretaceous of North America and has traditionally been

considered the nearest known well-understood relative of extant birds (16, 17). Thus, *Ichthyornis* is essential to estimation of ancestral avian traits. Recent studies have cast uncertainty over the phylogenetic affinities of *Ichthyornis* recovering Late Cretaceous toothed bird *Hesperornis* as more closely related to extant birds (18, 19). Well-preserved skull material from *Ichthyornis* is rare, and although recent work has provided valuable insights on its cranial anatomy (18), crucial gaps remain, including the palatal and brain morphology. Early reconstructions of the brains of *Ichthyornis* and *Hesperornis* (16) were later shown to be hypothetical illustrations, lacking anatomical basis (20). The brain of *Ichthyornis* has been proposed based on a previously reported braincase (FHSM 18702) (18) to have a brain shaped like extant birds, including an expanded cerebrum and ventrally shifted optic lobes, although details about the brain shape in this specimen are obscured. Now, our only other published fossil insights into bird brain morphology in the Mesozoic come from the skulls of ~150-million-year (Ma) *Archaeopteryx lithographica* (1, 21) and *Cerebavis cenomanica* (22–24). *Archaeopteryx*, the earliest known potentially volant avialan (25), had a brain shape more like non-avian maniraptoran dinosaurs (e.g., *Zanabazar* and *Incisivosaurus*; figs. S1 and S2) than extant birds. By contrast, *Cerebavis* shows an expanded cerebrum and ventrally shifted optic lobes, although it is known only from an isolated partial skull, and its phylogenetic affinities remain unclear (22–24). Better understanding of the *Ichthyornis* condition can help fill our >70-Ma gap in neuroanatomical data separating *Archaeopteryx* from extant birds.

We describe a specimen of *I. dispar* preserving a nearly complete skull (Fig. 1 and figs. S1 to S14) and use x-ray computed tomography (CT) to digitally reconstruct the facial skeleton (Fig. 1) and partial brain endocast (Fig. 2, A and B). We reinvestigate phylogenetic relationships within Avialae using a matrix of 223 morphological characters scored for 43 avian and non-avian birds. We test the effects of stem taxon sampling by first estimating ancestral avian body and relative brain size using a sample of 2003 avians, *Archaeopteryx*, and seven non-avian dinosaurs. We then reestimate ancestral body mass with the addition of two sets of stem birds: First, we add data for 26 stem birds with well-understood phylogenetic affinities. Then, to that sample, we add data for 16 additional stem birds with poorly

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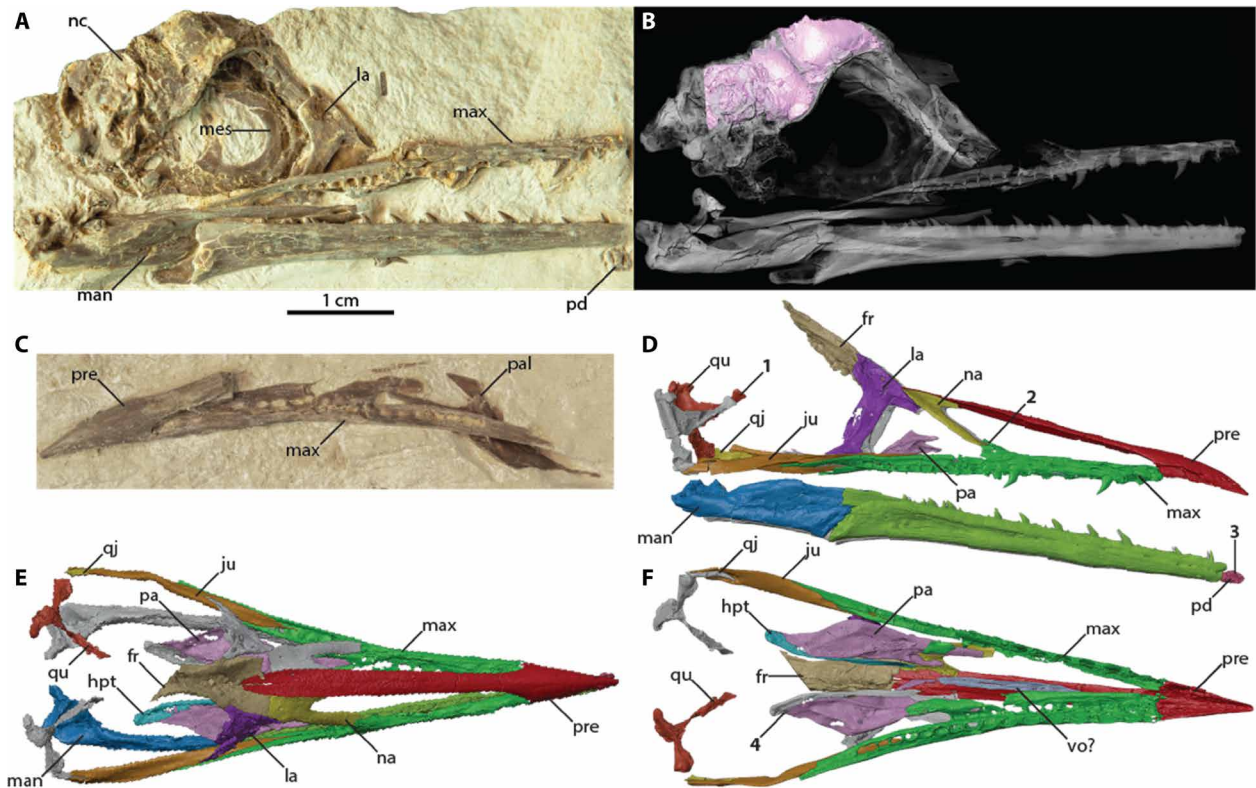


