Article

Late Cretaceous neornithine from Europe illuminates the origins of crown birds

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Our understanding of the earliest stages of crown bird evolution is hindered by an exceedingly sparse avian fossil record from the Mesozoic era. The most ancient phylogenetic divergences among crown birds are known to have occurred in the Cretaceous period[1–3], but stem-lineage representatives of the deepest subclades of crown birds—Palaeognathae (ostriches and kin), Galloanserae (landfowl and waterfowl) and Neoaves (all other extant birds)—are unknown from the Mesozoic era. As a result, key questions related to the ecology[4,5], biogeography[3,6,7] and divergence times[1,8–10] of ancestral crown birds remain unanswered. Here we report a new Mesozoic fossil that occupies a position close to the last common ancestor of Galloanserae and fills a key phylogenetic gap in the early evolutionary history of crown birds[10,11]. *Asteriornis maastrichtensis*, gen. et sp. nov., from the Maastrichtian age of Belgium (66.8–66.7 million years ago), is represented by a nearly complete, three-dimensionally preserved skull and associated postcranial elements. The fossil represents one of the only well-supported crown birds from the Mesozoic era[12], and is the first Mesozoic crown bird with well-represented cranial remains. *Asteriornis maastrichtensis* exhibits a previously undocumented combination of galliform (landfowl)-like and anseriform (waterfowl)-like features, and its presence alongside a previously reported *Ichthyornis*-like taxon from the same locality[13] provides direct evidence of the co-occurrence of crown birds and avialan stem birds. Its occurrence in the Northern Hemisphere challenges biogeographical hypotheses of a Gondwanan origin of crown birds[3], and its relatively small size and possible littoral ecology may corroborate proposed ecological filters[4,5,9] that influenced the persistence of crown birds through the end-Cretaceous mass extinction.

By any measure, crown birds (Neornithes) are among the most diverse and conspicuous of the extant tetrapods, yet their early evolutionary history is poorly understood. Apart from birds, all major groups of extant tetrapods—lissamphibians[14], squamates[15], turtles[16], mammals[17] and crocodylians[18]—are well-known from pre-Cenozoic crown-group fossils. By contrast, the Mesozoic record of well-supported crown birds is restricted to a single latest Maastrichtian taxon, *Vegavis iaai*[12]. Several fragmentary Mesozoic fossils have at times been referred to Neornithes[19], although the justifications for such assignments are questionable and these records have not unambiguously withstood re-evaluation[20,21].

We report a new crown bird from the Late Cretaceous of Belgium. The fossil is between 66.8 and 66.7 million years old—making it the oldest unambiguous crown bird fossil yet discovered—and provides important insight into the extent of Mesozoic neornithine diversification before the end-Cretaceous mass-extinction event, 66.02 million years ago (Ma)[22]. Uniquely among crown birds from the Mesozoic and earliest Palaeocene, the new fossil includes a nearly complete, three-dimensionally preserved skull, yielding direct insights into the nature of the crown bird skull early in neornithine evolutionary history. The specimen exhibits a previously unseen combination of features that are diagnostic of Galliformes and Anseriformes, which together form the crown clade Galloanserae—one of the most deeply diverging clades of crown birds and the sister group to the hyperdiverse extant clade Neoaves[1–3]. Our most parsimonious phylogenetic hypothesis suggests that the fossil sits on the stem lineage of Galloanserae, which would make it the only stem galloanseran yet known and would fill a conspicuous phylogenetic gap in the neornithine fossil record.

Systematic palaeontology

Avialae Gauthier, 1986
Neornithes Gadow, 1892
Neognathae Pycraft, 1900
Pangalloanserae Gauthier and de Queiroz, 2001
Asteriornis maastrichtensis gen. et sp. nov.

Remarks. We use Avialae to refer to theropods crownward of Dromaeosauridae and Troodontidae. Neornithes is equivalent to the bird crown

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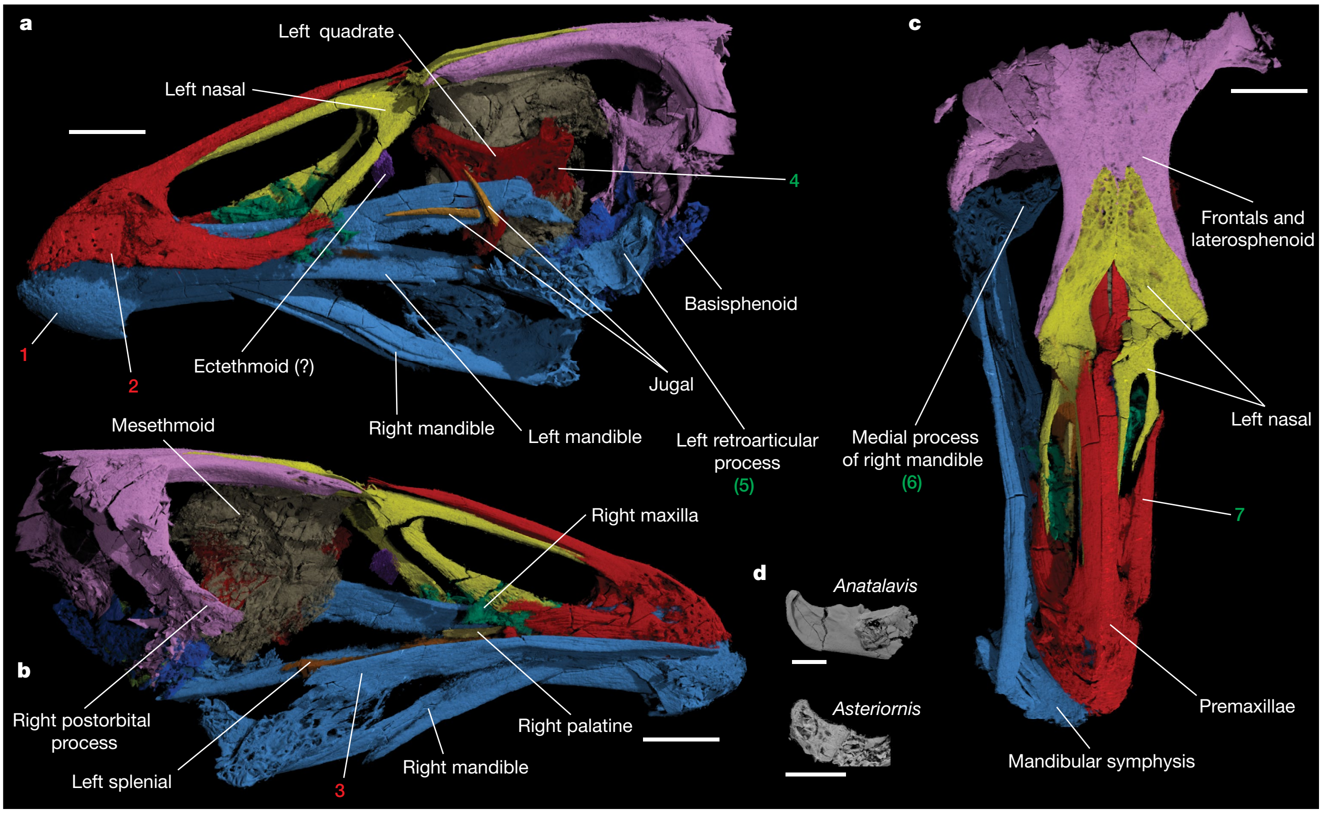

Fig. 1 | Digitally segmented skull of *Asteriornis maastrichtensis*. **a**–**c**, Left lateral view (**a**), right lateral view (**b**) and dorsal view (**c**) of the *A. maastrichtensis* skull. **d**, Comparison of retroarticular processes in lateral view of *Anatalavis oxfordi* (right side) and *Asteriornis* (left side, reflected). Selected synapomorphies are denoted with numbers (red, Neornithes; green, Galloanserae[37–39]): 1, bony mandibular symphysis; 2, toothless beak; 3, no coronoid bone; 4, bicondylar mandibular process of quadrate; 5, retroarticular process long, curving, strongly compressed mediolaterally; 6, dorsally oriented internal articular process of mandible; 7, maxillary process of premaxilla dorsoventrally deep and lateromedially compressed. Scale bars, 5 mm.

group (Aves sensu Gauthier, 1986[23]). Pangalloanserae defines the most inclusive clade including *Anser anser* and *Gallus gallus* but not *Passer domesticus* (that is, the galloanseran total group). Further phylogenetic definitions are presented in the Supplementary Information.

Etymology. *Asteriornis*, from the name of the Titan goddess *Asteria* and the Greek *ornis* for bird. In Greek mythology Asteria is the goddess of falling stars and transforms herself into a quail—attributes that are reflected by both the impending Cretaceous–Palaeogene (K–Pg) asteroid impact and the galloanseran affinities of *Asteriornis*. The specific epithet *maastrichtensis* reflects the provenance of the holotype—the Maastricht Formation (the type locality of the Late Cretaceous Maastrichtian stage).

Holotype. Natuurhistorisch Museum Maastricht (NHMM) 2013 008, a nearly complete, articulated skull including mandibles and associated postcranial remains preserved in four blocks (Fig. 1, Extended Data Figs. 1–7; see Supplementary Information for videos, character information, measurements, additional description and discussion). Preserved elements include the premaxillae, maxillae, nasals, frontals, laterosphenoid, basisphenoid, mesethmoid, left quadrate, left jugal, right palatine and lower jaws. Associated postcranial elements include incomplete femora, tibiotarsi, tarsometatarsus and radius.

