Earliest evidence for frugivory and seed dispersal by birds

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Abstract

The Early Cretaceous diversification of birds was a major event in the history of terrestrial ecosystems, occurring during the earliest phase of the Cretaceous Terrestrial Revolution. Frugivorous birds play an important role in seed dispersal today, and may have done so since their origins. However, evidence of this has been lacking. *Jeholornis* is one of the earliest-diverging birds, only slightly more derived than *Archaeopteryx*, but its cranial anatomy has been poorly understood, obscuring diet-related functional interpretations. Originally hypothesised to be granivorous based on seeds preserved as gut contents, this interpretation has become controversial. We conducted high-resolution synchrotron tomography on an exquisitely preserved new skull of *Jeholornis*, revealing remarkable cranial plesiomorphies combined with a specialised rostrum. We use this to provide a near-complete cranial reconstruction of *Jeholornis*, and exclude the possibility that *Jeholornis* was granivorous, based on morphometric analyses of the mandible (3D) and cranium (2D), and comparisons with the 3D alimentary contents of extant birds. We show that *Jeholornis* was at least seasonally frugivorous, providing the earliest evidence for fruit consumption in birds, and indicating that seed dispersal was present from early in the avian radiation. As highly-mobile seed dispersers, early frugivorous birds could expand the scope for biotic dispersal in plants, and may explain, in part, the subsequent evolutionary expansion of fruits, indicating a potential role of bird-plant interactions in the Cretaceous Terrestrial Revolution.

Introduction

Birds are among the most speciose extant vertebrate groups, playing unique ecological roles through their diverse flight and dietary adaptations (Prum et al., 2015). Modern birds include both specialised and opportunistic frugivores, that collectively are major consumers of fruits and important agents of seed dispersal. The early ecological diversification of birds

in the Early Cretaceous (>130 Ma) (Yang et al., 2020) was a landmark event in the evolution of terrestrial ecosystems, adding considerably to species richness of terrestrial ecosystems (Benson, 2018; Yu et al., 2021), and with impacts on the evolutionary histories of other flying groups (Benson et al., 2014b; Clapham and Karr, 2012). The origin and early diversification of birds in the Early Cretaceous was followed by a considerable long-term expansion of the abundance and disparity of fruits and fruit-like structures (Eriksson et al., 2000a; Eriksson, 2008), as part of the major floral transition from gymnosperm- to angiosperm-dominated floras that is central to the evolution of modern terrestrial ecosystems (Benton, 2010; Hultine et al., 2008). A macroevolutionary connection between early birds and this important event of fruit evolution has been suggested (Pejchar et al., 2008; Sekercioglu, 2006; Tiffney, 2004), but is so far unsubstantiated by fossil evidence of frugivory, presenting an obstacle to our understanding of the evolutionary origins of an important aspect of plant-animal interactions.

The Jeholornithiformes from the Early Cretaceous Jehol Biota of China are one of the earliest-diverging avian lineages, retaining a plesiomorphically elongate, bony tail, which is absent in all other birds except for the Late Jurassic *Archaeopteryx* (Wang et al., 2018; Zhou and Zhang, 2002). They also possess several advanced, flight-related morphologies, suggesting a unique form of powered flight (Chen et al., 2015; Zhou and Zhang, 2002). The most representative jeholornithiform, *Jeholornis*, has been interpreted as the earliest granivorous bird, based on the reportedly 'deep' mandible and traces identified as seeds preserved in the abdominal area (Zhou and Zhang, 2002). Reduced dentition and the presence of a gastric mill further suggest a herbivorous diet (Chen et al., 2015). However, there is no consensus on whether seeds entered the gut of *Jeholornis*, and other early birds, through deliberate seed consumption (granivory), or through consumption of fleshy propagules such as true angiosperm fruits or gymnosperm arils (frugivory) (Ksepka et al.,

and a recent review identified these two hypotheses (Müller and Pittman, 2021). Clarifying between these two hypotheses has significant implications with regards to the early evolution of bird-plant interactions, because frugivory results from beneficial co-evolutionary mutualism, whereas granivory does not. This therefore is relevant to understanding whether early birds could have been important agents of seed dispersal with a potential co-evolutionary influence on plant evolution during the KTR.

