

Review

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Remarkable insights into modern bird origins from the Maastrichtian type area (north-east Belgium, south-east Netherlands)

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Abstract

For centuries, fossils from the Maastrichtian type locality and adjacent quarries have provided key evidence of vertebrate diversity during the latest Cretaceous, yet until recently the Maastrichtian type area had revealed no important insights into the evolutionary history of birds, one of the world's most conspicuous groups of extant tetrapods. With the benefit of high-resolution micro-CT scanning, two important avian fossils from the Maastrichtian type area have now been examined in detail, offering profound, complementary insights into the evolutionary history of birds. The holotype specimens of these new taxa, *Janavis finalidens* Benito, Kuo, Widrig, Jagt and Field, 2022, and *Asteriornis maastrichtensis* Field, Benito, Chen, Jagt and Ksepka, 2020, were originally collected in the late 1990s, but were only investigated in detail more than twenty years later. Collectively, *Janavis* and *Asteriornis* provide some of the best evidence worldwide regarding the factors that influenced stem bird extinction and crown bird survivorship through the Cretaceous-Palaeogene transition, as well as insights into the origins of key anatomical features of birds such as an extensively pneumatized postcranial skeleton, a kinetic palate, and a toothless beak. *Asteriornis* also provides scarce evidence of a Cretaceous-aged divergence time calibration within the avian crown group, while together, *Janavis* and *Asteriornis* constitute the only documented co-occurrence of crown birds and non-neornithine avialans. Here, we review key insights into avian evolutionary history provided by these discoveries from the Maastrichtian stratotype, document undescribed and newly discovered Maastrichtian fossils potentially attributable to Avialae and provide the first histological data for the holotype of *Asteriornis*, illustrating its skeletal maturity at the time of its death.

Introduction

To date, only a handful of phylogenetically controversial fossils have been put forward that cast light on the early morphology of crown birds (Neornithes), precluding robust assessment of the nature of the last common ancestor of arguably the world's most conspicuous clade of terrestrial vertebrates. Molecular divergence time hypotheses generally suggest that crown birds arose in the Late Cretaceous, somewhere between 110 and 70 million years ago (Brown et al., 2008; Jarvis et al., 2014; Prum et al., 2015; Kimball et al., 2019; Brocklehurst and Field, 2024), meaning that any insight into the fossil record of birds from the uppermost Cretaceous has particularly strong potential to illuminate the earliest stages of crown bird evolutionary history. Moreover, the entirety of the avian stem group appears to have gone extinct at the K/Pg boundary (Longrich et al., 2011), meaning that crownward avialan fossils from this time interval may have unique potential to provide data on the factors separating extinction victims and survivors. Recent fossil discoveries in the type area of the Maastrichtian Stage of north-east Belgium (~66.7 million years ago) provide insight into both sides of this stem-crown divide, illuminating important aspects of cranial and postcranial morphology early in the evolutionary history of crown birds (Figs. 1–6). Together, *Asteriornis maastrichtensis* (among the world's oldest-known crown birds; Field et al., 2020a, 2020b) and *Janavis finalidens* (a crownward stem bird; Benito et al., 2022b) represent the first documented example of co-occurring crown birds and non-neornithine avialans, and the excellent three-dimensional preservation of both specimens enables long-sought inferences into the origins of key avian morphological features. Here, we review the remarkable insights into the origin of crown birds afforded by these recent discoveries, document as-yet undescribed and newly discovered fossils from the Maastrichtian type area of north-east Belgium and the south-east Netherlands that may be attributable to Avialae, and reveal new palaeohistological data on the holotype of *Asteriornis* with implications for assessing its ontogenetic stage at death.



Figure 1. Main matrix blocks comprising the holotype specimens of *Asteriornis maastrichtensis* (NHMM 2013 008; upper right) and *Janavis finalidens* (NHMM RD 271; lower left).

Methods

Materials

The avialan material studied includes the holotype specimen of *Asteriornis maastrichtensis* NHMM 2013 008 (Field et al., 2020b), consisting of four associated matrix blocks containing most of a skull and disarticulated postcranial elements, as well as the holotype specimen of *Janavis finalidens* NHMM RD 271 (Benito et al., 2022b), consisting of a main matrix block with postcranial remains, as well as associated cranial and postcranial elements extracted from the block, both originating from the Valkenburg member of the Maastricht Formation at Eben Emael, province of Liège, north-east Belgium. Additional specimens collected from the Maastricht Formation are surveyed here: NHMM K 4925 is a previously reported fragmentary distal tarsometatarsus collected from the Emael Member at Eben Emael, Belgium (Dyke et al., 2008); NHMM 2015 027x, a pedal phalanx possibly attributable to *Avialae*, and NHMM JJ 11919, a fragment of uncertain nature, are both newly discovered possible avialan specimens originating from the Emael and Gronsveld Members, respectively, at Sint-Pietersberg, Maastricht, the Netherlands.

Micro-CT scanning of new fossil remains

Specimens were μ CT scanned at the Cambridge Biotomography Centre using a Nikon 49 Metrology XT H 225 ST High-Resolution CT Scanner. Scans were reconstructed and digitally segmented using VGSTUDIO MAX 3.30 and 3.40 (Volume Graphics, Heidelberg, Germany) and Avizo 2019.3 (Thermo Fisher Scientific, Waltham, Massachusetts, US), to generate and export 3D surface meshes of individual elements. Scan data and surface meshes of *Asteriornis* are available for download from Zenodo (10.5281/zenodo.3610225) and of *Janavis* are available from MorphoSource (Project ID: 000444955). All associated postcranial elements from the holotype of *Asteriornis* were assembled into a skeletal reconstruction (Fig. 4) in Autodesk Maya 2023, with the exception of a fragmentary element of uncertain nature, tentatively identified as a possible humerus or femur fragment (Field et al., 2020b). Paired elements (femora and tibiotarsi) were mirrored and reconstructed into a single (left side) element each, along the approximately matching regions preserved on both sides, the

proximal surface of the distal femoral condyles on both femora and the exactly matching narrowest point of the shaft on both tibiotarsi.

Histological sampling, preparation methods and histological imaging

A small fragment of the right femoral diaphysis of the *Asteriornis maastrichtensis* holotype, NHMM 2013 008, was removed for histological thin sectioning before the specimen was treated with consolidant. This fragment is from the ventrolateral side of the bone, just proximal to the mid-diaphysis. It was removed along natural breaks, along with the underlying sediment adhering to it (Fig. 2).

This fragment was embedded in Silmar 41 Clear Polyester Casting Resin (US Composites, West Palm Beach, Florida, USA) catalysed with methyl ethyl ketone peroxide (MEKP; US Composites) at 1.5% by mass and allowed to cure at room temperature for 72 hours. Two 1.2-mm-thick slices were removed from the embedded block using an IsoMet 1000 Precision Cutter (Buehler, Lake Bluff, Illinois, USA). The mounting sides of each thick section were ground on a Plato E-series 10" grinder-polisher (Precision Surfaces International, Inc., Houston, Texas, USA) to remove saw marks using silicon carbide grit papers (600 and 1200 grit; Precision Surfaces International, Inc.) wet with tap water. Thick sections were allowed to dry for two hours, then mounted to glass microscope slides using Devcon clear 2 Ton Epoxy (ITW Performance Polymers, Danvers, Massachusetts, USA) and allowed to cure for 24 hours. The slides were ground to 0.3 mm specimen thickness using silicon carbide grit papers (180, 320, and 600 grit; Precision Surfaces International, Inc.) wet with tap water on the Plato grinder-polisher, then hand ground to the point where the specimens transmitted light when dry using 600- and 1200-grit silicon carbide grit papers. Finally, they were polished using a thick slurry of Hi-Purity alumina powder (5.0 micron and 1.0 micron, Precision Surfaces International, Inc.) and tap water on the Plato grinder-polisher.

The slides were numbered DF-1 and DF-2, with DF-1 the more proximally positioned sample. Both slides were imaged using a DS-Fi2 digital camera (Nikon Inc., Melville, New York, USA) mounted to an Eclipse LV100ND transmitted light microscope (Nikon Inc.) with a ProScan III motorised stage (Prior Scientific, Inc., Rockland, Massachusetts, USA). Slides were imaged dry or wet with tap water under two or more of the following light regimes: brightfield (single plane polariser), under crossed (90°) plane polarisers, and using a single plane polariser plus full wave retarder ($\lambda = 530$ nm) at 90°. In all images, the microscope was set to the darkfield photography setting to improve image quality in reduced light (polarisers) and the 2-ND neutral density filter was engaged. Slides were photographed using the 'Scan Large Image' feature in NIS-Elements: Basic Research (Nikon Inc.). The resulting images were measured, cropped, and adjusted to improve contrast using the brightness/contrast and levelling tools in Photoshop CC 2019 (Adobe Inc., San Jose, California, USA).

Histological comparisons with other taxa were made using specimens in the published literature or direct observation of histological slides in museum collections by one of us (SW).

Repositories

NHMM – Natuurhistorisch Museum Maastricht, Maastricht, The Netherlands (K – Kuypers Collection); USNM – Division of Birds,



Figure 2. The four matrix blocks comprising the holotype of *Asteriornis maastrichtensis* (NHMM 2013 008); the one containing the skull is in the upper left. An ovoid depression just above the femur shaft on that block illustrates the location of the femur shaft sample for palaeohistology. Scale bar equals 10 mm.