Fig. 1. Photographs and digital renderings of new *Ichthyornis* (AMNH FARB 32773) craniofacial anatomy showing evidence of a segmented palate. (A) Photograph of skull block including the neurocranium and partial upper and lower jaws. (B) Rendering of the skull block showing the position of the endocast (pink) relative to the cranium and nearby preserved facial elements (translucent white). (C) Photograph of the block including the premaxilla, left maxilla, and left palatine. Digital reconstructions of the facial skeleton in (D) lateral, (E) dorsal (mandible removed), and (F) ventral (mandible removed) views. Preserved elements are colored; symmetrical elements mirrored from the opposite side are in gray. Numbers correspond to novel insights from this specimen: 1, complete orbital process of the quadrate; 2, complete nasomaxillary contact; 3, segmented hemipterygoid. den, dentary; fr, frontals; hpt, hemipterygoid; ju, jugal; la, lacrimal; max, maxilla; mes, mesethmoid; na, nasal; nc, neurocranium; pa, palatine; pd, predentary; pman, posterior mandible; pre, premaxilla; qj, quadratojugal; qu, quadrate; vo?, tentative vomer. Photo credit: Christopher R. Torres, University of Texas at Austin.

understood phylogenetic affinities but that provide insight into avialan body size immediately preceding the K-Pg mass extinction (see Materials and Methods) (19).

RESULTS AND DISCUSSION

The endocast from the new specimen shows that *Ichthyornis* lacks the expanded cerebrum and ventrally shifted optic lobes characteristic of extant birds (Figs. 2 and 3). The braincase preserves impressions of the lateral sides of the telencephalon, optic lobes, and cerebellum, but the dorsal-most and ventral surfaces and rostral and caudal ends are lost to mediolateral crushing (Fig. 2, A and B). These data shed new light on the timing of the multiphase acquisition of the extant bird brain shape (Fig. 3). Basally diverging non-maniraptoran theropods (e.g., *Tyrannosaurus* and *Alioramus*) retained ancestrally linear brains with unexpanded cerebella and cerebra (26). Non-avian maniraptoran dinosaurs (e.g., *Zanabazar* and *Incisivosaurus*) are marked by relative expansion of both these brain subregions coinciding with ventral deflection of the midbrain (including the optic lobes) and dorsal deflection of the cerebrum (1, 27, 28). Further expansion of the cerebellum occurred near the divergence of Avialae (e.g., *Archaeopteryx*), resulting in exclusion of the midbrain from the dorsal brain margin

by contact between the cerebellum and the cerebrum (1, 21). Last, an episode of relative brain and cerebrum expansion has been shown to have occurred sometime after the divergence of Avialae (21), with optic lobes positioned entirely ventral to the cerebrum. Although the new endocast is incomplete, the position of the optic lobes relative to the mediolaterally widest point of the cerebrum strongly suggests that *Ichthyornis* had an *Archaeopteryx*-like brain shape. Thus, the most recent phase of bird brain shape change occurred near the origin of, and is synapomorphic for, extant birds. Unique expansion of the avian visual system may have been a driver of this reshaping. Among extant birds, eye size has been proposed to be correlated with and may constrain deflection of the optic lobes and cerebrum, relative cerebrum size, and relative brain size (29, 30). Despite the crown clade being marked by a derived brain shape, previous studies fail to recover shifts at the divergence of Aves in evolutionary rates of relative volume of either the total brain or individual regions (2, 31). However, these studies necessarily exclude data from stem birds due to a dearth of samples, obscuring any evolutionary shifts that might have occurred along the >70-Ma branch separating the divergences of Avialae and Aves. Better understanding of the sensory systems of non-avian dinosaurs will be crucial for elucidating the potential role of visual expansion as a driver of these shifts.

Ichthyornis exhibits an incipient wulst (Fig. 2), a derived cerebral structure previously thought to be restricted to living birds based on virtual reconstructions of osseous braincase architecture (1). In Aves, the wulst is a dorsal expansion of the cerebrum unique to birds among

extant reptiles and that corresponds to a subregion of the cerebrum thought to be homologous to parts of the mammalian neocortex (32–34). On the right dorsolateral surface of the *Ichthyornis* cerebrum, there is a shallow sulcus associated with a change in slope of the endocranial surface. Among extant birds, sulci in the dorsolateral surface of the brain correspond to the vallecular groove, demarcating the lateral margin of the wulst (Fig. 2) (7). A similar feature was tentatively identified in *Archaeopteryx* but was later shown to be a taphonomic artefact (1, 21). The original scan data of the corresponding preserved skull region in *Ichthyornis* where the dorsal deflection in slope is marked show no crushing and confirm that the structure observed here is natural (Fig. 2). The wulst is a visual processing center with a proposed role in flight but is more generally involved in somatosensory integration (32, 35). Although the presence of a wulst has been proposed to be the only recognized neuroanatomical correlate for flight among avialans (21, 35), if the wulst arose in response to increasingly efficient integration of sensory input imposed by flight, powered flight should have arisen first. This prediction is consistent with the apparent lack of a wulst in *Archaeopteryx*, the earliest known dinosaur capable of powered flight (25). However, as mentioned, the wulst is a brain structure with diverse functions not limited to those deployed in flight (32).

Ichthyornis is only the third Mesozoic taxon for which we have direct data on brain shape after *Archaeopteryx* and *Cerebavis*, and the new endocast sheds some light on the latter of these birds. The enigmatic 93-million-year-old *C. cenomanica* is known just from a poorly preserved, disarticulated braincase (22–24). The phylogenetic affinities of *Cerebavis* are uncertain; it exhibited the expanded cerebrum and ventrally shifted optic lobes characteristic of Aves, but lacked the wulst here recovered as characteristic of at least the clade comprising *Ichthyornis* and Aves (24). If recovered either within Aves or as a closer relative to Aves than *Ichthyornis*, *Cerebavis* would represent a secondary loss of a projected wulst visible on the external surface of the brain, although not necessarily the underlying neuronal structures. Alternatively, *Cerebavis*, like some derived pterosaurs (36), may represent a taxon with an independent gain of an expanded cerebrum and deflected optic lobes.