Locality and age. CBR-Romontbos Quarry, Eben-Emael, Liège, Belgium. Valkenburg Member (66.8–66.7 million years old[24]), Maastricht Formation, Late Maastrichtian, Cretaceous. Additional details regarding the locality and stratigraphic setting are presented in the Supplementary Information.

Diagnosis. *Asteriornis* is unique among known taxa in exhibiting caudally pointed nasals that overlie the frontals and meet at the midline of the skull, and a slightly rounded, unhooked tip of the premaxilla. Additional character combinations from phylogenetic analyses that differentiate *Asteriornis* are presented in the Supplementary Information.

Description

Asteriornis maastrichtensis is a small pan-galloanseran, with an estimated mean body mass from hindlimb scaling regressions of 394 g (around the 21st percentile among extant Galloanserae[25]; Extended Data Fig. 8). Complete measurements of NHMM 2013 008 are provided in the Supplementary Information.

Most major cranial components are in their original anatomical positions. The general appearance of the premaxillary beak resembles that of extant Galliformes, particularly in its gently down-curved tip and delicate construction, with no ossified joints among the rostral components[26]. The contralateral frontal processes of the premaxillae are unfused along their length, and the premaxillae and nasals are unfused at both their tomial and narial contacts. The beak tip is unhooked, which distinguishes *Asteriornis* from most Galloanserae except certain Anatidae and Presbyornithidae.

The skull lacks a distinct nasofrontal hinge. As such, the architecture of this region more closely resembles that of extant Galliformes than Anseriformes. At the midpoint of the orbits the frontals are constricted, yielding an hourglass-shaped cranial roof with wider rostral and caudal extremities. In dorsolateral view, the right postorbital process sweeps strongly ventrally before deflecting rostrally to define part of the ventral margin of the orbit.

The left quadrate is well-preserved in three dimensions and is generally similar to the quadrate of the fossil pan-anseriform *Presbyornis*[27]

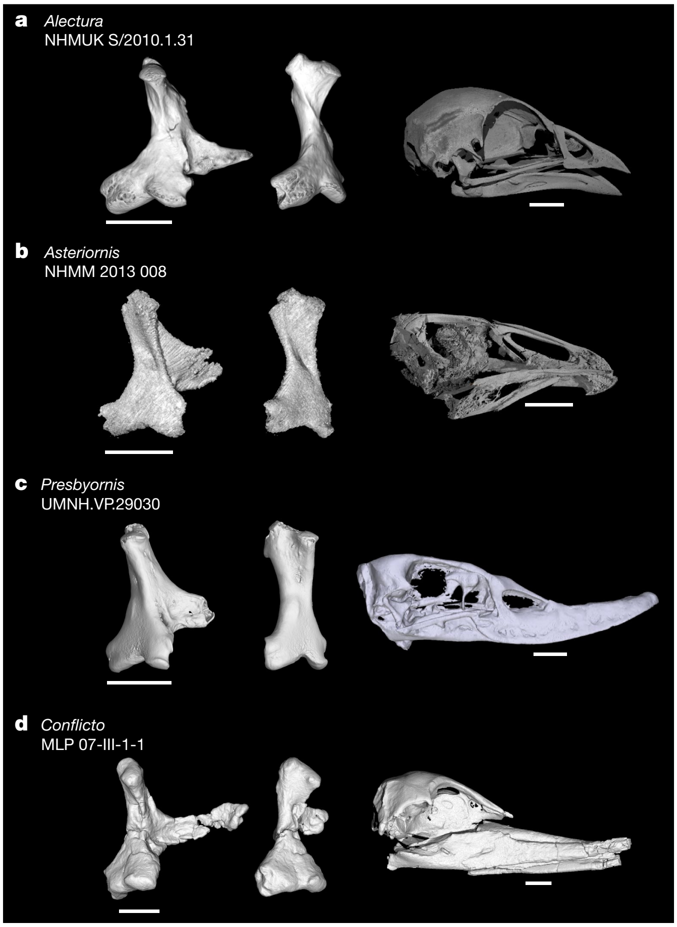

Fig. 2 | Comparative quadrate and skull morphology of selected total-group Galloanserae. a–**d**, Left quadrates (and reflected right quadrate of *Presbyornis*) in medial view (left) and caudal view (middle). Skulls are in right lateral view, except *Alectura* which is in reflected left lateral view. The skull of *Presbyornis* USNM 299846 is shown. Scale bars, 5 mm (quadrates); 1 cm (skulls). See Extended Data Fig. 4 for additional high-resolution images of these taxa and other extant and fossil Galloanserae.

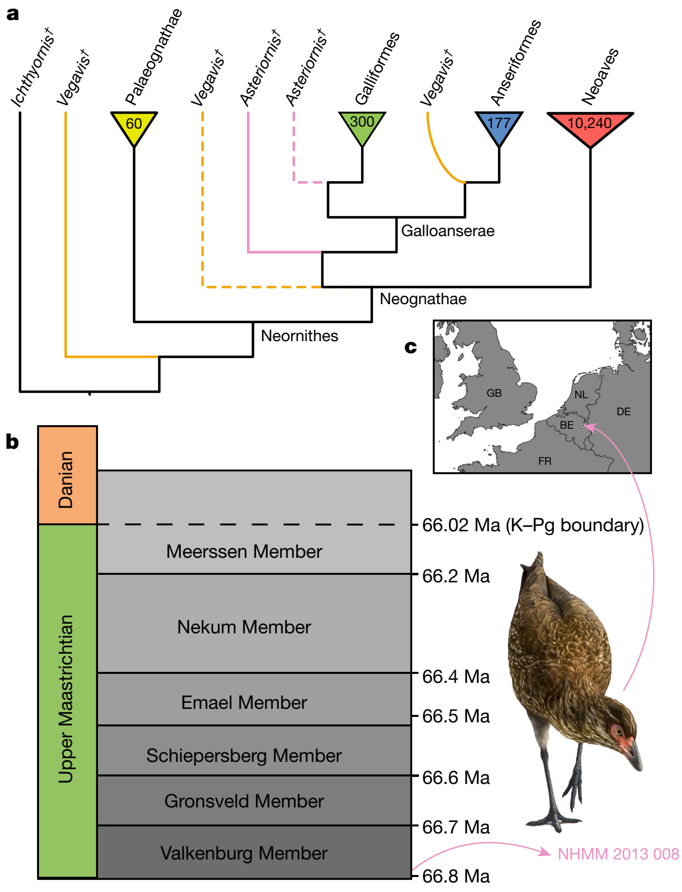

Fig. 3 | Relationships of *A. maastrichtensis* and stratigraphic provenance of holotype. a, Cladogram showing the phylogenetic position of *Asteriornis* and *Vegavis* inferred under parsimony (solid coloured lines) and tip-dated Bayesian analyses (dashed lines). A position for *Vegavis* allied with Anseriformes, as previously found[12,28,34], is also shown (curved branch). Numbers within clades denote extant species richness. The analysis is based on a newly modified dataset; see Extended Data Fig. 9 and Supplementary Information for full phylogenetic results. Extinct taxa are denoted with daggers. **b**, Simplified stratigraphy of the Maastricht Formation, exposed in the vicinity of the holotype locality and surrounding areas[24]. **c**, Location of the CBR-Romontbos Quarry near Eben-Emael, Belgium.

(Fig. 2, Extended Data Fig. 4). The prootic and squamosal heads are divided by a well-developed incisure, as in almost all Neognathae; this contrasts with the condition in crownward stem birds such as *Ichthyornis*, in which the division between these condyles is poorly marked, and Palaeognathae, in which the condyles merge into a single head. Two pneumatic foramina pierce the quadrate: the foramen pneumaticum rostromediale and the foramen pneumaticum basiorbitale. A tuberculum subcapitulare is moderately developed on the lateral face of the otic process. This characteristic has been considered a derived feature of Galloanserae[27]; however, it is present in many Neoaves, and given its absence in Palaeognathae and *Ichthyornis* it might instead represent a synapomorphy of Neognathae. The cotyla quadratojugalis of the quadrate is fairly deep, with a complete, un-notched rim. The pterygoid articulation is more widely separated dorsally from the mandibular condyle than in most extant Galloanserae, and is very similar to that of *Presbyornis*.

As in all known Galloanserae, the mandible of *Asteriornis* exhibits two cotylae for articulation with the bicondylar quadrate and a blade-like retroarticular process. This process is strongly hooked, and in its shape and proportions bears a strong resemblance to the condition in the pan-anseriform *Anatalavis oxfordi* (Fig. 1d, Extended Data Fig. 5). An elongate, slightly dorsally oriented processus medialis is preserved on the right jaw, as in all Galloanserae.

The left distal femur is well-preserved, exhibiting a medial condyle with a bluntly angular profile between the articular surface of the condyle and its cranial margin. A detailed anatomical description of the skull and postcranium is provided in the Supplementary Information.