National Museum of Natural History (Smithsonian), Washington DC, USA.

Results

New and as-yet undescribed avialan remains from the Maastrichtian type area

NHMM K 4925 is a fragmentary left tarsometatarsus (Fig. 7) collected from the middle Emael Member at the CBR-Romontbos quarry (Eben Emael, province of Liège, north-east Belgium), previously reported and figured by Dyke et al. (2008) (Fig. 7). Although the specimen currently preserves only the distal portion of the tarsometatarsus and is missing most of the second and fourth metatarsal trochleae, a large portion of the shaft was present when the element was discovered in the field, revealing that it was very elongate. Unfortunately, the shaft was broken during excavation and was not collected (Rudi W. Dortangs, pers. comm., December 2022).

The preserved portion of the bone (Fig. 7) reveals a gracile and lightly built tarsometatarsus with a proportionally large third metatarsal trochlea, which is slightly asymmetrical. Despite the fragmentary nature of the specimen, it is apparent that the third and fourth metatarsals fully enclosed a rather large distal vascular foramen, found within a deep groove and exhibiting two exits, one plantar and one distal, as in *Neornithes* and unlike the condition in *Ichthyornis* and more stemward avialans (Clarke & Norell, 2002; Clarke, 2004; Benito et al., 2022a). The second metatarsal was plantarily displaced, and its trochlea likely did not overlap with that of the third metatarsal in medial view, defining a concave and deeply excavated plantar surface. This condition is unlike that of *Ichthyornithes* (Benito et al., 2022a), where all three trochleae are coplanar, and is instead reminiscent of the condition in most non-neornithine Euornithes, such as *Yanornis* and *Gansus* (Zhou & Zhang, 2001; Wang et al., 2016), as well as many extant birds such as *Anseriformes*, *Gruiformes*, and many *Charadriiformes*.

Together with the reportedly elongate nature of the now-missing shaft when first discovered (Rudi Dortangs, pers. comm. 2022), the morphology of NHMM K 4925 is reminiscent of certain early total-clade *Anseriformes* such as *Presbyornis*. The size of NHMM K 4925 and the cross-section of the preserved portion of its shaft fit well with the elongate tarsometatarsus shaft of *Asteriornis* (Field et al., 2020b). Although the midshaft diameter of NHMM K 4925 cannot be assessed, the mediolateral width of the shaft at its proximal-most preserved point is 3.6 mm. Although undoubtedly a slight overestimate given its distal position, incorporating this measurement into an allometric equation for estimating body mass from the midshaft of the tarsometatarsus yields a mean body mass estimate of 486.7 g (Field et al., 2013). This clear overestimate nonetheless compares reasonably closely with the 394 g mass estimated for the holotype of *Asteriornis maastrichtensis* (Field et al., 2020b). As such, it is entirely plausible that NHMM K 4925 belonged to *Asteriornis maastrichtensis* or a closely related taxon, especially as similarities to *Presbyornis* extend to other aspects of the anatomy of *Asteriornis* (Field et al., 2020b).

An additional possible avialan element (NHMM 2015 027x), a well-preserved pedal phalanx (Fig. 8), has recently been recovered from the basal Emael Member at the now disused ENCI-HeidelbergCement Group quarry (Sint-Pietersberg, Maastricht, the Netherlands). The element was found in close association with a mosasaur skeleton, suggesting that it might correspond to mosasaur gut contents. The small phalanx (maximum proximo-distal length: 7.9 mm) is proportionally short and stout, similar to the shortened second and third phalanges of the fourth pedal digit of primarily ground-dwelling birds such as *ratites*, *Galliformes*, *Pteroclitiformes*, *Otidiformes* and *Cariamiformes*. This shortened phalangeal morphology of the fourth digit is not widespread among Mesozoic avialans, but does occur in some euornithines which have been reconstructed as primarily land-dwelling such as *Patagopteryx* (Chiappe, 2002), *Eogranivora* (Zheng et al., 2008), *Archaeorhynchus* (Zhou et al., 2013; Wang & Zhou, 2017) and *Apsaravis* (Clarke & Norell, 2002), contrasting with the more

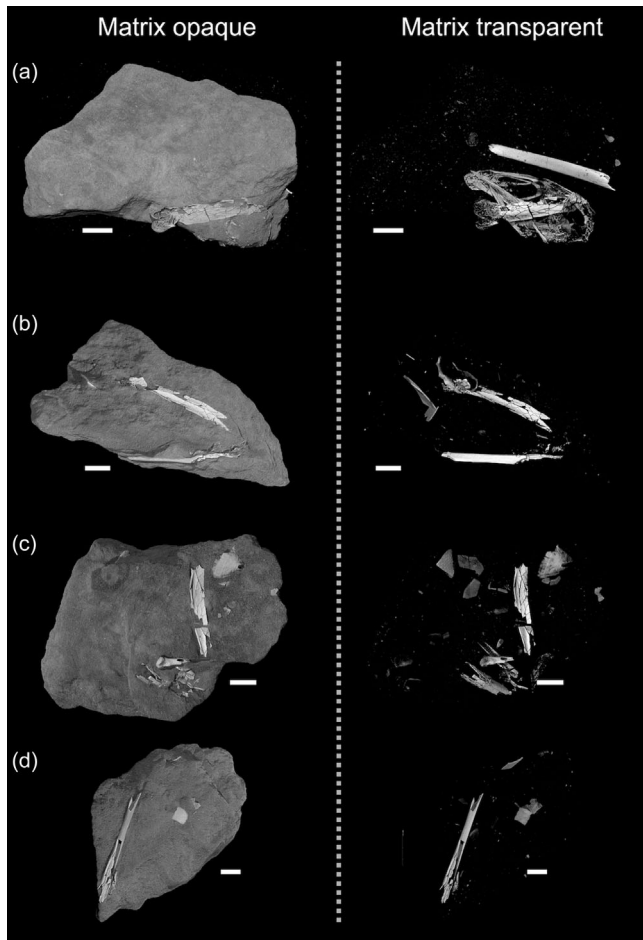


Figure 3. Position of the skeletal elements of *Asteriornis maastrichtensis* within the four matrix blocks comprising the holotype specimen (NHMM 2013 008), with the matrix rendered (left) and digitally removed (right). Scale bar equals 10 mm (modified from Field et al., 2020b).

elongate phalangeal morphology in most aquatic or semi-aquatic euornitheans (Wang et al., 2016; Benito et al., 2022a). The phalanx exhibits ginglymoid articulations and preserves deep, ventrally displaced collateral ligament pits on its distal end. The deeper of these pits is on the left (medial) side, consistent with this being a phalanx from the right pes. Although its small size is consistent with an avialan identity, it is also feasible that the phalanx could derive from a small-bodied, non-avian theropod dinosaur, which exhibit pedal phalangeal morphologies that are broadly consistent with those of many extant and fossil birds (Dececchi & Larsson, 2011), and which are known to be present, albeit rarely, in strata assigned to the Maastricht Formation (Jagt et al., 2003).

A second element possibly attributable to an avialan is more difficult to identify given its highly fragmentary nature (Fig. 7). The specimen, NHMM JJ 11919, originates from the basal Grönsvelde Member of the now disused ENCI-HeidelbergCement Group quarry. The element appears to correspond to a fragment of a vaguely cylindrical structure, with a flat surface on one side delimited by a marked ridge, and a rounded broken surface extending from it. The interior of the element is exposed, revealing a trabecular structure perforated by many small foramina. A large, rounded foramen on the flat side of the element opens into the trabecular interior of the bone and might correspond to a pneumatic opening, consistent with an avialan, but also potentially

non-avian theropod or pterosaur identity. The shape of the element is reminiscent of a vertebral centrum, where the flat surface could correspond to a flat or concave vertebral articular surface, yet it is worth noting that neither theropods (including birds) nor pterosaurs exhibit pneumatic openings on their vertebral articular surfaces. In reference to its small size, the element could also correspond to a fragment of a cranial bone; however, given its incomplete preservation it is difficult to interpret which element it might correspond to if that is the case.

A fragmentary long bone (NHMM K 4101) from the basal Emael Member (Maastricht Formation) of the Marnebel quarry complex (Eben Emael, province of Liège, north-east Belgium) was identified as a proximal left radius by Dyke et al. (2008). This specimen was tentatively referred to Enantiornithes on the basis of a distinct longitudinal groove on the ventral surface of the bone and small, paired bicipital tubercles near the proximal articular surface.

Histological description of Asteriornis maastrichtensis (NMMH 2013 008)

Our histological terminology follows that of Francillon-Vieillot et al. (1990). The mid-diaphyseal cortex of the femur of the *Asteriornis maastrichtensis* holotype NMMH 2013 008 is relatively thin, ~0.41 mm from periosteum to endosteum. In both slides, the outer bone surface is slightly crushed and degraded along most of the preserved margin, and the innermost endosteal margin is also slightly worn in places, possibly due to resorption, so this is likely a slight underestimate of cortical thickness. Neither slide shows evidence of trabeculae nor other spicules (e.g., medullary bone) projecting into the medullary cavity. Of the two slides, DF-2 shows less damage and is therefore the focus of the present description and discussion (Fig. 9).