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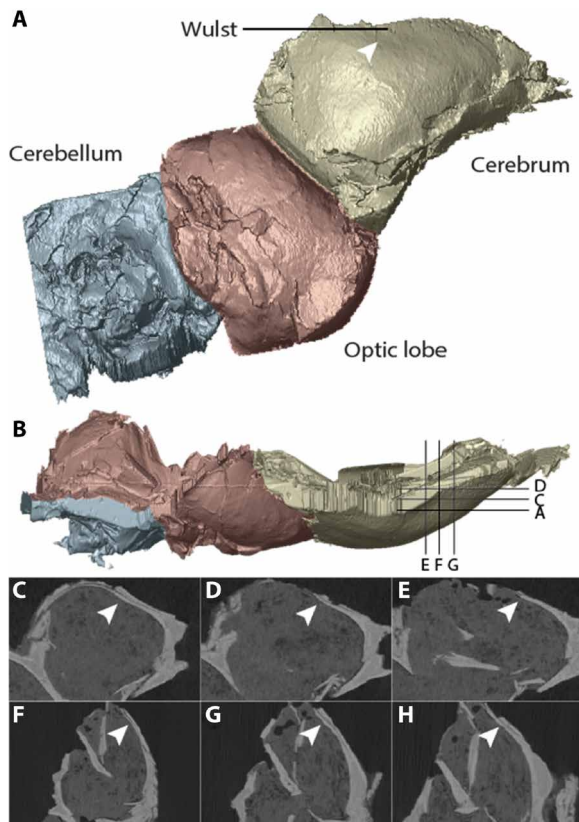


Fig. 2. Evidence of a wulst in *Ichthyornis*. (A and B) Reconstruction of the *Ichthyornis* endocast in (A) right lateral and (B) dorsal views. (C to H) CT slice data showing the endocranial surface in the area of the vallecula (arrowheads) in (C to E) coronal and (F to H) sagittal planes. Yellow, telencephalon; red, optic lobe; blue, cerebellum.

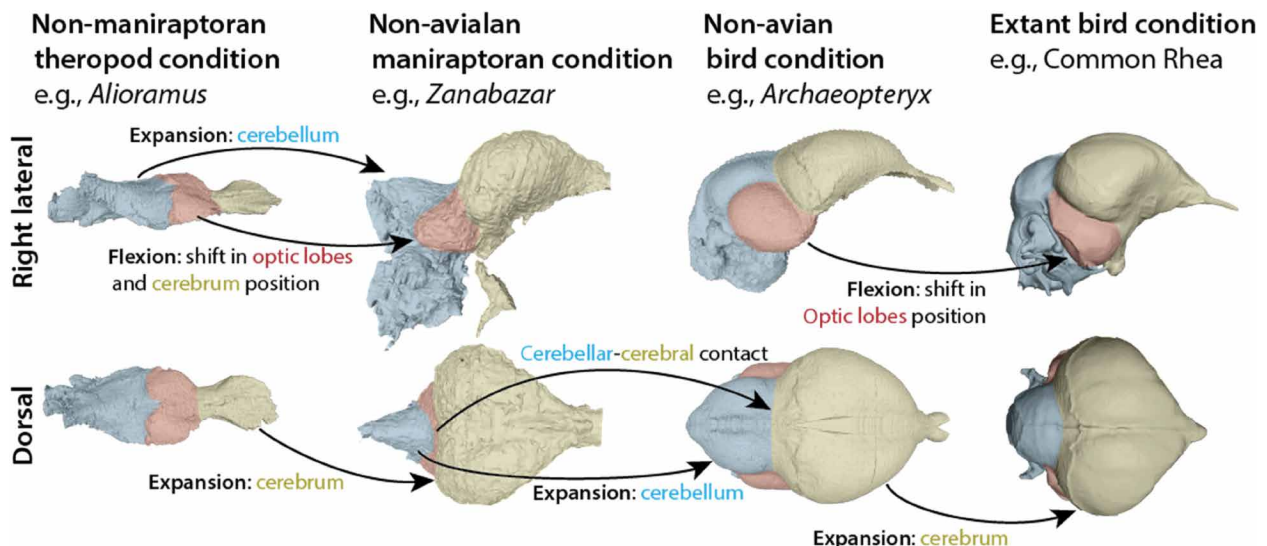


Fig. 3. Multiphase acquisition of the avian brain shape.

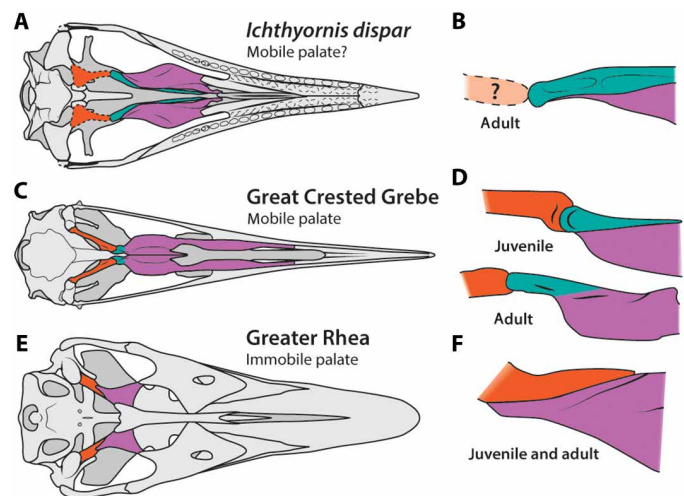


Fig. 4. Evidence of the presence of a neognath-like palate in *Ichthyornis*. (A to F) Orange, pterygoid; purple, palatine; teal, hemipterygoid.