Phylogenetic analysis

We investigated the phylogenetic position of *Asteriornis* under alternative optimality criteria, with and without molecular scaffolds[1,2], using a matrix of 39 taxa and 297 characters modified from previous studies[28,29] (Fig. 3, Extended Data Fig. 9; see Methods and Supplementary Information). We added recently described taxa such as *Protodontopteryx*[30], and revised the scorings for several taxa, including *Anatalavis*, *Presbyornis* and *Conflicto*. Our analyses were uniformly consistent with a position of *Asteriornis* near the last common ancestor of Galloanserae. Under parsimony we recovered a single most parsimonious tree with *Asteriornis* as the sister taxon to crown Galloanserae, and analyses under a tip-dated Bayesian framework recovered *Asteriornis* as the stemward-most pan-galliform. We are cautious in the interpretation of this result because few unambiguous synapomorphies can be optimized in support of a sister group relationship between *Asteriornis* and Galliformes to the exclusion of Anseriformes. The few potential synapomorphies for such a clade that are observable in *Asteriornis* also occur in early pan-anseriforms such as *Conflicto* (see Methods and Supplementary Information). Likewise, only one or two steps are required to move *Asteriornis* to an alternate placement as a stem anseriform or stem galliform, respectively, in the parsimony analysis. The difficulty in resolving the precise placement of the fossil, as well as its notable combination of anseriform- and galliform-like anatomical features, is consistent with *Asteriornis* occupying a short phylogenetic branch proximal to the most recent common ancestor of Galloanserae—one of the deepest nodes in the neornithine tree of life[31].

Discussion

The latest Cretaceous fossil record of crown birds is extremely sparse. Other than *Asteriornis*, *Vegavis iaai* (dated to around 66.5 Ma[32]) is the only Cretaceous neornithine known from a partial skeleton to have been thoroughly examined[12]. However, its phylogenetic position is debated[33]—studies have suggested variable positions within Neognathae[12,28,33–35] and even outside Neornithes[36]—emphasizing the importance of obtaining new information on *Vegavis* and Mesozoic crown birds in general. Under parsimony, we recovered *Vegavis* as the sister taxon to Neornithes (that is, the crownward-most stem bird), whereas under a Bayesian framework *Vegavis* was recovered in an unresolved position at the base of Neognathae.

Galloanseran cranial anatomy

All discernible character evidence is consistent with neornithine (crown bird) affinities for *Asteriornis*, and supports its hierarchical placement within Neornithes (local synapomorphies such as a toothless beak; no coronoid bone; a bony mandibular symphysis), crown Neognathae (for example, palatine–premaxilla contact; an incisure between the prootic and squamosal cotylae of the quadrate) and Pangalloanserae (for example, a dorsoventrally deep and lateromedially compressed maxillary process of the premaxilla; palatines that are long, thin and widely separated rostrally; a bicondylar mandibular process of the quadrate; a long, dorsally oriented internal articular process of the mandible; a retroarticular process that is long, curving and strongly compressed lateromedially)[37–39] (Fig. 1). Given the scarcity of three-dimensional skulls from the earliest stages of the crown bird radiation, *Asteriornis* provides a key reference point for understanding how the marked variability of the crown bird skull came to be, and will inform estimates of early neornithine cranial disparity and rates of phenotypic evolution[40,41].

With the exception of the autapomorphic morphology of the posterior nasals, almost none of the discernible cranial anatomy of *Asteriornis* falls outside of the range of variation that is exhibited by extant galloanserans, despite the widely differing cranial morphology of extant Galliformes and Anseriformes[26]. Although galloanseran monophyly is now widely accepted (and was first suggested on the basis of basicranial morphology as early as the mid-nineteenth century[42]), the validity of this clade has been questioned[26,43], with some authors listing numerous anatomical dissimilarities between these groups[26]. Notably, *Asteriornis* reveals a previously undocumented combination of 'galliform' features, such as weakly fused rostral elements and rostrally forked nasals, and 'anseriform' features, such as a rostrally projecting postorbital process and a tall and strongly hooked retroarticular process (Fig. 1, Extended Data Figs. 1–6)—revealing the plesiomorphic condition of the galloanseran skull. The fact that such distinctive features of extant galloanseran anatomy are observable in this approximately 66.7-million-year-old fossil corroborates the hypothesis of beak shape canalization arising early in, or predating, crown bird evolutionary history[44,45], emphasizing the modular nature of the skull and bill of crown birds[40].

Biogeography and the origin of Neornithes

Much of the species-level and higher clade diversity of extant birds is confined to vestiges of Gondwana, which suggests that crown birds originated in the Southern Hemisphere[3]. Reports of Mesozoic crown birds in Antarctica appear to support this hypothesis[12,34]. However, the Palaeogene fossil record provides many examples of crown bird fossils that are well outside of the ranges of their closest extant relatives[6,21,46,47], which casts some doubt on the hypothesis of a Gondwanan cradle for crown bird evolution and suggests that factors such as Cenozoic climate shifts may have overprinted ancestral neornithine biogeographical patterns[7,48]. As the oldest and one of the most deeply diverging crown birds yet identified, *Asteriornis* provides conclusive Mesozoic evidence of Neornithes in the Northern Hemisphere, emphasizing that the discovery of further Mesozoic fossils will be necessary to convincingly identify the neornithine centre of origin.

Asteriornis provides a firm calibration point for the minimum age of divergence of the major bird clades Galloanserae and Neoaves. We recommend that a minimum age of 66.7 million years is assigned to this pivotal neornithine node in future divergence time studies, reflecting the youngest possible age of the *Asteriornis* holotype including geochronological uncertainty. The paucity of crown bird remains from the Mesozoic is such that our current understanding of the deepest stages of the neornithine evolutionary timescale depends on the outcome of molecular divergence time analyses[9]. However, molecular-clock-based estimates for the deepest divergences of crown birds differ markedly depending on factors such as node calibration decisions and alternative parameterizations of statistical probability distributions[8,10]. Furthermore, such estimates could be affected by the interplay of nucleotide substitution rates and deep-time directional selectivity on life history variables and body size, leading to disagreement as to the extent of neornithine survivorship across the end-Cretaceous mass-extinction event[8–10]. We suggest that the terminal-Cretaceous age and rootward phylogenetic position of *Asteriornis* are consistent with a limited diversification of crown birds in the Late Cretaceous, and restricted survivorship of crown birds across the end-Cretaceous mass-extinction event. This interpretation is in line with the emerging consensus from molecular divergence time studies[1,2,8–10], as well as evidence for a mass extinction of stem birds at the K–Pg boundary[20]. Furthermore, the oldest credible occurrences of crown birds in both the Northern (this study) and Southern Hemispheres[12] derive from terminal Mesozoic sediments, which might confirm the recently proposed null expectation of a rapid evolutionary transition between stem birds and crown birds[31]. The occurrence of a large *Ichthyornis*-like avialan[13] from the same horizon and quarry as the *Asteriornis* holotype (with temporal separation amounting to no more than tens of thousands of years; see Supplementary Information) provides evidence of crown birds and avialan stem birds occurring in the same environment in the immediate lead-up to the K–Pg mass extinction.

Considerable discussion has focused on hypothetical scenarios of neornithine survivorship across the end-Cretaceous mass extinction[4]. A consensus hypothesis is emerging in which survivors are thought to have exhibited a suite of features that proved selectively beneficial through the extinction event, including a relatively small body size to limit total metabolic requirements[9], flying ability and a non-arboreal ecology[4,11]; an advanced digestive system[49]; and dietary flexibility to capitalize on sparse resources that might have included insects and seeds[5]. However, owing to the scarcity of latest Cretaceous and earliest Palaeocene neornithine fossils, little direct fossil evidence can be applied to this question. *Asteriornis* could therefore provide the best direct insight into the probable biology of neornithine K–Pg survivors, and—notably—no discernible aspects of its palaeobiology are inconsistent with these hypothetical expectations. Indeed, its relatively small size (less than 50% of the median body size of known latest Maastrichtian avialans[9]), narrow and elongate hindlimbs (Supplementary

Information) and provenance from nearshore marine sediments might indicate a littoral ecology, which could validate an ecological—though not a phylogenetic—prediction of the hypothesis of 'shorebird'-like origins for much of crown bird diversity[50].

Fossils that clarify the Mesozoic origins of the extant bird radiation are among the rarest and most sought-after palaeontological discoveries. *Asteriornis* helps to fill a phylogenetic and stratigraphic gap between the most crownward-known stem birds and the rich Cenozoic neornithine fossil record. This record of a Mesozoic neornithine from Europe provides key insights into the origin of extant bird diversity, and shows that future discoveries of even earlier Cretaceous neornithines could be as likely to derive from the Northern as the Sourthern Hemisphere.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41586-020-2096-0.

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Methods

Preparation and imaging of specimens

Owing to the fragility of the *Asteriornis* holotype, only minor mechanical preparation was performed to reduce the volume of rock matrix for improved computed tomography (CT) scans. Scans of NHMM 2013 008, UW *Presbyornis* specimens and all extant taxa were performed at the Cambridge Biotomography Centre (CBC). *Presbyornis* UMNH.VP.29030 and UMNH.VP.29031 were scanned at the small-animal-imaging core research facilities of the University of Utah Health Science Cores. *Anatalavis oxfordi* NHMUK PV A5922 was scanned at the Natural History Museum London. All scanned material was digitally segmented and rendered using VGStudio Max 3.3.0. Full CT scanning details are provided in the Supplementary Information.

Phylogenetic analyses

To assess the phylogenetic position of *Asteriornis*, we scored it into a considerably modified version of a recent phylogenetic matrix that targets deep neornithine divergences and focuses on Galloanserae[29], which in turn was modified from a previous study[28]. We also added the crownward stem bird *Ichthyornis dispar* as an outgroup taxon to improve the inference of character polarity at the base of crown birds, on the basis of direct examination of specimens and previously published literature[51,52]. We scored the stem galliform *Gallinuloides wyomingensis* through direct examination and reference to published descriptions[53,54], and scored the pelagornithids *Protodontopteryx ruthae*[30] and *Pelagornis chilensis*[55] on the basis of published literature. The phylogenetic position of Pelagornithidae is debated, and they have been posited as early-diverging pan-neognaths or pan-galloanserans in previous studies[56,57]. A right humerus and ulna associated with the *Protodontopteryx* holotype are of questionable assignment to the taxon[30] and were therefore disregarded for the purposes of scoring. Additional details of matrix modifications and taxon sampling are presented in the Supplementary Information.