The cortex is almost entirely composed of primary parallel-fibred bone. The inner two-thirds of the cortex are less organised and better vascularised than the outer third. Osteocyte lacunae are more oval internally and become flatter once the parallel-fibred bone transitions to a more organised state towards the outer cortex. A thin band of inner circumferential lamellae (ICL) is visible on the inner margin in both sections; this region is 3–5 lamellae (~0.02–0.03 mm) thick. A slightly thicker (7–9 lamellae, ~0.05 mm) band of outer circumferential lamellae (OCL) is also present in both sections. The OCL is more apparent in DF-2, which has less damage (fewer cracks) along the outer margin of the bone. The divisions between lamellae are less distinct in the ICL than in the OCL, and the osteocyte lacunae of the ICL are more oval compared to the flat osteocyte lacunae in the OCL. Neither the ICL nor the OCL are vascular. No annuli or lines of arrested growth (LAGs) are visible in the middle layer of primary bone or in the OCL, and the bone seems to grade from parallel-fibred bone of the cortex into the lamellar bone of the OCL rather than forming a distinct boundary, the condition in many neognath taxa of similar size (Ponton et al., 2004).

All the vascular canals in this section are longitudinal or slightly oblique in orientation. Most of these do not anastomose with adjacent canals, but some canals in the inner third of the cortex exhibit short circumferential anastomoses between two adjacent canals. Most of the vascular canals in the inner third of the cortex are primary osteons, whereas all the canals in the outer third are simple primary canals. Notably, the primary osteons in the inner cortex are ringed with parallel-fibred bone rather than lamellar bone. No secondary osteons are present in either slide.

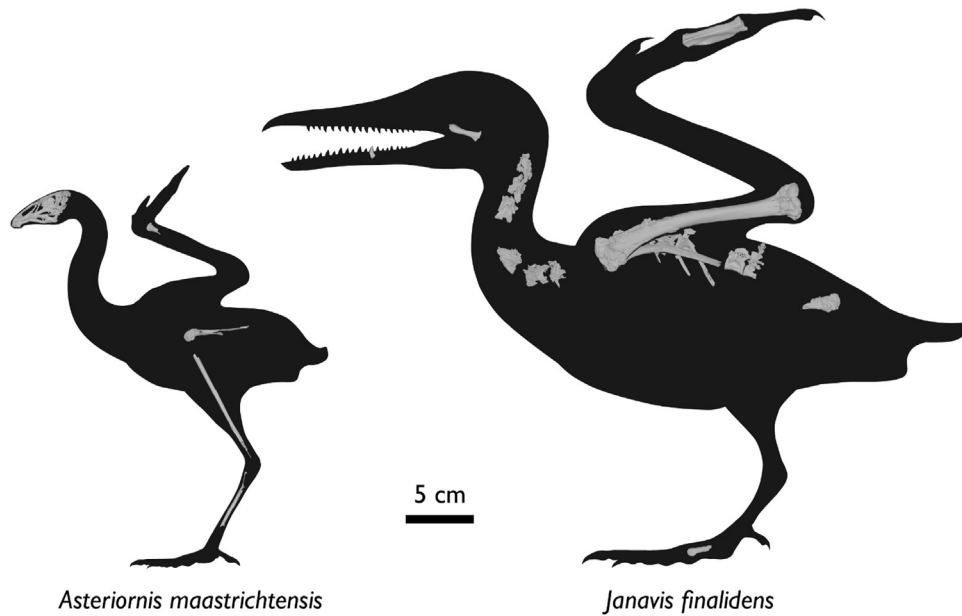


Figure 4. Skeletal reconstructions of *Asteriornis* and *Janavis*. Hindlimbs of *Asteriornis* are longer than previously reconstructed (Field et al., 2020b), bolstering the interpretation that *Asteriornis* was a long-legged bird with a possible wading ecology.



Figure 5. 3D-printed physical model of the holotype skull of *Asteriornis maastrichtensis* as preserved (above), and high-resolution CT scan rendering (below). Scale bar equals 10 cm.

Discussion

Asteriornis: long-sought insight into the origin of crown birds from the Maastrichtian type area

As one of the few uncontroversial representatives of the avian crown group (Neornithes) yet recovered from Mesozoic sedimentary rocks, *Asteriornis* has outsized potential to inform numerous longstanding questions related to the evolutionary origins of crown birds. Such insights range from anatomical to ecological and to temporal and biogeographical.

Anatomically, *Asteriornis* exhibits a range of character states optimising as synapomorphies of crown group birds, including a toothless beak, a fused mandibular symphysis, and a proportionally large premaxilla (Field et al., 2020b). Additional character states optimise as synapomorphies of the more exclusive subclades Neognathae (i.e. contact between the palatine and premaxilla; incisure between the otic and squamosal cotylae) and Galloanserae (i.e. a dorsoventrally deep and lateromedially compressed maxillary process of the premaxilla; palatines that are long, narrow, and widely separated rostrally; a bicondylar mandibular



Figure 6. Artist's reconstruction of *Asteriornis* and *Janavis* in their natural habitat, along the shore of a shallow sea in the Maastrichtian of northern Europe. Illustrations courtesy of Phillip Krzeminski. Used with permission.

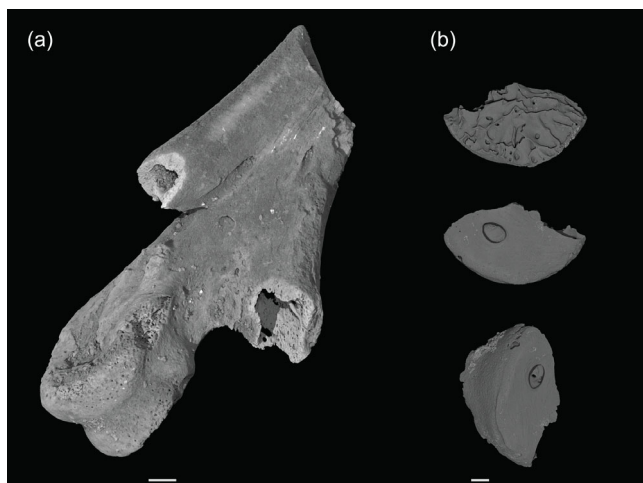


Figure 7. A. NHMM K 4925, distal end of left tarsometatarsus in oblique plantar view; B. NHMM JJ 11919, unidentified avialan-like fragment in three alternative views (standard anatomical orientations not possible given the uncertain nature of the fragment), both from the Maastrichtian type locality (see text for details). Scale bars equal 1 mm.

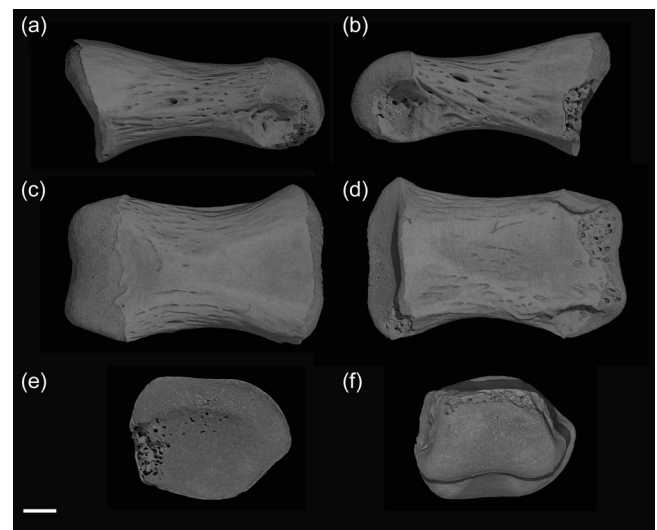


Figure 8. Newly discovered avialan-like pedal phalanx from the Type Maastrichtian (NHMM 2015 172x) in (A) right lateral, (B) left lateral, (C) ventral, (D) dorsal, (E) proximal, and (F) distal views. The specimen represents possible gut contents from a mosasaur. Scale bar equals 1 mm.

process of the quadrate; a long, dorsally oriented internal articular process of the mandible). Indeed, virtually all discernible character states suggest that *Asteriornis* provides some of the clearest evidence yet of a fossil phylogenetically proximal to the most recent common ancestor of crown Galloanserae, the extant avian clade uniting 'waterfowl' (Anseriformes) and 'gamebirds' (Galliformes). Certain attributes of the skull of *Asteriornis* are reminiscent of the condition observed in many crown anseriforms, such as the rostrally projecting postorbital process, while others are reminiscent of extant Galliformes, such as the contralateral frontal processes remaining unfused along their entire length, and the unfused tomial and narial contacts of the premaxillae and nasals. Notably, however, these 'galliform' features could also be indicative of an early ontogenetic status for the holotype of *Asteriornis maastrichtensis* (Parker, 1868; Jollie, 1957; Field *et al.*, 2020b),

necessitating the investigation of the skeletal maturity of the specimen undertaken herein.