The new specimen sheds new light on the ancestral avian palate (Fig. 4). In the new specimen, both palatines are preserved as elongate, mediolaterally broad elements with rostral processes projecting mediodorsally from the medial margins and conformed as rostrally oriented hooks (Figs. 1F and 4, A and B, and figs. S11 and S12). This is unlike the condition previously described for *Ichthyornis* (18) and observed in extant birds (Fig. 4, C to F) but is like other near-crown avialans, the Hesperornithiformes (37, 38). The right hemipterygoid is preserved in life position medial to the right palatine (Figs. 1F and 4A), the first evidence for the presence of this element in *Ichthyornis*. Shortly after most neognaths hatch, the pterygoid becomes segmented, with the anterior part (hemipterygoid) fusing to the palatine and the posterior part becoming the element recognized as the pterygoid in the adult bird (Fig. 4, C and D) (39). This process of pterygoid segmentation has been proposed as a synapomorphy for Neognathae and to be the prerequisite innovation to all other characteristics of the mobile neognath palate (40). This process is absent in all known palaeognaths, wherein the unsegmented pterygoid overlaps the palatine, and the palate is immobile (Fig. 4, E and F). This condition has historically been inferred as primitive for extant birds (41).

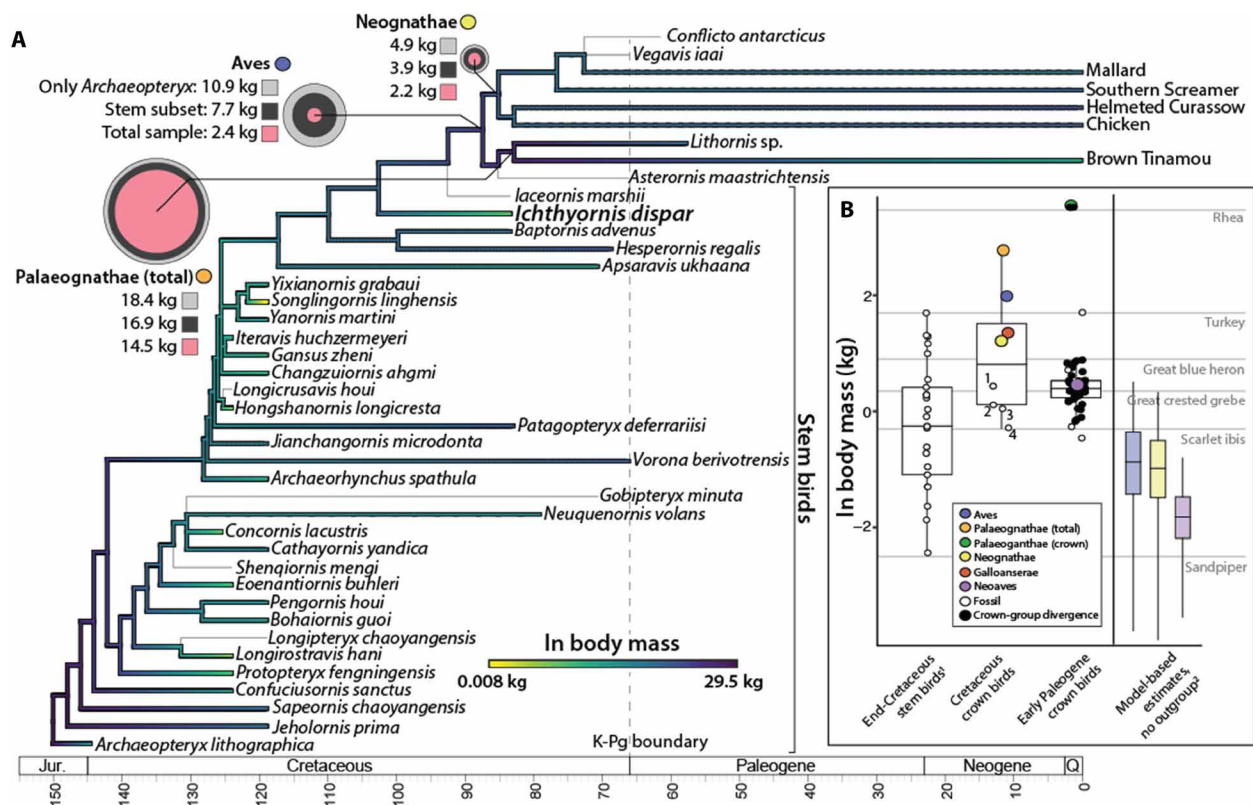


Fig. 5. The impact of including stem data on estimating body size evolution in birds. (A) Body mass evolution across the avian stem. Ancestral body masses were estimated including 26 stem birds with well-supported phylogenetic affinities and mapped across the strict consensus tree from our primary phylogenetic analysis. Gray branches indicate taxa that were used to estimate phylogeny but not ancestral body mass reconstructions. Circles correspond to ancestral body masses estimated for major basal divergences within Aves including data from the total stem bird sample (pink), only stem birds with well-supported phylogenetic affinities (dark gray), and no stem birds except *Archaeopteryx* (light gray) and are to scale. (B) Comparison of body mass estimates of ¹Cretaceous birds known from within 300 ka (thousand years) of the K-Pg boundary (19) to our body mass estimates for divergences within the crown clade and taxa from the Late Cretaceous and Early Paleogene, as well as ²model-based ancestral body masses for Aves, Neognathae, and Neoaves estimated previously (11) without inclusion of outgroup taxa. Cretaceous crown birds: 1, *Conflicto antarcticus*; 2, *Asteriornis maastrichtensis*; 3, *Polarornis gregorii*; 4, *Vegavis iaai*.