Maximum parsimony analyses were conducted in TNT v.1.5[58]. After increasing the maximum number of trees to 10,000, a new technology search was run in which a minimum length tree was found in 10 replicates and default parameters were set for sectorial search, ratchet, tree drift and tree fusion. After this, the maximum number of trees was set to 100 and a traditional search with default parameters was run on the trees in RAM to explore treespace more extensively. Absolute bootstrap frequencies were obtained from 1,000 replicates under a traditional search with default parameters. The tree length induced by alternative phylogenetic topologies was evaluated by unchecking the 'lock trees' option in TNT and manually moving branches to alternative phylogenetic positions.

Bayesian phylogenetic analyses were conducted in MrBayes[59] using the CIPRES Science Gateway[60]. Data were analysed under the Mkv model[61], taking into account the absence of invariant characters in our dataset. To allow for variation in evolutionary rate across different characters, gamma-distributed rate variation was assumed. Analyses were conducted using four chains and two independent runs, with a tree sampled every 4,000 generations and a burn-in of 25%. We performed Bayesian tip-dating under the fossilized birth–death model[62], implemented in MrBayes following established procedures[63]. An independent-gamma rates (IGR) clock model was used. The clock rate prior was set at a diffuse, uninformative rate, whereas the IGR variation, speciation, extinction and fossilization priors were set at the MrBayes default distributions: exp(10) for the former two parameters and beta(1,1) for the latter two. These settings follow other recent tip-dating studies[64,65]. Given that our extant taxon sample did not reflect the relative diversity of extant bird groups—focusing primarily on galloanserans (which represent 72% of our extant taxon sample, in contrast with around 4% of extant bird diversity based on recent species counts[66])—we assumed a random instead of a diversified sampling strategy. Taxon sampling probability was assigned a value of 0.0023, based on the fact that our extant taxon sample covers roughly 0.23% of extant bird diversity[66].

To account for ongoing controversies about the timing of crown bird diversification, two tip-dating analyses were run, each with different prior age probability distributions. In one analysis, a soft-maximum upper bound was set at 86.5 Ma for crown birds, following previous justifications[1]. This represents the age of the Niobrara Formation, a well-sampled Upper Cretaceous fossil-bearing formation from which no crown bird fossils have been recovered despite an abundance of small vertebrates and crownward stem-bird fossils[52,67]. A previous study[9] found evidence for increased nucleotide substitution rates at the base of Neornithes. The authors suggested that this phenomenon might be partially responsible for the older ages estimated by other studies[68,69] and outlined criteria under which the use of "appropriately conservative" age priors are justified, concluding that crown birds—like placental mammals[70]—are one clade for which such conservative treatment could be warranted[9]. As such, a more restrictive soft maximum of 72.72 Ma was used for the second tip-dating analysis, based on the estimated age of crown birds in a previous study[1]. For both tip-dating analyses, a soft maximum of 120 Ma was assigned to the root (the divergence between *Ichthyornis* and Neornithes) reflecting the minimum age of the Jiufotang Formation, the youngest phase of the Jehol Biota[71]. This assemblage preserves an abundance of Lower Cretaceous avialan fossils, but none that are phylogenetically crownward of *Ichthyornis*[72]. Given that no fossil crown neoavians were included in our dataset, a prior age probability distribution was assigned to the neoavian clade Gruiformes, with a minimum age of 53.95 million years (the age of *Pellornis mikkelseni*, the oldest well-established crown gruiform[73]) and a soft maximum of 66 million years (the age of the K–Pg boundary, prior to which no well-corroborated crown neoavian fossils have been identified[74]). An exponential distribution was used for all of these age priors, allowing for a 5% prior probability of each clade having originated earlier than its specified soft maximum.

The ages of fossil taxa were fixed at the minimum age constraints for the specimens that were used to score our morphological dataset, in line with best practices[75] and the results of experimentally testing alternative calibrations on an empirical dataset[76]. *Asteriornis* was accordingly assigned a minimum age of 66.7 million years. Most minimum age calibrations for taxa previously included in our dataset follow published ages[28]. Following the recommended ages of relevant fossil-bearing localities, *Gallinuloides* from the Green River Formation was assigned an age of 51.57 million years and *Anatalavis* from the London Clay Formation was assigned an age of 53.5 million years[32]. Despite being known from younger strata, *Presbyornis* was also assigned an age of 51.57 million years because it had been scored into the dataset on the basis of specimens held at the National Museum of Natural History in Washington, DC[77], which had primarily been collected from the Green River Formation. *Ichthyornis* was assigned an age of 86.5 million years[78], *Conflicto* was assigned an age of 61 million years[29], *Pelagornis* was assigned an age of 4.8 million years[55] and *Protodontopteryx* was assigned an age of 61.5 million years[30].

Undated Bayesian analyses were run for 30,000,000 generations, whereas tip-dated analyses were run for 60,000,000 generations. Analytical convergence was assessed using standard diagnostics provided in MrBayes (average standard deviation of split frequencies < 0.02, potential scale reduction factors $= 1$, effective sample sizes > 200). Results of independent runs of the same analyses were summarized using the sump and sumt commands in MrBayes. Morphological synapomorphies were optimized under parsimony onto resulting tree topologies using TNT. Molecular scaffolds followed the consensus from previous phylogenomic studies[1,2,79–81].

Estimation of body size

The minimum mediolateral cross-sectional diameter of the tarsometatarsus shaft (3.32 mm) was taken from high-resolution CT scans.

This measurement was incorporated into a published scaling equation for estimating the body masses of volant birds[25] ($R^2 = 0.93$) and compared with a published compilation of the body sizes of extant galloanserans[82].

Reporting summary

Further information on research design is available in the Nature Research Reporting Summary linked to this paper.

Data availability

The holotype specimen of *A. maastrichtensis* is deposited in the permanent collection of the Natuurhistorisch Museum Maastricht under collection number NHMM 2013 008. Digital models of the *A. maastrichtensis* skull and postcranial elements, .tre files from phylogenetic analyses and CT scans of the *A. maastrichtensis* holotype are available at Zenodo (doi: 10.5281/zenodo.3610226). The Life Science Identifier for *Asteriornis* is urn:lsid:zoobank.org:pub:32192A46-4A43-48CE-8F17-447900FCC6DF.

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Author contributions J.W.M.J. provided the material and stratigraphic data; D.J.F. prepared the specimens; D.J.F. and J.B. acquired CT scans and discovered the skull; D.J.F., J.B. and A.C. performed digital segmentation of the material and created figures; D.J.F., J.B., A.C. and D.T.K. performed anatomical comparisons; J.B. and A.C. performed the phylogenetic analyses; and D.J.F. wrote the paper, with contributions from all authors.

Competing interests The authors declare no competing interests.