Notably, an important aspect of galloanseran cranial morphology cannot be confirmed in the holotype specimen of *Asteriornis maastrichtensis* despite originally being interpreted as present by Field *et al.* (2020b). Long, dorsally deflected retroarticular processes are a well-established synapomorphy of Galloanserae (Cracraft, 1988; Livezey, 1997; Cracraft & Clarke, 2001), and a retroarticular process virtually indistinguishable from those of both stem anseriforms (e.g. *Nettapterornis*, *Presbyornis*) and crown anseriforms was interpreted as being clearly discernible in the holotype skull of *Asteriornis maastrichtensis* (Field *et al.*, 2020b). However, examination of digital models of the caudal mandible under rendering settings with enhanced shadow contrast reveals unmistakable impressions corresponding to the quadrate cotylae

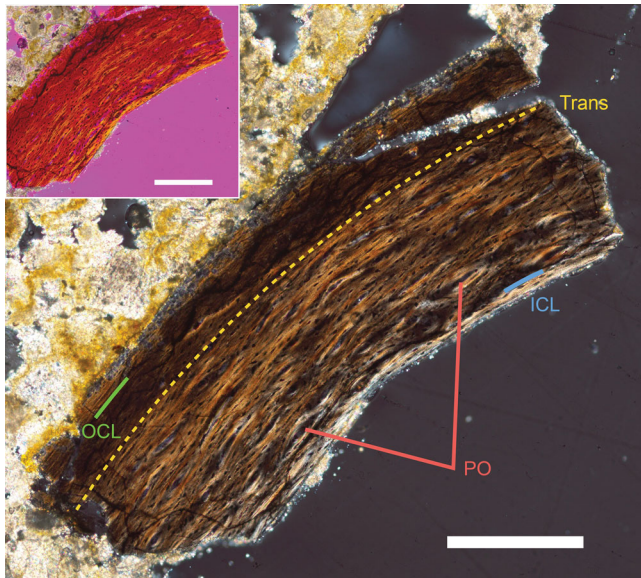


Figure 9. Histological section through the holotype femur of *Asteriornis maastrichtensis* (NMMH 2013 008), section DF-2. ICL: inner circumferential lamellae; OCL: outer circumferential lamellae; PO: primary osteons within parallel-fibred bone; Trans: transition to more organised, parallel-fibred bone. Scale bar equals 1 mm. Inset shows the same section imaged under a single plane polariser plus full wave retarder ($\lambda = 530$ nm) at 90° .

on the supposed retroarticular process (Crane et al., 2023), illustrating that the process must instead correspond to the medial process of the same mandible that was taphonomically displaced and twisted from a mediolaterally elongate, medial position into a dorsoventrally elongate, caudodorsal position (Fig. 10). The shape of the retroarticular and medial processes in some pan-galloanserans can be remarkably similar, as illustrated by the pan-anseriform *Conflicto* (Tambussi et al., 2019), and we hypothesise that this may have been the case in *Asteriornis* as well.

In light of the potential phylogenetic influence of pronounced retroarticular processes being coded as present in the original phylogenetic investigation of *Asteriornis*, Crane et al. (2023) re-examined the caudal ends of the mandible of *Asteriornis maastrichtensis* to assess the potential presence or absence of these structures and evaluate resultant phylogenetic implications. Crane et al. (2023) concluded that the caudal extremities of both the left and right mandibular rami extend to the surface of the fossil block containing the holotype skull, where the caudal ends have eroded away. However, anatomical comparisons with a wide phylogenetic sample of extant birds illustrate that the possibility of retroarticular processes having originally been present cannot be excluded; as such, the presence/absence of retroarticular process for *Asteriornis* is best treated as unknown at present.

Using an updated version of the phylogenetic matrix from Field et al. (2020b) in which the presence and shape of the retroarticular were scored as unknown in *Asteriornis*, a phylogenetic position within total-clade Galloanserae was still obtained (Crane et al., 2023), with *Asteriornis* resolving as a stem galliform under both Parsimony and Bayesian optimality criteria. Thus, these updated results support the initial interpretation of *Asteriornis* as a member of total-group Galloanserae, and potentially as a member of total-group Galliformes (Field et al., 2020b).

While the caudal ends of the mandibles of *Asteriornis* have proved to be less well preserved than originally interpreted, other aspects of the cranial osteology of *Asteriornis* are sufficiently

complete and well preserved to be incorporated into three-dimensional investigations of avian skeletal evolution. For instance, the quadrate of *Asteriornis* (Fig. 11) was pivotal for constraining anatomical reconstructions in a macroevolutionary investigation of Galloanserae (Kuo et al., 2023), demonstrating that the quadrate morphology of the ancestral crown galloanseran would have been substantially more similar morphologically and functionally to that of extant galliforms than to extant anseriforms, conflicting with reconstructions based on extant taxa alone. Those results demonstrate the necessity of incorporating fossil taxa into ancestral state reconstructions of skeletal geometry whenever possible – a conclusion applicable well beyond Galloanserae. Moreover, subsequent work by Kuo et al. (2024) has illustrated widespread decoupling between quadrate morphology and feeding specialisation across the avian tree of life, emphasising the potential value of quadrate morphology in assessments of fossil phylogenetic affinities. As such, the morphological similarity of the quadrate of *Asteriornis* to those of extant Galliformes is likely to reflect genuine phylogenetic proximity.

Histological implications for age and maturity of *Asteriornis maastrichtensis*

The galliform-like nature of several features exhibited by *Asteriornis*, particularly the unfused nature of the contacts between the premaxillary contralateral processes, the tomial and narial contacts of the premaxillae and nasals, and the unfused splenial in the lower jaw could also be related to an early ontogenetic age. The contacts between these cranial and lower jaw bones usually fuse or obliterate during post-hatchling development in Neornithes (Plateau et al., 2024) however, they remain unfused or poorly fused in adult galliforms (Parker, 1868; Jollie, 1957; Field et al., 2020b). As such, to clarify the ontogenetic stage of the *Asteriornis maastrichtensis* holotype NMMH 2013 008 is of utmost importance in order to fully evaluate the extent of its galliform affinities. Overall, the histology observed in the studied femoral section of *Asteriornis* is comparable to that of similarly sized extant birds. The femoral histology suggests that growth was slowing and that this bird had either reached its growth asymptote (i.e. skeletal maturity) or was close to it. Features that support this hypothesis include the marked transition from disorganised, moderately well-vascularised parallel-fibred bone in the inner cortex to more organised and less vascular tissue in the outer cortex, the presence of true primary osteons in the inner cortex, and the presence of a thin ICL and OCL along the inner and outer margins of the bone, respectively.

The degree of organisation of collagen fibres in primary bone matrix inversely correlates with bone deposition rate (Newell-Morris & Sirianni, 1982; de Buffrénil & Pascal, 1984), with more organised tissues deposited at slower rates. In NMMH 2013 008, the more disorganised parallel-fibred bone of the inner cortex would have been deposited at higher rates than the more organised parallel-fibred bone of the outer cortex. Absolute rates of bone deposition ($\mu\text{m}/\text{day}$) are likely taxon-specific (Werning & Nesbitt, 2016) and, in the absence of LAGs or annuli, cannot be reliably estimated. Vascular canal density correlates with bone deposition rate in a broad range of taxa (Montes et al., 2010; Cubo et al., 2012); therefore, the lower vascular density in the more organised tissues of the outer cortex is also consistent with an ontogenetic decrease in overall growth rate.

The bones of living and fossil birds commonly form three distinct layers within the cortex (Enlow and Brown, 1957), and the

Figure 10. Mandible of the holotype of *Asteriornis maastrichtensis* in dorsal and ventral views. LMP: left medial process; RMP: right medial process. The right medial process was originally identified as the right retroarticular process by Field et al. (2020b). Subsequently, this structure was reidentified as the twisted and displaced medial process of the right mandible. Scale bar equals 10 mm. Figure modified from Crane et al. (2023).