The presence of a hemipterygoid in *Ichthyornis* and multiple hesperornithiforms (37, 38) indicates that a segmented pterygoid, and possibly a mobile palate, arose before the divergence of extant birds and is likely ancestral for all of Aves. Zusi and Livezey (42) suggested that the intrapterygoid joint of *Hesperornis* was analogous to that observed in Neognathae rather than homologous based on the unique shape of the hesperornithine palatine. If so, the presence of such a joint in *Ichthyornis* would represent a third independent gain among closely related taxa. Instead, the presence in *Ichthyornis* of hesperornithine-like palatine and pterygoid morphologies in a neognath-like configuration of elements suggests that the intrapterygoid joint, and possibly the mobile palate observed in extant neognaths, was present at least as early as the divergence of *Hesperornis*. Fusion of the hemipterygoid to the palatine is absent in known near-crown stem birds and is so far unique to extant neognaths, and an unsegmented pterygoid is likely derived within Palaeognathae. This pattern may indicate that Aves was marked by a shift in palatal ontogeny, as the adult *Ichthyornis*-hesperornithine condition is only observed in juveniles among extant birds (39, 41, 42).

Adaptive plasticity of the beak associated with a mobile palate has been suggested to explain why neognaths, but not palaeognaths, explosively radiated in the Paleogene (8) but cannot alone explain the unique survivorship of Aves out of the Cretaceous. The mobile neognath palate has three components: articulation of the palatine and segmented pterygoid to the exclusion of the vomer; a mobile articulation between the palatine and pterygoid; and articulation between the parasphenoid and either the palatine, pterygoid, or both (42). Only the third of these components remains unknown in *Hesperornis* and, now, *Ichthyornis*, suggesting that these and possibly other Late Cretaceous near-crown stem bird had an incipient mobile palate (e.g., *Iaceornis*). The failure of these lineages, but not palaeognaths, to survive across the K-Pg boundary indicates that a detached palate alone likely did not influence survivorship dynamics.

Our phylogenetic analyses (see also the Supplementary Materials) recover *Ichthyornis* in its traditional place crown-ward of Hesperornithiformes as sister to a clade comprising Aves and the Late Cretaceous *Iaceornis* (Fig. 5A and figs. S15 to S20). Our results also shed further light on the phylogenetic affinities of two other Late Cretaceous birds, *Vegavis* and *Asteriornis*. Initially proposed to be a stem anatid within waterfowl (Anseriformes), the phylogenetic affinities of the Antarctic *Vegavis* have been controversial (43–45). We recover *Vegavis* in its traditional place within crown group waterfowl in a polytomy with the Mallard (*Anas platyrhynchos*) and the Early Paleocene Antarctic bird *Conflicto* (Fig. 3) (46). The Belgian *Asteriornis* was initially recovered with affinities to Galloanserae or with Galliformes (47). We instead recover *Asteriornis* as potentially a stem palaeognath with very limited support (Fig. 3 and fig. S15). This result underscores the need for additional data to confidently resolve its phylogenetic affinities. Our unconstrained phylogenetic analyses including the 16 fragmentary single-element end-Cretaceous stem birds from Longrich *et al.* (19) resulted in uninformative polytomies (fig. S19) due to missing data, so we constrained their relationships to match those recovered by the original authors (fig. S20) for ancestral state reconstructions including these taxa.

Estimates of avian body mass evolution are highly sensitive to outgroup sampling, underscoring the need to interpret the results of these analyses with extreme caution. Our analyses including data from only those stem birds with well-resolved phylogenetic affinities recovered an ancestral avian body mass of 7.7 kg (Wandering Albatross-sized)

Table 1. Body masses and brain volumes estimated for major basal avian divergences. Ancestral body masses were estimated from three alternative outgroup samples: Total, total sample including stem birds with poorly resolved phylogenetic affinities (19); Sub, taxonomic subsample including only stem birds with well-resolved phylogenetic affinities; AO, *Archaeopteryx* only.

Divergence	Body mass (kg)			Brain volume (cm ³)
	Total	Sub	AO	
Aves	2.4	7.7	10.9	7
Palaeognathae (total)	14.5	16.9	18.4	9.6
Palaeognathae (crown)	34	35	35.6	16.2
Neognathae	2.4	3.4	4	5.6
Galloanserae	2.2	3.9	4.9	5.9
Neoaves	1.4	1.5	1.6	5.4

compared to 10.9 kg (swan-sized) when stem bird outgroups other than *Archaeopteryx* were excluded (Fig. 5A). This difference was even more pronounced when we expanded outgroup sampling to include poorly understood end-Cretaceous stem birds known from isolated elements. If these stem birds are included, we recover an ancestral body mass of 2.4 kg (eagle-sized). Our results demonstrate the disproportionate effect that mostly large-bodied palaeognaths and non-avian dinosaurs had on states recovered by previous studies at the crown node in the absence of data from stem birds (2, 31). Total exclusion of any outgroup data results in an opposite phenomenon, with what are likely artificially low underestimates of ancestral avian body mass. Previous investigations relying on model-based approaches in lieu of outgroup sampling resulted in body mass estimates smaller than most Late Cretaceous stem birds (Fig. 5B) (11).

Our analyses failed to recover patterns in bird body mass evolution across the K-Pg boundary consistent with hypotheses that small body masses contributed to the unique survival of extant birds. We recovered an increase in body size from at least the divergence of Hesperornithiformes through the origin of extant birds, followed by continued increase in Palaeognathae and decrease early in Neognathae (Fig. 3A). Avian birds from either side of the K-Pg boundary were generally larger-bodied than end-Cretaceous stem birds (Fig. 5B) (11), albeit without statistically significant difference. Ancestral body masses for most major basal divergences within extant birds (i.e., Aves, Neognathae, Galloanserae, and Neoaves) were estimated to be larger than most end-Cretaceous stem birds regardless of which taxonomic subsample we used (Table 1). Our analysis represents one of the broadest samplings of body mass from stem birds yet published, but our understanding of Mesozoic bird diversity remains highly incomplete, and trends in body mass evolution may significantly change with future discoveries. These recovered trends will be influenced by revision of our understanding of stem bird phylogenetics. Inclusion of highly fragmentary, small-bodied birds from the Latest Cretaceous had a profound influence on estimated ancestral body masses (Fig. 5), but the phylogenetic affinities of these taxa are poorly understood. The relationships of several of these taxa to the crown clade, or even their inclusion within it, are ambiguous, and their treatment is likely to severely bias inferred ancestral trait values.