Additional information
Supplementary information is available for this paper at https://doi.org/10.1038/s41586-020-2096-0.
Correspondence and requests for materials should be addressed to D.J.F.
Peer review information *Nature* thanks Jingmai O'Connor and Kevin Padian for their contribution to the peer review of this work.
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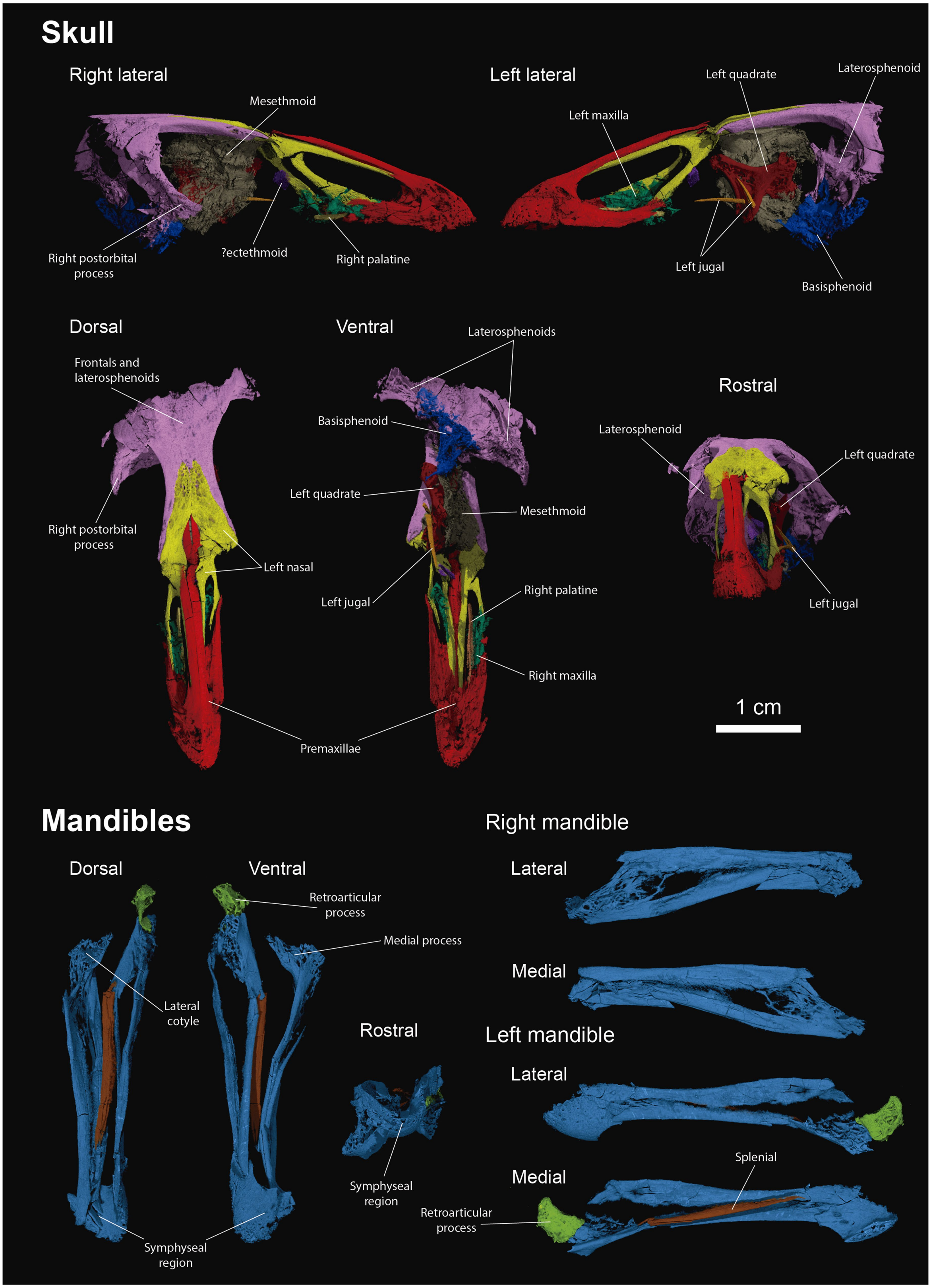
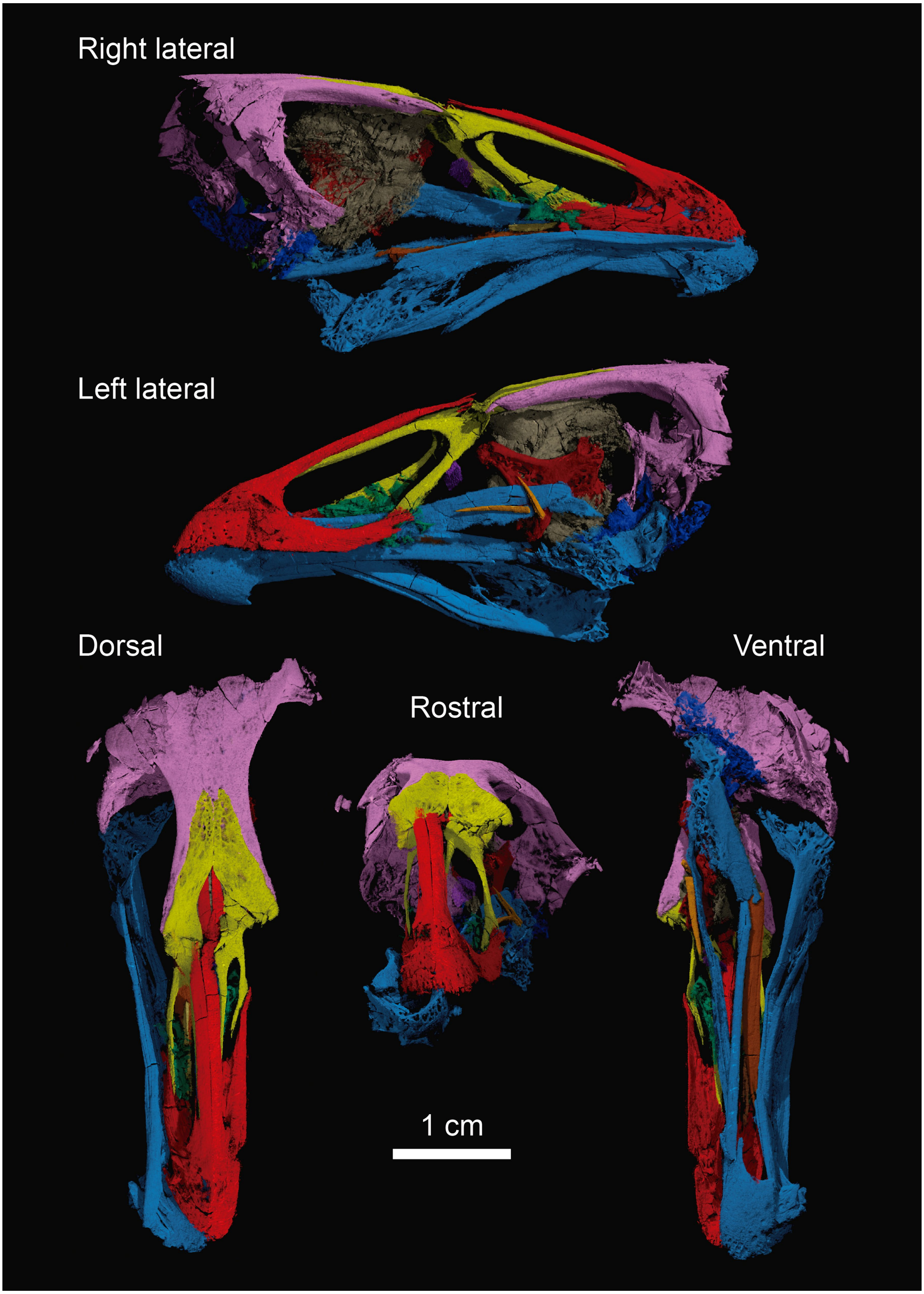
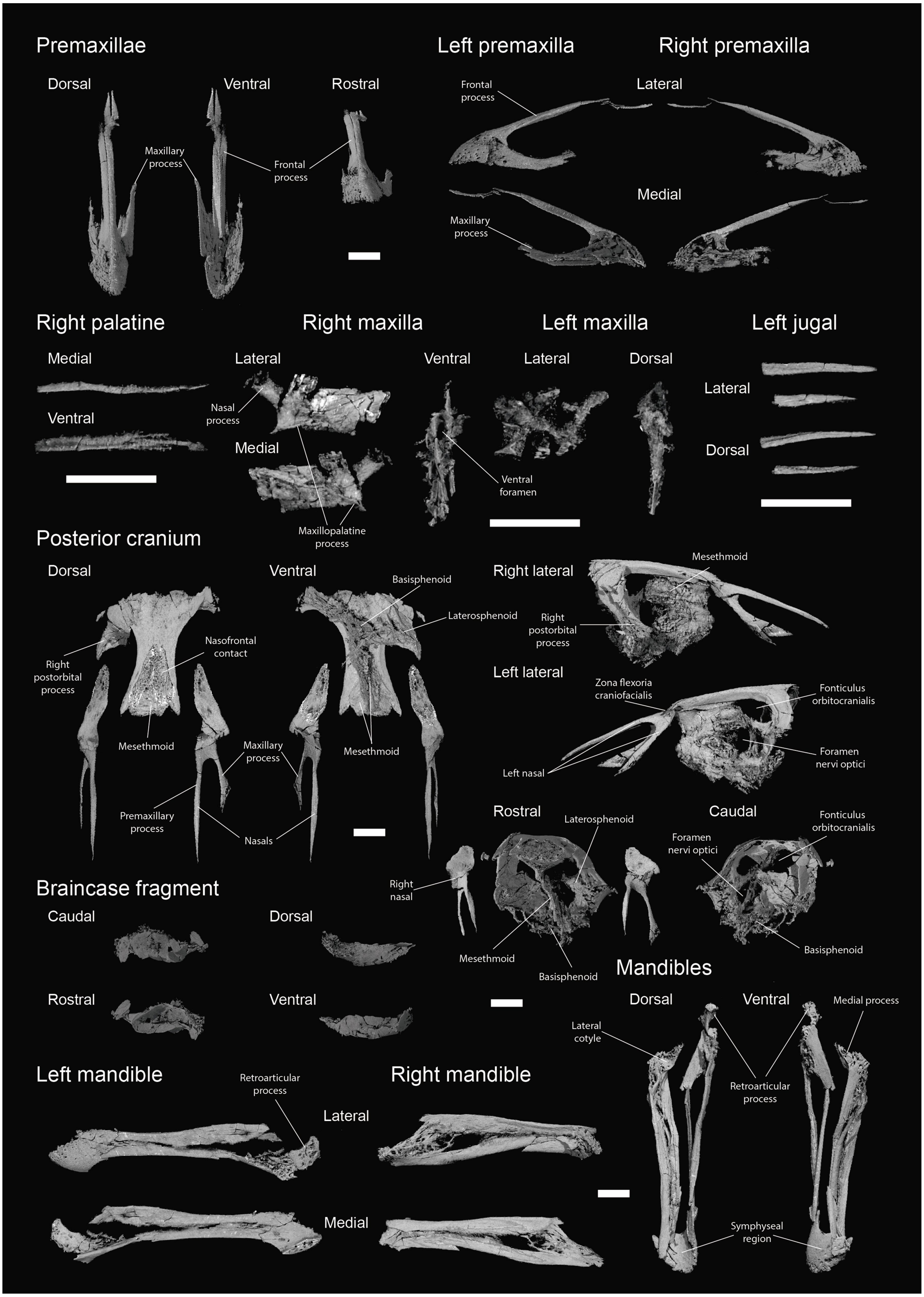