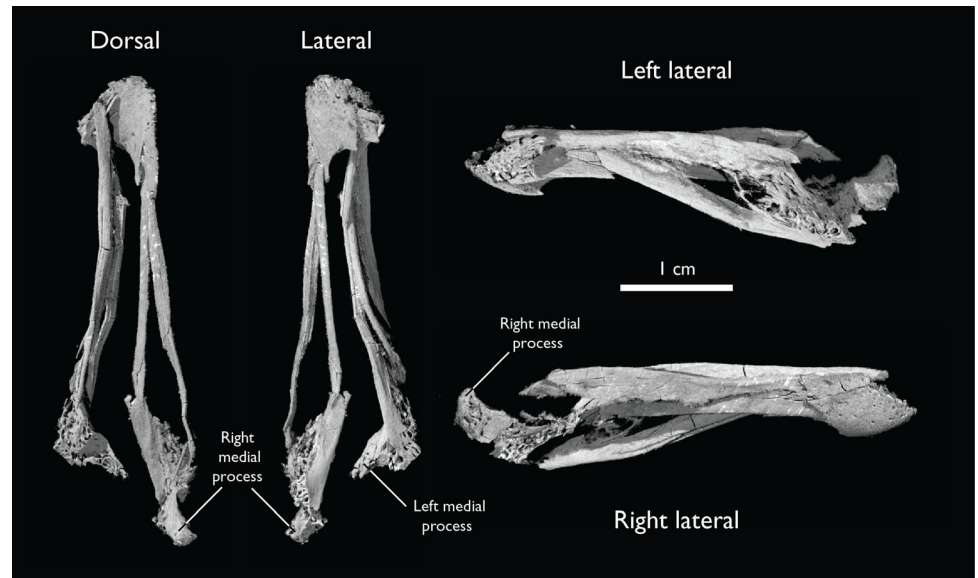
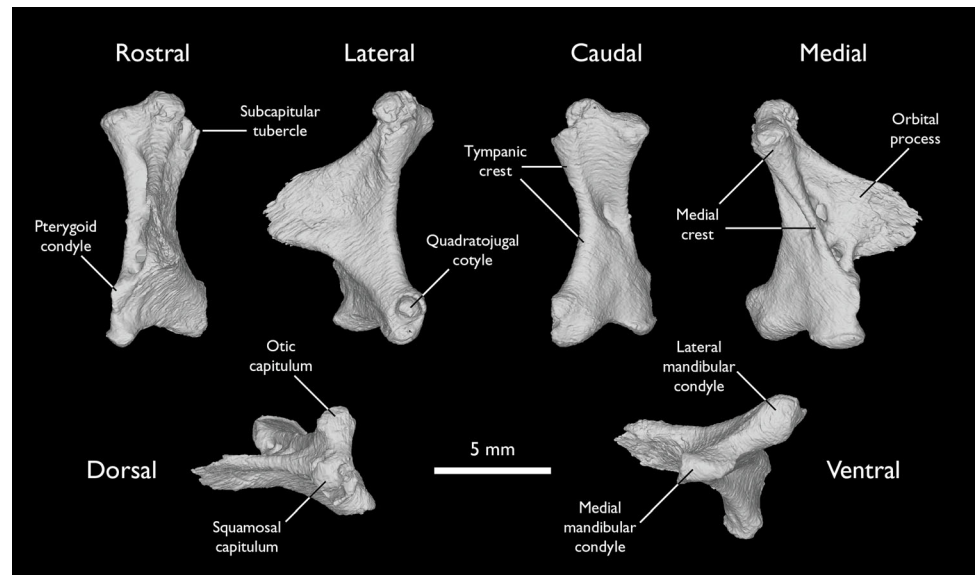


Figure 11. Detailed morphology of the quadrate of the holotype of *Asteriornis maastrichtensis* (NHMM 2013 008), modified from Kuo et al. (2023).



relative thickness of these can be indicative of ontogenetic stage. The innermost is the ICL, a band of circumferential lamellar or parallel-fibered bone that forms the endosteal margin. In extant taxa, the ICL is often moderately vascularised by radial canals. The OCL forms along the periosteal margin. It is also composed of circumferentially oriented lamellae or parallel-fibered bone but is nearly always avascular. The OCL is homologous to the external fundamental system (EFS) of other tetrapods. However, unlike the EFS of reptiles and mammals, the OCL of extant birds usually forms over a period of weeks or months, rather than years (Chinsamy-Turan, 2005). Between these regions is a middle layer of periosteally deposited bone, usually reported as woven-fibered in extant taxa and always vascularised. Ornithuran birds do not generally produce growth marks in the middle, woven-fibered layer, because most reach full body size within a year, and often in a matter of weeks or months (Chinsamy-Turan, 2005). In many neognaths, a line of arrested growth (LAG) marks the boundary

between the middle layer and the OCL, but this becomes less common as body mass increases. When growth marks are present, they almost always occur in the OCL, with birds that continue to grow after a year constituting a notable exception (Chinsamy-Turan, 2005; Turvey et al., 2005; Bourdon et al., 2009; Heck & Woodward, 2021). LAGs in the OCL are not annual like those of the primary cortex, but they are more numerous in taxa with longer periods of 'residual' growth as the individual approaches their size/growth asymptote or after reaching sexual maturity (Ponton et al., 2004).

As such, the presence of both an ICL and an OCL in NHMM 2013 008 provides additional evidence that this individual had either reached skeletal maturity or was close to the end of its most active growth phase when it died. Both layers are very thin in terms of numbers of lamellae (3–5 in the ICL and 7–9 in the OCL), so it is possible that these regions were just beginning to form at the time of death and some growth remained. The ICL is inconsistently

preserved in both slides. Incomplete preservation of the ICL is known among extant taxa, such as the galliform *Crax rubra* (e.g., tibiotarsus of specimen USNM 19918), and the extant alcid *Alca torda* (Drozdowska & Meissner, 2014). Inconsistent preservation of the ICL around the endosteal margin may be one reason that age estimates based on layers in the ICL are unreliable (Drozdowska & Meissner, 2014).

Neither slide shows LAGs within the OCL. LAGs are present in the OCL of extant galliforms, including species with larger body sizes than this individual; for example, in the tibiotarsus of *Crax rubra* (USNM 19918), a LAG marks the boundary between the middle layer of primary cortical bone and the OCL, and a second LAG lies within the OCL (pers. obs). The absence of LAGs in the OCL of NHMM 2013 008 may represent a more rapid truncation of growth compared to some extant galliforms, or it may reflect that NHMM 2013 008 had yet to finish depositing a complete OCL at the time of its death.

Cortical LAGs are fairly common in Mesozoic avialans (e.g. Chinsamy et al., 1994; Chinsamy & Elzanowski, 2001; de Ricqlès et al., 2003; Wang et al., 2017). Within crown birds, they are common in very large-bodied and often flightless species (e.g. Turvey et al., 2005; Bourdon et al., 2009; Angst et al., 2017) but are otherwise rare. As such, the absence of LAGs and other growth lines in the middle layer of primary cortical bone in NMMH 2013 008 might be indicative of *Asteriornis* reaching full body size in less than a year, similar to most extant birds.

Phylogenetic, ecological and biogeographical implications of *Asteriornis maastrichtensis*

Phylogenetic analyses undertaken by Field et al. (2020b) and Crane et al. (2023) have recovered *Asteriornis* either as the sister taxon to crown Galloanserae or as the sister taxon to the remainder of total-group Galliformes. Mayr (2022), referencing aspects of skull morphology originally noted by Field et al. (2020b) such as elongate, rostrally projecting postorbital processes, suggested that a phylogenetic position for *Asteriornis* among total-clade Anseriformes might be the most plausible, noting similarities with screamer-like birds from the Eocene London Clay Formation of south-east England. Mayr (2022) additionally hypothesised that *Asteriornis* could be an early representative of the lineage ultimately giving rise to the large-bodied flightless Gastornithidae of the lower Palaeocene. This latter hypothesis is weakly justified at present, so much the more so given that the phylogenetic position of gastornithids among total-clade Galloanserae may be in need of re-evaluation (Worthy et al., 2017; Benito et al., 2022a).

This phylogenetic uncertainty is as expected for a fossil whose topological position sits close to a phylogenetic divergence; regardless of whether *Asteriornis* represents a crownward stem galloanseran, a stemward stem galliform, or a stemward stem anseriform, internal branch lengths between *Asteriornis* and any of these alternative phylogenetic positions are expected to be extremely short, limiting the potential for unambiguous phylogenetic resolution. Nonetheless, other alternative phylogenetic hypotheses that have been put forward for *Asteriornis* seem less tenable. For instance, Torres et al. (2021) included *Asteriornis* in a matrix focused on the crownward stem bird *Ichthyornis*. In their analyses under parsimony, *Asteriornis* resolved as the sister taxon to Palaeognathae with weak support, attributable to a single inferred synapomorphy: 'deeply caudally forked dentary with dorsal and ventral forks of approximately equal caudal extent'. However, the coding for this character in the Torres et al. (2021)

dataset is dubious, as a caudally forked mandible is exhibited by many Galliformes, wherein the dorsal ramus is considerably shortened relative to the ventral ramus. The dentary of *Asteriornis* thus more closely resembles the condition in most galliforms than the condition in palaeognaths, in which the dorsal and ventral rami are of roughly equal length (Crane et al., 2023). It is worth noting that the updated version of the Torres et al. (2021) dataset analysed by Benito et al., (2022a, b) also recovered *Asteriornis* as sister to Palaeognathae under maximum parsimony, but as a total-clade galloanseran when the same dataset was analysed under Bayesian inference. However, these results should be viewed with caution, as the construction of the Torres et al. (2021) dataset was primarily focused on reconstructing relationships among non-crown avialans, with a very limited sample of crown birds (Benito et al., 2022a).

While the incomplete nature of the skeleton of *Asteriornis* precludes detailed insights from being drawn regarding its ecological habits, preliminary hypotheses regarding both its foraging ecology and substrate preferences can be drawn from its cranial and hindlimb remains. For instance, the overall morphology of the bill of *Asteriornis* resembles that of generalist galloanseran foragers such as anhimids and some phasianids – perhaps reflecting a degree of dietary generalism that may have characterised at least some K/Pg boundary-crossing bird lineages. Seed-based (Larson et al., 2016) and insect-based diets (Field et al., 2020b) have been hypothesised to have been selectively favoured among avian survivors across the K/Pg boundary, as these resources may have remained comparatively abundant in the aftermath of the end-Cretaceous asteroid impact. Indeed, the relatively small size of *Asteriornis*, estimated at ~394 g from hindlimb-based scaling equations (Field et al., 2013, 2020b), may have been compatible with a predominantly insect-based diet, a foraging strategy generally restricted to relatively small-bodied extant terrestrial vertebrates due to its energy-intensive nature (Cooke et al., 2022). Furthermore, if *Asteriornis* is representative of the ancestral condition for Galloanserae, its body mass of 394 g (less than 50 per cent of the median body size of known latest Maastrichtian avialans; Longrich et al., 2011; Berv & Field, 2018), might also be compatible with the hypothesis that filtering for reduced body size may have contributed to patterns of extinction and survivorship across the K/Pg boundary (Berv & Field, 2018; Field et al., 2020b). Strong directional selectivity for reduced body size among surviving crown bird lineages across the K/Pg boundary has been hypothesised on the basis of fossil data and has been associated with a potential transient increase in avian nucleotide substitution rates as a result of the negative relationship between body size and nucleotide substitution rates in extant birds (Berv & Field, 2018; Field et al., 2020a).