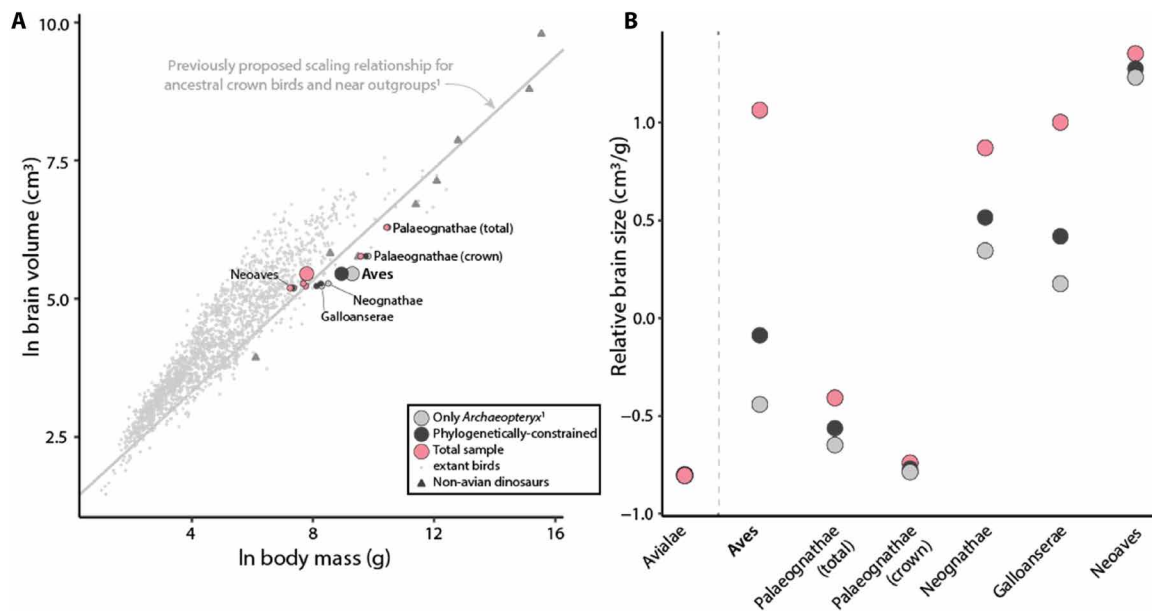


Fig. 6. The impact of outgroup sampling on inferred ancestral relative brain size in Aves and major subclasses. (A) Brain size versus body size for extant birds (gray) and select non-avian dinosaurs (triangles) and a regression representing the ancestral avian and near-crown scaling relationship from (2). Increasingly dense outgroup body mass sampling (dark and pink) recovers ancestral avian relative brain size more consistent with extant birds than non-avian dinosaurs. **(B)** The same data depicted in (A) showing that increased outgroup body mass sampling recovers an increasingly marked shift in relative brain size from the divergences of total birds (Avialae) to major extant clades. ¹Data for extant birds and non-avian dinosaurs and regression from (2).

Estimation of ancestral avian brain size and other allometrically scaling traits that may have influenced end-Cretaceous extinction dynamics is highly sensitive to outgroup body mass sampling (Fig. 6 and Table 1). This effect is especially pronounced at the divergence of crown-group birds, with increased outgroup sampling recovering ancestral avian brain sizes more consistent with extant birds than non-avian dinosaurs (Fig. 6A). The recovered shift in relative brain size from the divergence of Avialae to the divergence of extant birds is increasingly marked based on sampling strategy (Fig. 6B). Thus, it is perhaps expected that recent investigations have failed to detect a significant shift in evolutionary rates of either total or regional brain volume at or near the divergence of extant birds in the absence of data from the avian stem (2, 31). Despite our increased body mass sampling along the avian stem, neuroanatomical data from these taxa remain lacking, suggesting that our estimates of ancestral avian brain size are likely still influenced by taxonomic bias. It is likely that our understanding of ancestral avian brain size will shift markedly with improved sampling.

Ancestral maniraptoran brain shape was retained by birds until at least the divergence of *Ichthyornis* (Fig. 2). Aves was marked by a major neuroanatomical reshaping relative to known outgroups, including inflation of the telencephalon and ventral deflection of the optic lobes (fig. S21). Our identification of this condition as synapomorphic for extant birds implicates it as a trait so far unique to the Paleogene survivors. Aves may also have been marked by a major increase in relative brain size (Fig. 6), but our understanding of brain size evolution remains highly sensitive to outgroup sampling. Small body size characterizes many volant birds from lineages that are not known past the latest Cretaceous (e.g., Enantiornithes and non-crown Ornithurae). Living bird lineages present before this event are estimated to have been larger than most contemporary stem birds (Fig. 5), inconsistent with previous hypotheses that relatively small body sizes

provided the ancestors of extant birds a selective advantage in the face of the K-Pg mass extinction (11, 19). However, our analyses underscore the extreme sensitivity of ancestral body mass reconstructions to stem taxon sampling, casting uncertainty on the fidelity of these estimates both here and in all other studies to the true ancestral avian condition. We estimate the wulst and a segmented and possibly mobile palate arose before Aves (fig. S21), despite previously being considered features of that clade or derived within. The segmented palate may have arisen as a consequence of general reshaping of the skull associated with expansion of the brain that has been proposed to be linked to elaboration of the visual system (48). A combination of changes in craniofacial ontogeny, brain size, and shape is recovered as characterizing crown birds and may signal as yet poorly understood shifts in ecology that are linked to dinosaur survivorship.