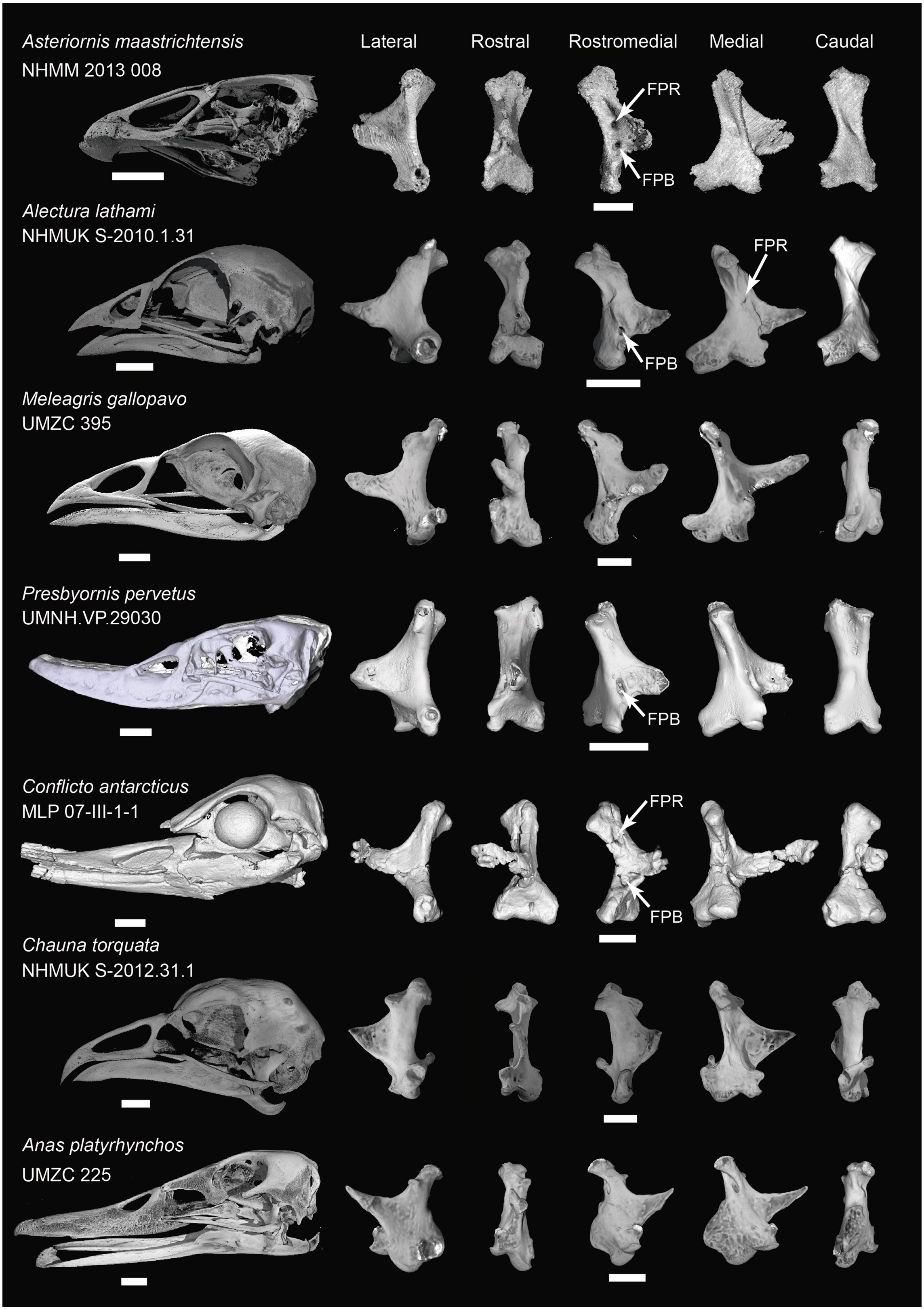
Extended Data Fig. 1 | Detailed cranial and mandibular anatomy of *A. maastrichtensis* (NHMM 2013 008). The views of the cranium are similar to those in Fig. 1, but with the jaws removed to illustrate the ventral portion of the skull.



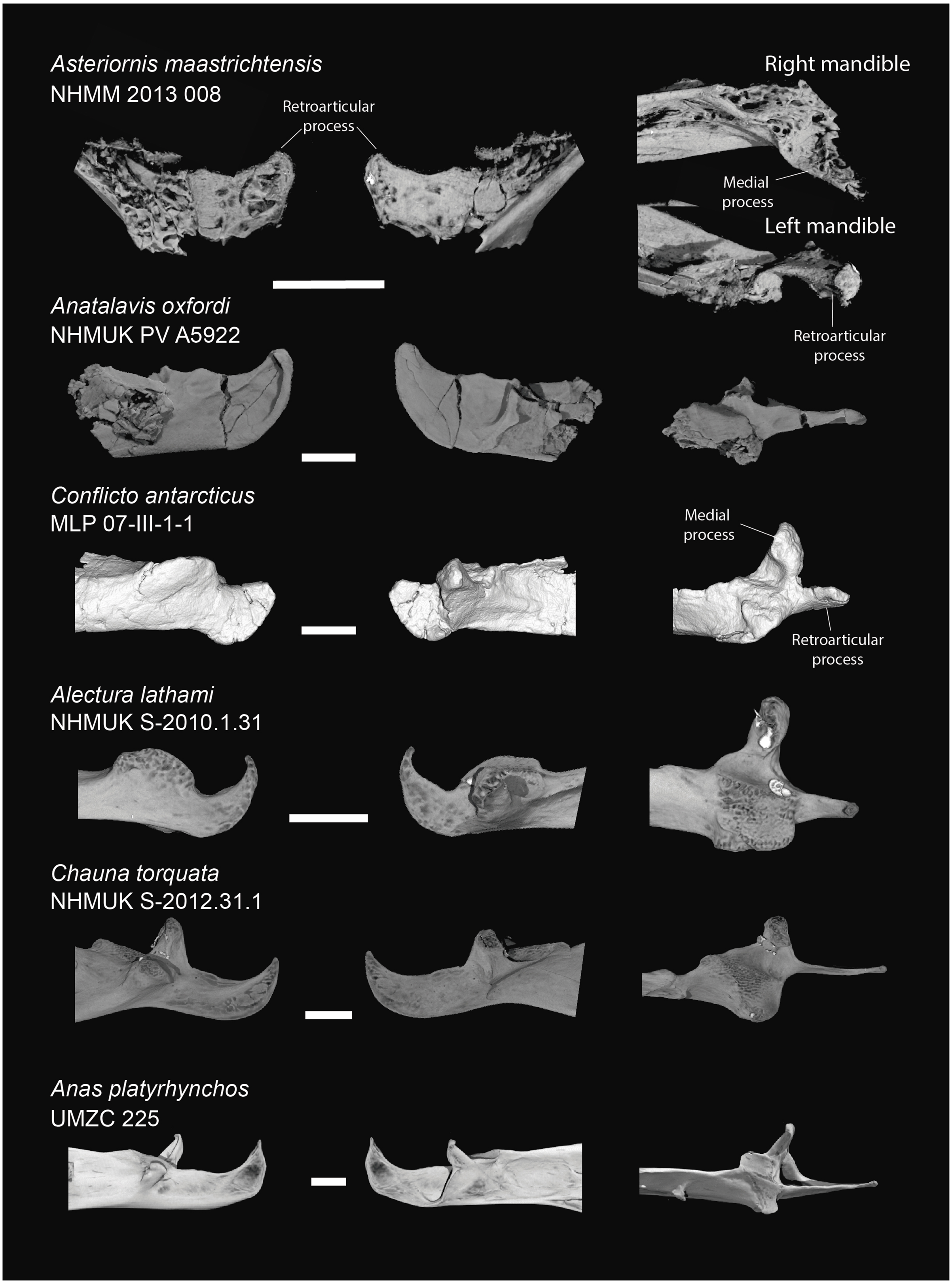
Extended Data Fig. 2 | Higher-resolution cranial and mandibular anatomy of *A. maastrichtensis* (NHMM 2013 008). Labels have been removed and images enlarged to show details.