The hindlimb elements of the holotype of *Asteriornis maastrichtensis* are incomplete, yet appear to represent portions of the tarsometatarsus, tibiotarsus, and femur, enabling minimum estimates of hindlimb proportions to be generated (Fig. 12). In fact, the three-dimensional reconstruction of the skeleton of *Asteriornis* undertaken here (Fig. 4) allows fuller insights into its postcranial anatomy and proportions than have previously been possible. By mirroring and digitally combining remains from the left and right sides, more complete reconstructions of the femur and tibiotarsus have been generated. These reconstructions show that both the femur and tibiotarsus were longer than previously appreciated. The complete femoral head is missing, yet the regions preserved on both femora enable an almost complete reconstruction of the distal femur, with a minimum length for this element of 47.97 mm. The

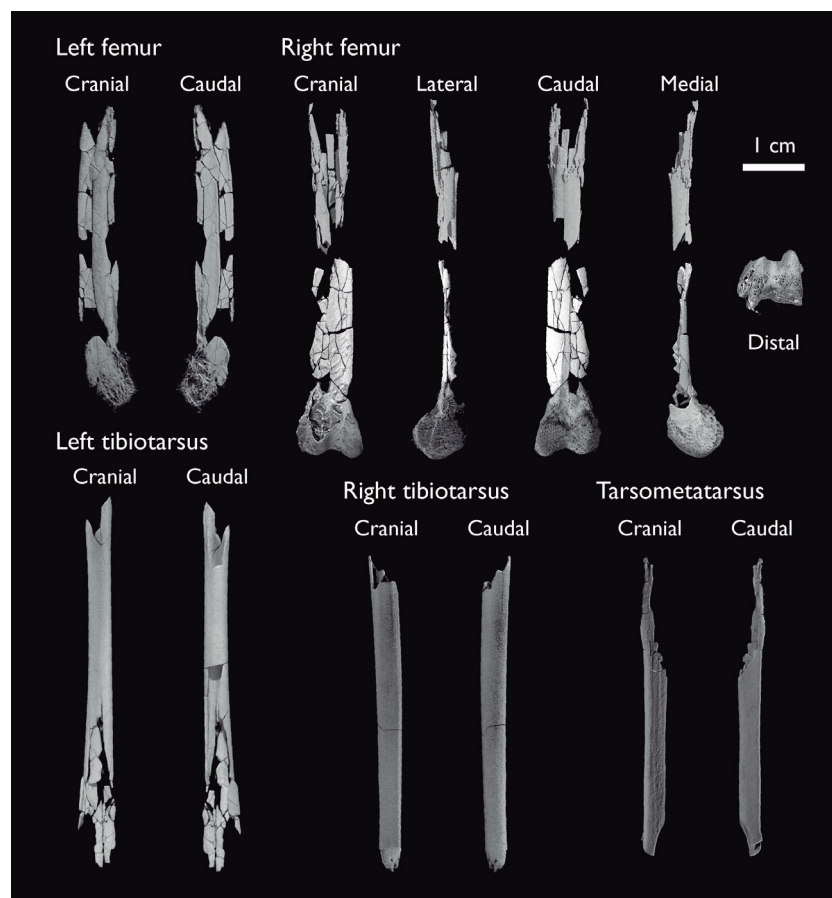


Figure 12. Hindlimb elements from the holotype of *Asteriornis maastrichtensis* (NHMM 2013 008). Scale bar equals 10 mm. Modified from Field et al. (2020b).

upper bound estimate on femur length from Field et al. (2020b), 53.4 mm, therefore may actually represent an underestimate as the complete proximal region of the element is missing, and the newly reconstructed composite femur appears to be missing much of its proximal end. The tibiotarsus was reconstructed by precisely matching portions of the midshaft of identical width from both tibiotarsi, yielding a minimum length of the tibiotarsus of 86.13 mm, 31 per cent longer than the previous estimate from Field et al. (2020b), based on the preserved right tibiotarsus and its contiguous impression (65.38 mm). Together with the long (62.54 mm), yet incomplete tarsometatarsus reported by Field et al. (2020b), these new measurements yield a minimum 'hindlimb index' (HI) [(length of tibiotarsus+length of tarsometatarsus)/(length of femur)] (Field & Hsiang, 2018) of 2.78 (vs a previous estimate of 2.41). This value, surely an underestimate given the incompleteness of the tarsometatarsus and tibiotarsus (both consisting exclusively of diaphyseal remains), falls within the range of predominantly ground-dwelling representatives of some major extant avian clades such as Otidimorphae, in which neomorphine ground-cuckoos, small bustards, and the presumed ground-dwelling stem turaco *Foro panarium* yield HI estimates in the range of 2.7–2.8 (Field & Hsiang, 2018). These estimates highlight the elongate hindlimb proportions of *Asteriornis*, consistent with its inferred ecology as a long-legged ground-dwelling bird. Similarly elongated hindlimbs are widespread across total-group galloanserans, including fossil representatives such as *Presbyornis* (Feduccia, 1976; Ericson, 2000), *Telmabates* (Howard, 1955), and *Conflicto* (Tambussi et al., 2019), which have long been proposed to have exhibited a wading ecology, as well as deeply diverging aquatic or

semi-aquatic crown anseriforms such as anhimids, *Anseranas* and *Dendrocygna*. The presence of such elongate hindlimbs in *Asteriornis*, perhaps also indicative of a wading ecology (Field et al., 2020b), may provide further support for the possibility that these could be plesiomorphic for Galloanserae.

Relatively narrow and relatively long hindlimb proportions like those of *Asteriornis* are generally associated with predominantly ground-dwelling lifestyles in extant non-passerines (Norberg, 1979; Field et al., 2018a; Field & Hsiang, 2018). The early Cenozoic fossil record of crown birds supports a survivorship model whereby avian taxa crossing the K/Pg boundary would have been predominantly non-arboreal (i.e. expected to exhibit relatively long hindlimbs; Field et al., 2018a), and ancestral state reconstructions suggest that hindlimbs exhibiting specialisations for arboreal perching may have arisen numerous times among higher landbirds (Telluraves) in the aftermath of the K/Pg mass extinction (Ksepka et al., 2017), indicative of non-arboreal antecedents repeatedly giving rise to arboreal descendants (Field et al., 2018a). As such, the relatively elongate and gracile hindlimbs of *Asteriornis maastrichtensis* may capture the general morphology of K/Pg-surviving bird clades. Palaeoecological reconstructions of the Type Maastrichtian generally indicate a nearshore marine environment, suggesting that the elongate hindlimbs of *Asteriornis* may have been associated with shore-dwelling habits. This latter interpretation recalls earlier hypotheses of a 'transitional shorebird' morphology being ancestral for several bird lineages and key for bird survival through the K/Pg (Feduccia, 1995). Indeed, although the phylogenetic basis for this hypothesis may be incompatible with an up-to-date understanding of crown bird phylogeny

(e.g. Jarvis et al., 2014; Prum et al., 2015), the ecological basis for this hypothesis may prove prescient. Indeed, stem group representatives of Anseriformes such as *Presbyornis* and *Conflicto* were generally long-legged (Tambussi et al., 2019), and Mirandornithes, which may represent the extant sister taxon to all other extant Neoaves (Jarvis et al., 2014; Braun & Kimball, 2021; Kuhl et al., 2021), may have been plesiomorphically long-legged, an attribute that has been elaborated in crown group flamingos (Phoenicopteridae) and reversed in crown group grebes (Podicipedidae) (Mayr, 2014, 2022).

Temporally and phylogenetically, *Asteriornis* contributes to bolstering particularly sparsely populated intervals of the neornithine fossil record. At roughly 66.7 million years old, *Asteriornis* is among the oldest uncontroversial crown bird fossils yet discovered, occurring within 700,000 years of the end-Cretaceous asteroid impact. Its apparent phylogenetic position within total-group Galloanserae – one of the three most deeply diverging crown bird subclades – is consistent with the hypothesis of a limited degree of crown bird diversification prior to the end-Cretaceous mass extinction event, with the corollary that much of the deep diversification among crown birds took place in the early Cenozoic, following the end-Cretaceous mass extinction event and potentially related to competitive release following the extinction of non-neornithine dinosaurs and pterosaurs. Although the temporal origins of Neornithes remain controversial, the striking concentration of all compelling Mesozoic fossil material attributable to Neornithes near the K/Pg boundary is suggestive of a limited degree of crown bird diversification prior to the Cretaceous-Palaeogene transition.