MATERIALS AND METHODS

Scanning and reconstruction

Cranial material of the new *Ichthyornis* specimen (AMNH FARB 32773; fig. S1) was scanned at the University of Texas (UT) High-Resolution X-ray CT Facility in Austin, Texas, on an NSI scanner with a Fein Focus High Power source. The block containing the neurocranium was scanned on 25 February 2019 with the following settings: x-ray beam power of 150 kV/0.19 mA, pixel dimensions of 1869 × 989, 3665 total slices, and voxel size of 17.9 μm. The blocks containing the premaxilla, left maxilla, and left palatine were scanned simultaneously on 11 February 2020 with the following settings: x-ray beam power of 160 kV/0.16 mA, pixel dimensions of 714 × 714, 1894 total slices, and voxel size of 30.8 μm. Scan data are freely available on MorphoSource (media ID 000367065 and 000367056). CT scan data of *Asteriornis* were taken from Field *et al.* (47). We segmented the

data using Avizo 2019.1 (Thermo Fisher Scientific) following the best practices proposed by Balanoff *et al.* (49), manipulated models in three-dimensional (3D) space using Netfabb 2019 (Autodesk), and rendered models using Avizo 2019.1 and Blender 2.91.0 (www.blender.org). Our retro-deformed reconstruction of the new skull is provided as STL files on MorphoSource (media ID 000367046).

Phylogenetic analysis

To reinvestigate the relationship of *Ichthyornis* to other avialans, we modified the morphological character matrix first constructed by Clarke and Norell (50) and subsequently modified by Clarke *et al.* (51), Li *et al.* (52), Huang *et al.* (53), and, most recently, Field *et al.* (18). We added scorings to this matrix for proposed Late Cretaceous stem galloanserine *Asteriornis maastrichtensis* from Field *et al.* (47) and our digital reconstruction of its skull (fig. S22), Early Paleocene stem anseriform *Conflicto antarcticus* from Tambussi *et al.* (46), and proposed Late Cretaceous stem anatid *Vegavis iai* from Clarke *et al.* (43). We made the following scoring changes for *Ichthyornis*: 8:1, 12:1, 43:1, and 222:1. We rescored character 221 for all birds lacking teeth from 1 (absent) to ? (unknown/noncomparable); the character describes the presence or absence of dental socketing along the region of the maxilla and dentary occupied by embryonic dental lamina, the presence of which we could not confirm in embryos of extant birds. We also removed two characters from the matrix. We considered original character 210, describing the anteroposterior location of the apex of the sternal carina, to be non-independent with character 72, describing the anterior extent of the carina proper. Original character 221, describing the relative contribution of the premaxilla to the margin of the jaw, was a duplicate of character 8. Last, to include the end-Cretaceous stem birds scored by Longrich *et al.* (19), we added 11 characters from their matrix, which was also a modification of the Clarke and Norell (50) matrix. Our final character matrix is provided in data file S1.

We analyzed the resulting character matrix in TNT 1.5 using an unconstrained traditional heuristic search with Wagner starting trees and all characters equally weighted. We performed 1000 replicates of random stepwise addition using the tree bisection and reconnection algorithm, with 10 trees saved per replication and branches with minimum lengths of 0 collapsed into polytomies. We used the resulting most parsimonious trees (MPTs) to calculate a strict consensus tree. That consensus tree was used in standard (sample with replacement) bootstrap analyses using a traditional search replicated 1000 times with results reported as absolute frequencies. To test the sensitivity of our results to taxonomic sampling, we analyzed our matrix using the following schema: Our primary unconstrained analysis included 9 avian birds, 32 stem birds plus *Archaeopteryx*, and Dromaeosauridae as outgroup (henceforth referred to as our core taxonomic sample). We then analyzed our core taxonomic sample plus *Gansus yumenensis* to test the sensitivity of our results to the latter taxon's inclusion. To test the sensitivity of our results to constraints on the position of *Asteriornis*, we reanalyzed our core taxonomic sample with *Asteriornis* constrained to within Galloanserae and then constrained as a stem galloanserine. Last, we analyzed our taxonomic sample plus the 16 end-Cretaceous stem birds from Longrich *et al.* (19), both without constraints and constrained to match the relationships recovered by those authors.

Supertree assembly and time calibration

To investigate the impact of data from the avian stem on estimates of ancestral avian body mass, we time-calibrated the strict consensus

trees we recovered from both the analysis of our core taxonomic sample and the constrained analysis of our core taxonomic sample plus the 16 additional stem birds from Longrich *et al.* (19). First, we added seven non-avian dinosaurs included in the analyses of Ksepka *et al.* (2) to our tree following the topology used by those authors. Then, for each extinct taxon in the tree, we obtained first and last appearance data from the literature, corresponding to the lower bound and upper bound of the formation(s) from which the taxon is known. Appearance data are provided in data file S2. We then used these data to calibrate the tree in R using the DatePhylo() function in the strap R package (54), with root length = 0.1 and using the equal method. Then, we extracted the clade comprising Aves from the Ksepka *et al.* (2) tree, scaled it to match the depth of that clade in our tree, and grafted it onto our time-calibrated tree. Last, we pruned the total tree to match those taxa for which we had either species body mass averages (extant species) or body mass estimates (extant plus extinct species).

Body mass estimation

Body masses for 26 stem birds were estimated using the correlation with femoral length estimated by Field *et al.* (55). The femoral lengths we used and their references, as well as estimated body masses, are provided in data file S3. Average species body mass for avians and all brain volume estimates were taken from Ksepka *et al.* (2). Our total body mass and brain volume dataset is provided in data file S4.