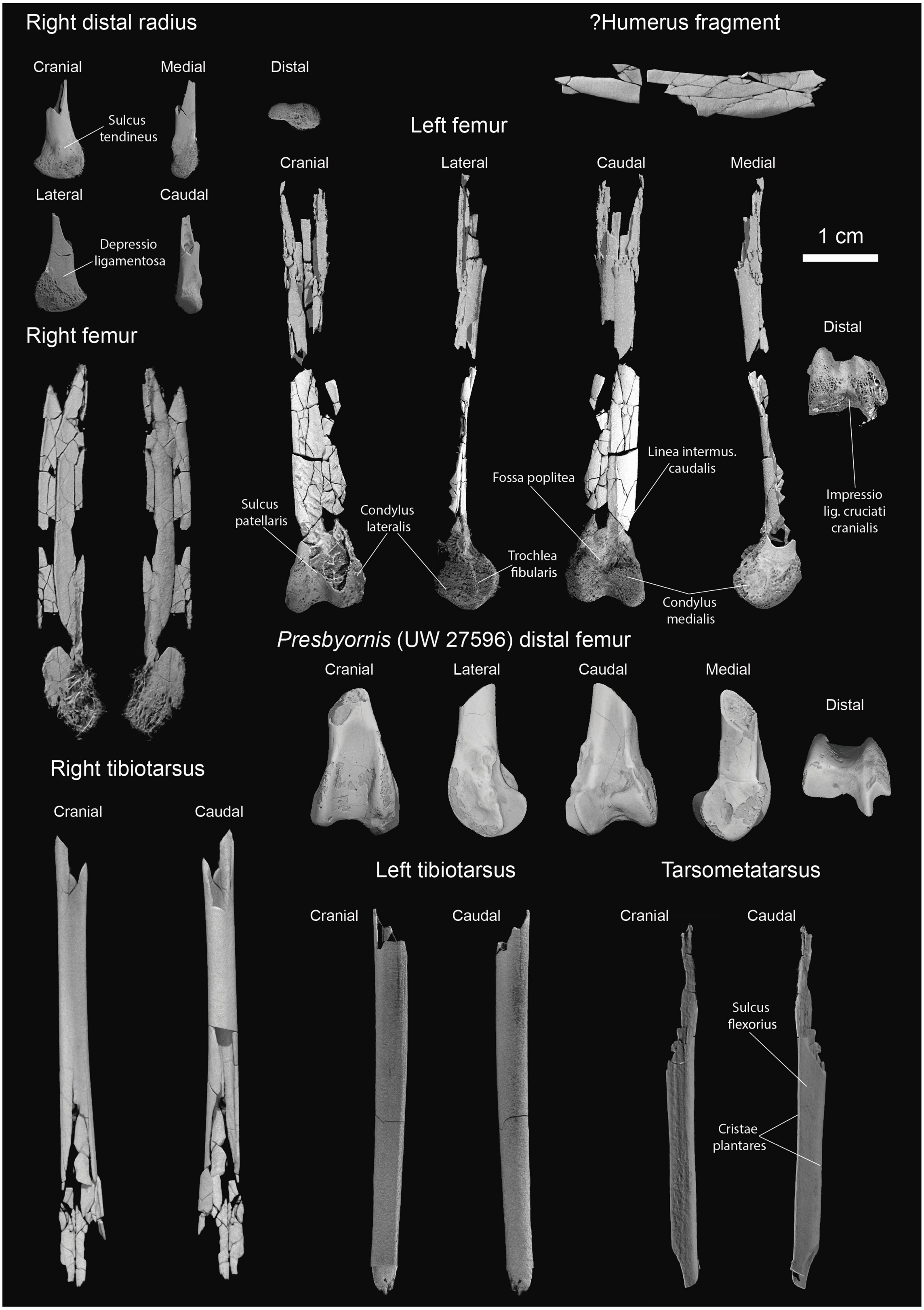
Extended Data Fig. 3 | Morphology of individually segmented skull elements from *A. maastrichtensis* (NHMM 2013 008). Dorsal, ventral and rostral views of the frontals show the nasals separated from their in situ position to illustrate the morphology of the nasofrontal contact. Scale bars, 1 cm.



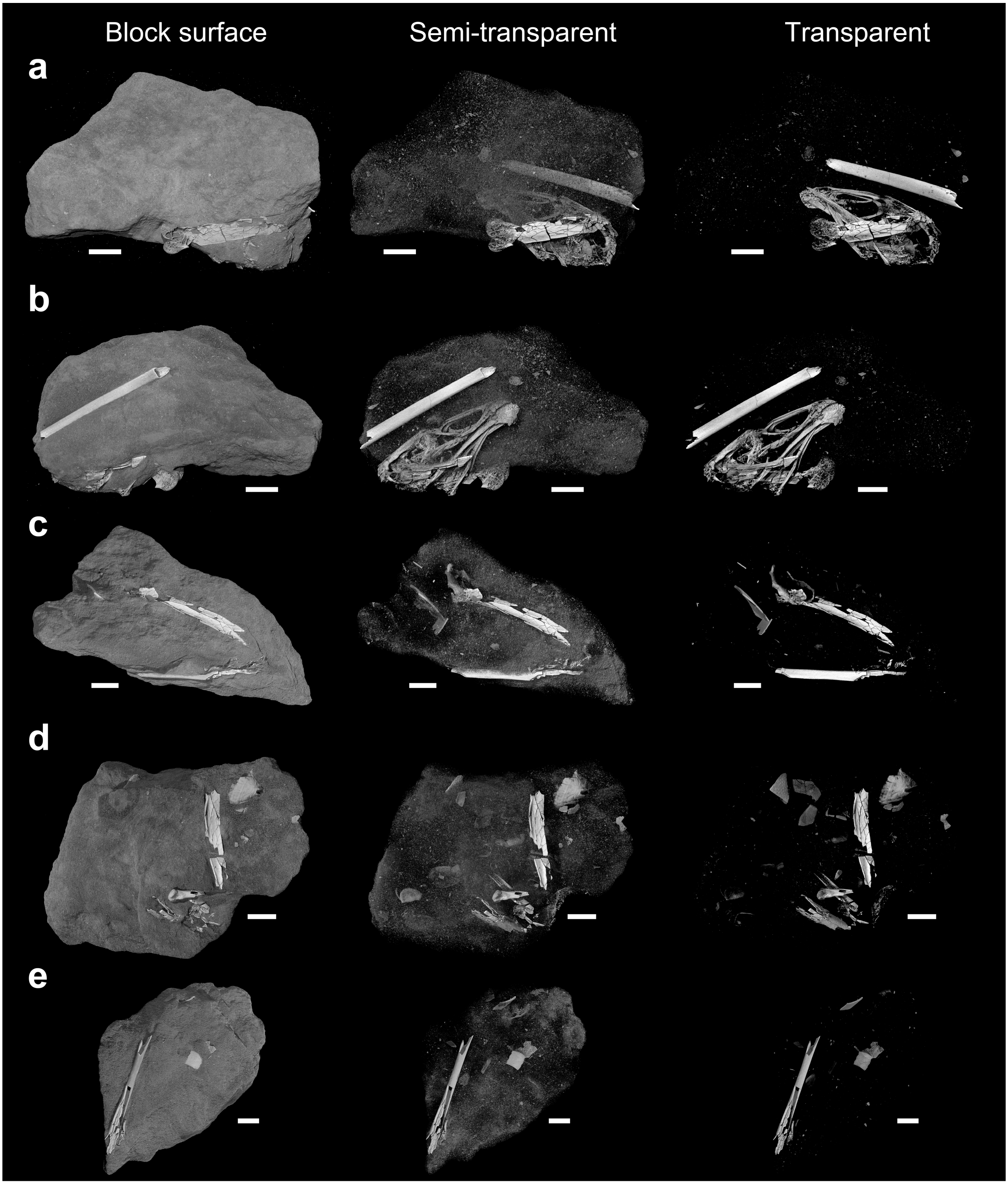
Extended Data Fig. 4 | Detailed comparisons of galloanseran quadrate morphology. Skulls and quadrates of extant Galliformes and total-group Anseriformes. The skull of *Presbyornis* USNM 299846 is shown. Scale bars, 5 mm (quadrates); 1 cm (skulls). Skulls are in left lateral view except *Presbyornis*, which is in reflected right lateral view. FPB, foramen pneumaticum basiorbitale; FPR, foramen pneumaticum rostromediale.



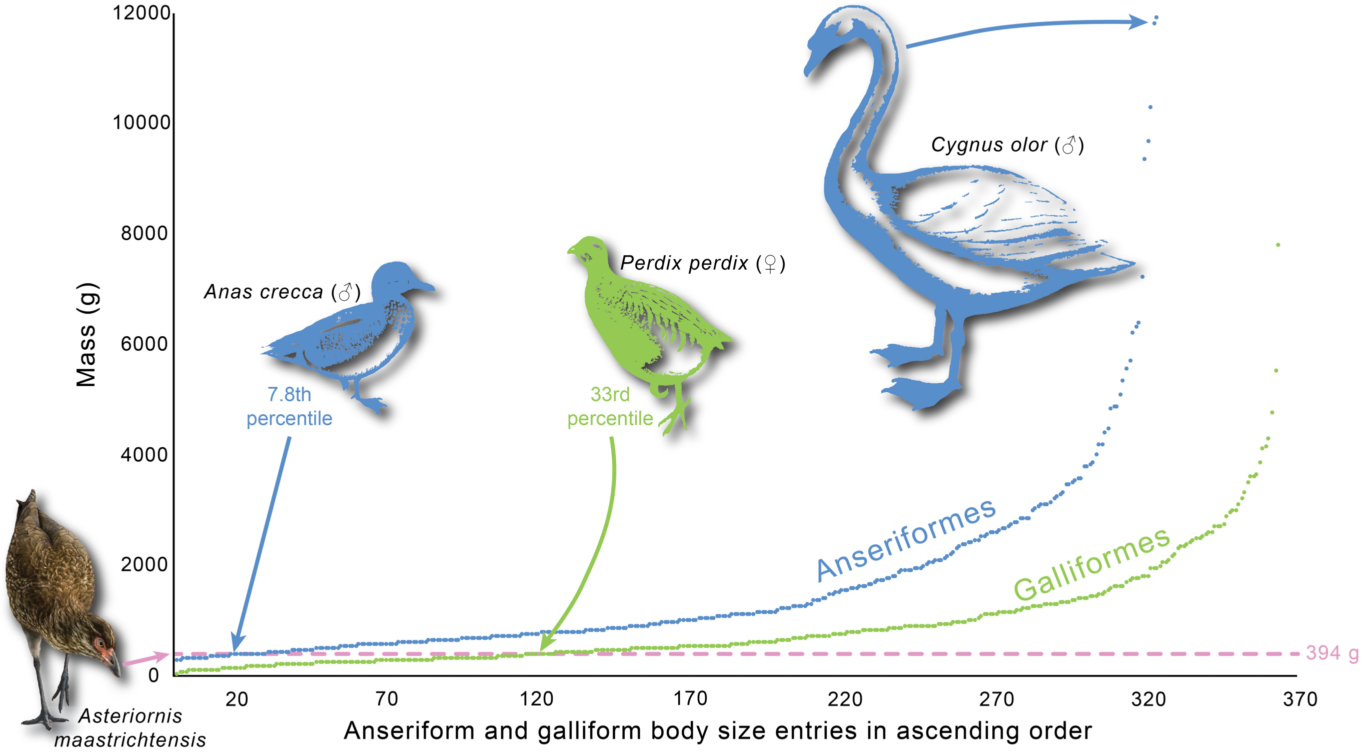
Extended Data Fig. 5 | Detailed comparisons of galloanseran retroarticular morphology. Retroarticular regions of left mandibles in lateral (left), medial (middle) and dorsal (right) views. Both the left and right mandibles of *Asteriornis* are shown in dorsal view, as the retroarticular process is only preserved on the left mandible and the medial process is only preserved on the right mandible. Images of *Anatalavis* are mirrored. Scale bars, 1 cm.