Biogeographically, the provenance of *Asteriornis* from the northern hemisphere is extraordinary in light of other purported crown bird remains from the uppermost Cretaceous. Indeed, other than *Asteriornis*, the best evidence of crown birds from the Cretaceous is provided by *Vegavis iaii* (Noriega & Tambussi, 1995; Clarke et al., 2005, 2016; Acosta Hospitaleche & Worthy, 2021), which has alternatively been interpreted as a crown anseriform, a stem anseriform, a neoavian-like neognath and a near-crown stem bird (Clarke et al., 2005; O'Connor et al., 2011; Clarke et al., 2016; Agnolín et al., 2017; Worthy et al., 2017; Mayr et al., 2018; Álvarez-Herrera et al., 2023). *Vegavis* derives from Vega Island, Antarctica, and, along with other early crown bird fossils from high latitude sites in the southern hemisphere, such as the early Palaeocene stem anseriform *Conflicto* (Tambussi et al., 2019) and the late Palaeocene stem penguin *Waimanu* (Slack et al., 2006), seemingly bolsters biogeographic reconstructions favouring a Cretaceous origin of crown birds in the southern hemisphere (Cracraft, 2001; Claramunt & Cracraft, 2015). However, a more in-depth assessment of the early Cenozoic fossil record of crown birds challenges assumptions regarding the geographic origins of many major crown bird clades in the southern hemisphere, suggesting that Cenozoic climate shifts have obfuscated the biogeographic centres of origin for many bird groups (Blondel and Mourer-Chauviré, 1998; Mayr, 2011; Saupe et al., 2019). Thus, the recovery of *Asteriornis* – a well-supported crown bird – in the Upper Cretaceous of Europe emphasises that much remains unknown regarding the biogeographic origins of crown group birds. Further discoveries of crown-grade Cretaceous birds from the Maastrichtian of North America (Brownstein, 2024) have provided further support for a more complex biogeographic early evolutionary history for Neornithes than previously appreciated, and future discoveries may therefore be just as likely to derive from the northern hemisphere as the southern hemisphere.

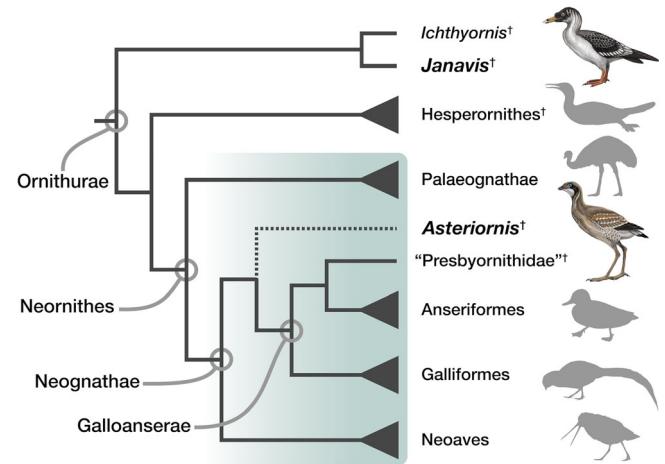


Figure 13. Phylogenetic interrelationships of Pygostylia, illustrating the inferred phylogenetic position of *Janavis finalidens* (NHMM/RD 271) as the sister taxon of *Ichthyornis*. Collectively, *Janavis* and *Ichthyornis* comprise the only valid representatives of Ichthyornithes, inferred to represent the sister group to the rest of Ornithurae. Illustration for Neornithes is a life reconstruction of *Asteriornis maastrichtensis*. Illustrations courtesy of Roc Olivé, used with permission. Topology simplified from Benito et al. (2022b).

Janavis: unexpected information on the origin of crown bird features from one of the youngest toothed avialans

The specimen that eventually became the holotype of *Janavis finalidens*, NHMM RD/271, was originally reported by Dyke et al. (2002), although limited mechanical preparation of the specimen at the time led to several skeletal elements being originally misidentified or unreported. As a stem group bird, *Janavis finalidens* has potential to cast light on the pattern and timing of the origin of features that today characterise crown group birds. Phylogenetic analyses recover *Janavis* as the sister taxon to *Ichthyornis* (Fig. 13; Benito et al., 2022a), an iconic Late Cretaceous fossil taxon that is among the morphologically best-understood members of Avialae (Marsh, 1880; Clarke, 2004; Benito et al., 2022b). However, *Ichthyornis* mainly derives from Santonian deposits within the Niobrara Formation of central North America, and the lower Campanian strata of the Mooreville Formation of Alabama. By contrast, the provenance of *Janavis* from the Maastrichtian type area implies at least a 20-million-year temporal extension of the clade, corroborating its persistence into the latest Cretaceous as hypothesised by Longrich et al. (2011), albeit on the basis of scant evidence.

While even the heaviest mean body mass estimates for *Ichthyornis* top out at less than 500 g (Benito et al., 2022a), body mass estimates for *Janavis* based on humeral least shaft circumference (Field et al., 2013) exceed 1,500 g, falling within the adult body size range of the Great Black-backed Gull (*Larus marinus*), the world's largest gull species (Olsen & Larson, 2004). This exceptionally large size contrasts with body size estimates for the co-occurring *Asteriornis* (mean body size estimate 394 g), which may be representative of the body size of early galloanserans. While data remain limited, the apparent contrast in size between crownward stem birds and early crown birds in the Maastrichtian Type Locality is in line with the hypotheses that size selectivity may have contributed to patterns of survival and extinction across the K/Pg boundary.

A trove of recent descriptions has supplemented the original material known from *Ichthyornis* and rendered it among the most

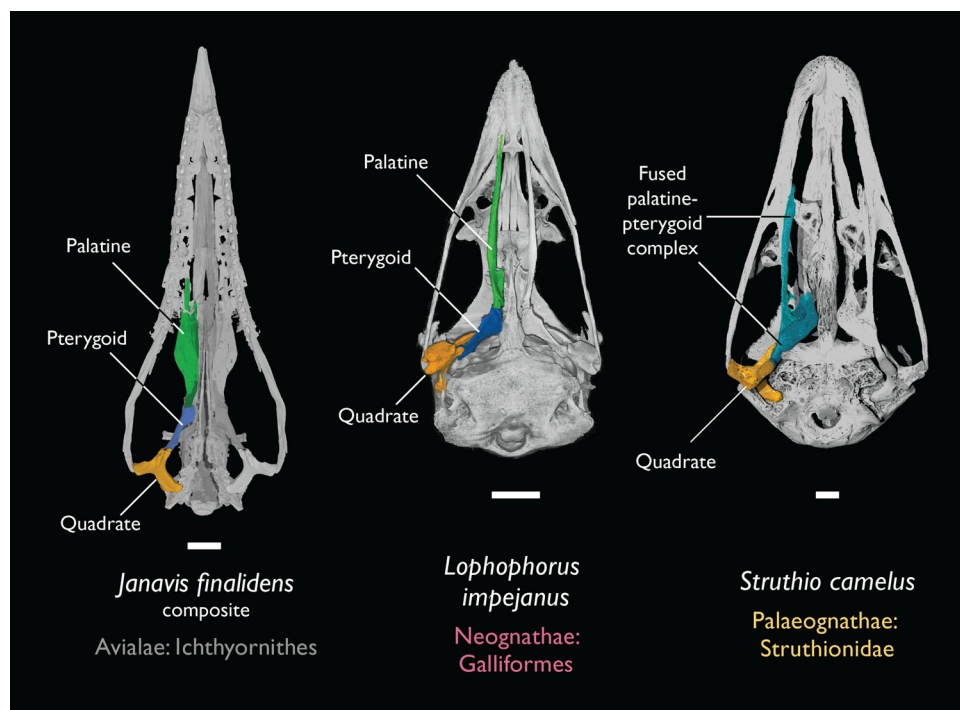


Figure 14. Reconstructed palate of *Janavis* based on the pterygoid of *J. finalidens* and several specimens of *Ichthyornis* (Field *et al.*, 2018b; Torres *et al.*, 2021), compared with an extant neognath and palaeognath. Scale bar equals 10 mm.

thoroughly understood Mesozoic avialans (Clarke, 2004; Field *et al.*, 2018b; Torres *et al.*, 2021; Benito *et al.*, 2022a), with virtually the entirety of its cranial and postcranial osteology now well understood. Only a small number of skeletal elements remain unreported from *Ichthyornis*, including the vomers and pterygoids from the skull, and the pygostyle from the postcranial skeleton. Serendipitously, the comparatively incomplete osteology of *Janavis* preserves a complete and essentially undistorted pterygoid, casting light on the palate morphology of ichthyornithine avialans and crownward stem birds more generally. When scaled to the body size of *Ichthyornis*, the pterygoid of *Janavis* fits well within the reconstructed *Ichthyornis* palate from Field *et al.* (2018b) and Torres *et al.* (2021) (Fig. 14; see Benito *et al.*, 2022b). On the rostral end of the pterygoid, a synovial socket accommodates the rounded caudal end of the *Ichthyornis* hemipterygoid, while on the caudal end of the pterygoid a single concave facet connects to the rostrally protruding pterygoid condyle on the quadrate. Strikingly, this configuration closely matches the condition of the palate in neognathous birds, in which a mobile joint connects the caudally positioned pterygoid and rostrally positioned hemipterygoid-palatine complex, providing a degree of flexibility within the palate, contributing to an improved capacity for cranial kinesis via dorsally directed upper jaw movements (Fig. 14; Simonetta, 1960; Bout & Zweers, 2001; Gussekloo & Bout, 2005). This revelation challenges long-held assumptions regarding the nature of the ancestral crown bird palate, which for over a century was assumed to have been palaeognathous (that is, lacking a mobile connection between the pterygoid and the hemipterygoid-palatine complex; Pycraft, 1901). *Janavis* has therefore revised our understanding of avian palatal evolution, suggesting that a mobile palatal configuration had already arisen among crownward stem birds, and therefore that the ‘neognathous’ palate of extant Galloanserae and Neoaves reflects the retention of the plesiomorphic crown bird condition. In this scenario, the comparatively rigid palates of

Palaeognathae reflect an apomorphic loss of palatal mobility along the palaeognath stem lineage.