Ancestral state reconstruction

Ancestral body mass and brain volume were estimated separately in R using the fastAnc() function in the phytools R package (56). To investigate the impact of data from the avian stem on reconstructed ancestral body masses, we used three subsets in our taxonomic sample. The primary subset used 2002 avians, 27 non-avian avialans, and 7 non-avian dinosaurs. The tree pruned to match this sample, as well as the reconstructed ancestral body masses, variances, and 95% confidence intervals are provided in data files S5 to S8. The second expanded taxonomic sample included the primary subset plus the 16 stem birds from Longrich *et al.* (19). The tree pruned to match this sample, as well as the reconstructed ancestral body masses, variances, and 95% confidence intervals are provided in data files S9 to S12. The final subset included only those taxa for which brain volumetric data were available (i.e., 2002 avians, *Archaeopteryx*, and seven non-avian dinosaurs). The tree pruned to match this sample, as well as the reconstructed ancestral body masses, variances, and 95% confidence intervals are provided in data files S13 to S16. Ancestral brain volume reconstruction used the latter sample and tree. Reconstructed ancestral brain volumes, variances, and 95% confidence intervals are provided in data files S17 to S19. Ancestral relative brain size (i.e., encephalization) could not be directly reconstructed for any non-avian avialan except *Archaeopteryx* due to a lack of brain volume data from 25 stem birds added here. Instead, we calculated the ratio of brain volume to body mass for selected nodes using the corresponding values estimated from each of the above ancestral state reconstructions.

Phylogenetics results and comparisons with previously published results

When *Gansus* was excluded, our analysis yielded six MPTs with 605 steps. These trees plus the strict consensus tree (fig. S16) are provided in data file S20. We recovered *Ichthyornis* in its traditional position next to a clade comprising *Iaceornis* plus Aves with weak bootstrap support (26), supported by six synapomorphies: completely fused

premaxillae (1:2), presence of ossified connective tissue bridging transverse processes of thoracic vertebrae (59:1), presence of three sacral vertebrae that are short with dorsally directed parapophyses just anterior to the acetabulum (62:1), presence of pneumatic foramen/foramina on the dorsal surface of the sternum (73:1), flat to convex area of the foramen n. supracoracoideus on the medial surface of the coracoid (98:1), and presence of a facet for articulation with the furcula on the acroracoid of the coracoid (227:1).

We recovered *Iaceornis* next to Aves to the exclusion of *Ichthyornis* with moderate bootstrap support (55) based on four synapomorphies: presence of paired, raised intermuscular ridges on the sternum (77:1); the tip of the extensor process of metacarpal I conspicuously surpasses articular facet by approximately the width of the facet, producing a pronounced knob (143:4); metacarpal III extends farther distally than metacarpal II (148:1); and conformation of the extensor canal on the tibia/tarsal formed condyles as a groove bridged by an ossified supratendinal bridge (182:2).

We recovered the Late Cretaceous *V. iaii* and the Early Paleocene *C. antarcticus*, both from the Antarctic Peninsula, in a polytomy with the Mallard with low bootstrap support (24) based on three synapomorphies: presence of pneumatization on the coracoid (91:0); metacarpal II is subequal to or surpasses metacarpal III in distal extent (149:0); and presence of a hypertrophied, “shelf-like” posterior trochanter on the femur (172:0). *Vegavis* was originally described as a stem anatiid (43), but subsequent analyses variously recovered it as a stem anseriform (57), stem galloanserine (45), or stem avian (47, 58). Our results are consistent with the original placement as a stem anatiid, but our low bootstrap support highlights the need for more data to confidently place *Vegavis*.

The Late Cretaceous *A. maastrichtensis* was originally described and recovered as a stem galloanserine (47). By contrast, our unconstrained analyses recovered *Asteriornis* as a stem Palaeognathae with low bootstrap support (12) based on one synapomorphy: a strongly posteriorly forked dentary with the dorsal and ventral rami approximately equal in posterior extent (42:1). Constraining *Asteriornis* to a clade also including the other galloanserines in our sample resulted in 24 MPTs with 606 steps (one more than when unconstrained; fig. S17), provided in data file S21. This analysis resulted in a weakly supported (bootstrap = 38) polytomy comprising *Asteriornis*, *Conflicto*, *Vegavis*, *Chauna torquata*, *Anas*, and Galliformes (*Pauxi pauxi* + *Gallus gallus*). Constraining *Asteriornis* to the stem of Galloanserae resulted in six MPTs with 606 steps (one more than when unconstrained; fig. S18), provided in data file S22. This analysis resulted in a moderately supported (bootstrap = 52) polytomy including *Asteriornis*, Palaeognathae, Galliformes, and Anseriformes. Together, these results indicate a need for more data before *Asteriornis* can confidently be placed within Aves.

When our analysis included *Gansus*, we recovered 14 MPTs with 616 steps (fig. S19). These trees are provided in data file S23. We recovered *Ichthyornis* in a polytomy also including Hesperornithiformes, *Iaceornis*, *Asteriornis*, Palaeognathae, Neognathae, and several other near-crown stem taxa with low bootstrap support (8).

When we included the 17 end-Cretaceous stem birds from Longrich *et al.* (19) and excluded *Gansus* in an unconstrained analysis, we recovered 4710 MPTs with 610 steps (fig. S20); MPTs and strict consensus are provided in data file S24. We recovered *Ichthyornis* in a polytomy also including Galliformes, Hesperornithiformes, and several other crown and near-crown taxa with very low bootstrap support (5). Because this unconstrained analysis failed to recover

the relationships recovered by Longrich *et al.* (19), we reanalyzed this matrix constrained to match those relationships, and we recovered 7030 MPTs with 610 steps (fig. S21); MPTs and strict consensus tree are provided in data file S25.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/7/31/eabg7099/DC1>

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