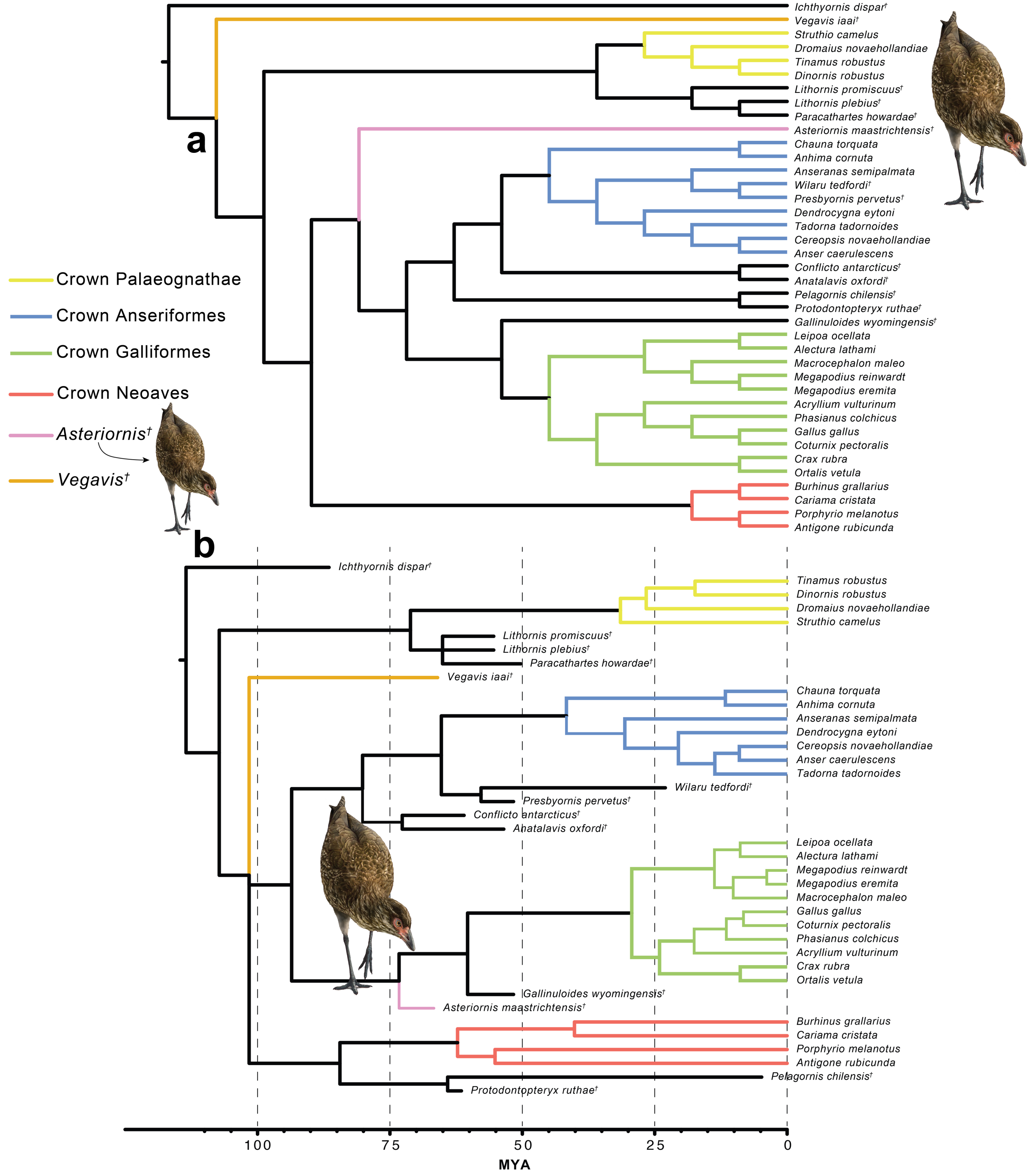
Extended Data Fig. 6 | Postcranial morphology of *A. maastrichtensis* (NHMM 2013 008). The left distal femur of *Presbyornis pervetus* (UW 27596) is shown for comparison.



Extended Data Fig. 7 | Internal composition of NHMM 2013 008 blocks. **a**, Block containing the left femur, left tibiotarsus and the main portion of the skull, viewed from the side with the femur exposed. **b**, Same block as in **a**, viewed from the side containing the tibiotarsus. **c**, Block containing the right femur and tarsometatarsus. **d**, Block containing the right distal radius, several unidentified bone fragments and a portion of the cranial roof near the frontoparietal suture. **e**, Block containing the right tibiotarsus. Numerous fragments of fossil echinoderms and molluscs are visible within the blocks. Scale bars, 1 cm.



Extended Data Fig. 8 | Relative body size of *A. maastrichtensis*. Estimate of the mean body size of the *Asteriornis* holotype[25] compared with extant Galloanserae[82], ranked on the *x* axis from smallest to largest. The mean body-size estimate for *Asteriornis* (394 g) is closest to that of male *Anas crecca* (392 g; 7.8th percentile among Anseriformes) and female *Perdix perdix* (393 g; 33rd percentile among Galliformes).



Extended Data Fig. 9 | Expanded phylogenetic results. a, Results of the parsimony analysis. *Asteriornis* (pink) resolves as the sister taxon to crown Galloanserae. **b**, Results of the tip-dated Bayesian analysis with a soft-maximum neornithine root age of 86.5 million years. An estimated timescale is shown on the *x* axis, although see caveats relating to divergence times in the Supplementary Information. *Asteriornis* (pink) resolves as the stemward-most member of Pangalliformes. Colours match those in Fig. 3 and extinct taxa are denoted with daggers. See Supplementary Information for full details of phylogenetic analyses, character information, synapomorphies of key clades, support values and tree files.

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Reporting Summary

Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed	
☒	☐	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement
☒	☐	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☒	☐	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☒	☐	A description of all covariates tested
☒	☐	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☒	☐	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☒	☐	For null hypothesis testing, the test statistic (e.g. *F*, *t*, *r*) with confidence intervals, effect sizes, degrees of freedom and *P* value noted *Give P values as exact values whenever suitable.*
☐	☒	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☒	☐	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☒	☐	Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	CT data segmentation was performed using VGStudio Max 3.3.0.
Data analysis	Phylogenetic analyses were performed using MrBayes 3.2 and TNT 1.5.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors/reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research guidelines for submitting code & software for further information.

Data

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All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

The holotype specimen of Asteriornis maastrichtensis has been deposited in the permanent collection of the Natuurhistorisch Museum Maastricht under collection number NHMM 2013 008. Tree files from phylogenetic analyses as well as digital models and CT scans of the A. maastrichtensis skull and postcranial elements are available at Zenodo.org (10.5281/zenodo.3610226).

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

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For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	Description of fossil material from the new Cretaceous fossil bird Asteriornis maastrichtensis.
Research sample	All known material from this taxon.
Sampling strategy	Osteology of A. maastrichtensis was digitally extracted from CT scans (the original bones are embedded in matrix). All discernible skeletal elements were sampled and described.
Data collection	The primary interpretation of the fossil was performed by Daniel Field, Juan Benito, Albert Chen, and Daniel Ksepka using digital reconstructions within the Field Palaeobiology Research Group in the Department of Earth Sciences at the University of Cambridge.
Timing and spatial scale	The specimen was CT scanned in December 2018, and segmentation and interpretation was carried out from January-November 2019.
Data exclusions	No data were excluded.
Reproducibility	Not applicable.
Randomization	Not applicable.
Blinding	Not applicable.

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

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☒	☐	Antibodies
☒	☐	Eukaryotic cell lines
☐	☒	Palaeontology
☒	☐	Animals and other organisms
☒	☐	Human research participants
☒	☐	Clinical data

Methods

n/a	Involved in the study	
☒	☐	ChIP-seq
☒	☐	Flow cytometry
☒	☐	MRI-based neuroimaging

Palaeontology

Specimen provenance	The holotype of Asteriornis maastrichtensis comes from the CBR-Romontbos Quarry, Eben Emael, Province of Liège, Belgium. Valkenburg Member (66.8-66.7 Ma24), Maastricht Formation, Late Maastrichtian, Cretaceous.
Specimen deposition	The holotype specimen of Asteriornis maastrichtensis is deposited in the permanent collection of the Natuurhistorisch Museum Maastricht under collection number NHMM 2013 008.
Dating methods	No new dates are provided; date estimates follow the most recent estimates for the type Maastrichtian (e.g., Keutgen 2018).

☒ Tick this box to confirm that the raw and calibrated dates are available in the paper or in Supplementary Information.