Geometric morphometric comparisons of pterygoids from across the avian crown group illustrate that extant Neognathae (i.e. the large clade uniting Galloanserae and Neoaves) fall closely in morphospace, whereas the pterygoids of extant palaeognaths are peripherally distributed (Fig. 15; Benito *et al.*, 2022b). The pterygoid of *Janavis* clusters with neognaths, close to galliforms and anseriforms, providing quantitative affirmation that the pterygoid of *Janavis* was morphologically, and presumably functionally, similar to that of extant neognathous birds, and of Galloanserae in particular, in which enlarged, sessile, ovoid basiptyergoid processes are present towards the rostral end of the element, as in *Janavis*. As such, extant galloanserans such as chickens and ducks most likely provide useful analogues of ancestral crown bird palate development and function – a convenient realisation as these taxa remain common avian model organisms.

The postcranial osteology of *Janavis* also provides insight into the origin of key attributes of the modern bird skeleton. Although the postcranial skeleton of *Janavis* closely resembles a considerably larger version of *Ichthyornis*, the centra of the thoracic vertebrae and ribs of *Janavis* are extremely pneumatic, contrasting with the entirely apneumatic nature of the same structures in *Ichthyornis*. These elements exhibit extremely thin bone walls, and in the case of the anterior thoracic vertebral centra, exhibit large ventrally positioned pneumatic openings entirely unknown from other fossil or extant avialans. Otherwise, the skeletons of *Janavis* and *Ichthyornis* appear to be most clearly distinguished by the apparent absence of an acromion process on the scapula of *Janavis*, a feature otherwise only seen in extant screamers (Anhimidae; Clarke, 2004) and magpie geese (*Anseranas semipalmata*; pers. obs.) among surveyed crown birds (Clarke, 2004). The degree of vertebral pneumaticity observed in *Janavis* is extreme, seemingly

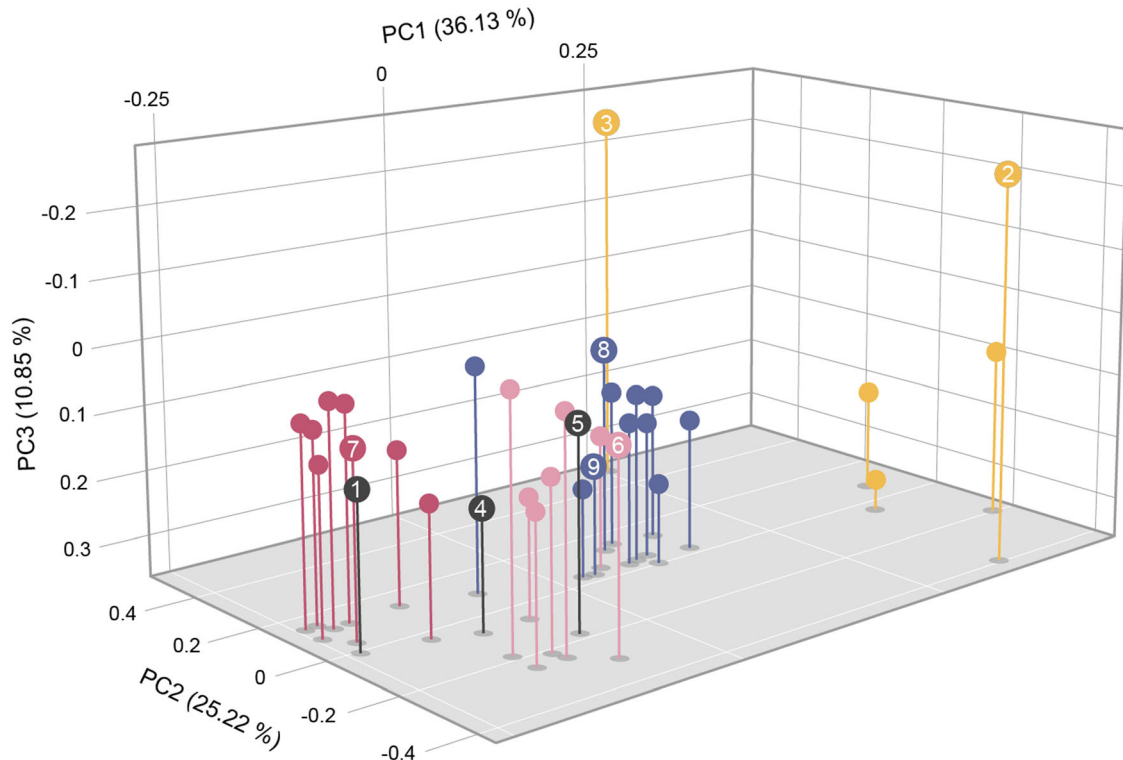


Figure 15. Three-dimensional geometric morphospace of extant Palaeognathae (yellow), Galliformes (red), Anseriformes (pink), and Neoaves (blue), combined with selected fossils including *Janavis* (1), *Dasornis* (4), and *Anatalavis/Nettapterornis* (5). Extant taxa labelled are *Struthio* (2) and *Rhea* (3), *Anas* (6), *Lophophorus* (7), *Scolopax* (8), and *Trogon* (9). Modified from Benito et al. (2022b).

comparing with some of the most extensively pneumatized vertebrae observed among extant birds (e.g., frigatebirds), although thorough quantitative comparisons employing modern approaches for quantifying pneumaticity have yet to be applied to the skeleton of *Janavis* (Burton et al., 2023). The extensive pneumatization of the vertebral column in *Janavis* presumably reflects an adaptation for weight reduction and flight efficiency as seen in many extant large-bodied soaring birds. In light of this presumed selection for mass reduction, the lack of any indication of appendicular pneumaticity in *Janavis* is notable, suggesting that the evolutionary origin of a developmental capacity for pneumatization of the appendicular skeleton postdates the phylogenetic divergence between Ichthyornithes and more crownward avialans. Given that pneumatization of the appendicular skeleton appears to be plesiomorphic for crown birds (Clarke, 2004; Turner et al., 2012; Burton et al., 2023), the evolutionary acquisition of this developmental capacity must therefore have taken place along the crownward-most portion of the avian stem lineage.

New discoveries: the continued potential of the Maastrichtian type area for clarifying avian evolution

While *Asteriornis* and *Janavis* remain the most complete bird fossils from the Maastrichtian type area yet recovered, additional discoveries provide cause for optimism regarding the potential of the Maastrichtian type locality for providing further insight into avian evolutionary history during the latest Cretaceous. Previously recovered elements from the Maastricht Formation include a

partial radius and tarsometatarsus, the latter of which is figured here (Fig. 7). Although fragmentary, the morphology of this element, including an elongate shaft that was reportedly destroyed during specimen collection, is consistent with that of early total-group anseriforms such as *Presbyornis*, and its similar size to the preserved tarsometatarsal shaft of *Asteriornis* raises the possibility that it might belong to *Asteriornis* or a closely related taxon. This tarsometatarsus originates from the Emael Member of the Maastricht Formation, contrasting with the older age of the *Asteriornis* holotype, which originates from the base of the Valkenburg member (Vellekoop et al., 2022), suggesting that *Asteriornis* or closely related taxa may have been relatively common faunal components of nearshore ecosystems during the deposition of much of the Maastricht Formation. However, more detailed morphological work on this and other Late Cretaceous isolated tarsal specimens will be necessary in order to fully establish the degree of phylogenetic and ecological information that can be gathered from such fragmentary fossil remains. Additionally, recent finds of an avialan-like pedal phalanx recovered in the summer of 2023 and a possible vertebral fragment (Figs. 7,8) indicate the continued and perhaps increasing potential of the Type Maastrichtian to yield avian fossil remains, even if the research insights to be gained from these elements are limited at present. Indeed, the recognition that small bone-bearing pieces of matrix can contain significant fossil bird remains, as exemplified by the holotype of *Asteriornis*, will hopefully encourage collectors to retain and donate promising specimens to natural history museums rather than jettisoning them in favour of more obviously aesthetic specimens. Hopefully, additional discoveries of more

complete specimens of *Asteriornis*, *Janavis*, and indeed as-yet undiscovered fossil birds from the Maastrichtian type area will be forthcoming in future years.

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