Interpretations regarding diet in *Jeholornis* and other potentially-granivorous early birds (Ksepka et al., 2019; Zheng et al., 2018, 2011) have previously been framed using qualitative observations and subjective assessments, with minimal formal comparison to extant species, and in the absence of a detailed understanding of jeholornithiform cranial anatomy (Lefèvre et al., 2021). We here report an exquisitely preserved new *Jeholornis* specimen, STM 3-8, from the Shandong Tianyu Museum of Nature, Pingyi, China. We use high quality three-dimensional (3D) data acquired through the synchrotron tomography to reveal the key cranial features of this taxon and build the most accurate cranial reconstruction of a stem bird to date. This information is used to test and determine the two diet hypotheses of *Jeholornis*, through geometric morphometric (GMM) analyses of the mandible (3D) and cranium (2D), and high-resolution computed tomography (CT) 3D visualisations of the alimentary contents of extant birds. Our approach demonstrates the importance of applying multiple methods simultaneously to solve complex palaeoecological questions.

Results

Cranial Anatomy

Due to its key phylogenetic position, *Jeholornis* has been frequently studied and cited, and many specimens are known. However, because specimens are often compressed, and are preserved in slabs, little unequivocal cranial information has been available (Lefèvre et al., & \$ % (/ ' C Ð 7 c b b c f ' Y h ' U ` " ž ' & \$ % , ž ' & \$ % ' ž ' & \$ % & / ' K U b Zhang, 2003, 2002). Our three-dimensional (3D) reconstruction of the exquisitely preserved skull of *Jeholornis* STM 3-8 (Figure 1; for detailed taxonomic information see Supplementary Information) reveals that *Jeholornis* retains a plesiomorphic diapsid skull, and provides considerable new anatomical data.

Although an unfused postorbital was previously inferred based on the basal phylogenetic position of *Jeholornis* (Wang and Hu, 2017), STM 3-8 provides the first direct evidence of this. The postorbital is proportionally large with a well-developed jugal process that contacts the jugal, forming a robust, complete postorbital bar (Figure 1). This is a plesiomorphy shared with non-avian theropods and other stem birds including *Archaeopteryx* and *Sapeornis* (Hu et al., 2020a; Rauhut et al., 2018), contrasting with the reduced or absent postorbital bar in the Ornithothoraces including modern birds (Hu et al., 2020b). The squamosal possesses a postorbital process that likely contacted the postorbital to form the supratemporal arch. The ventral process of the squamosal is short and would not have contacted the quadratojugal. The squamosal of *Jeholornis* is remarkably anteroposteriorly broad even compared to that of *Archaeopteryx* (Rauhut, 2014; Rauhut et al., 2018). A complete bony upper temporal bar is supposed to exist based on the articular facet in the postorbital, while this bar is broken and probably linked by ligament in Late Cretaceous bird *Ichthyornis* (Field et al., 2018).

The palatal complex is nearly completely preserved, including the palatine, pterygoid and vomer; the absence of the ectopterygoid is most likely preservational (Figure 1). The palate of *Jeholornis* exhibits few modifications from the non-avian theropod condition, and closely resembles that of *Archaeopteryx* (Elzanowski and Wellnhofer, 1996; Mayr et al.,

2007; Rauhut et al., 2018). The palatine is broad with a well-developed jugal process that contacts the maxilla. The pterygoid is elongated with no sign of the shortening that occurs in more derived birds and the pterygoid flange is well-developed, indicating the presence of an ectopterygoid. The vomer is dorsoventrally thin with bifurcated caudal flanges oriented nearly vertical to the rostral body, similar to the condition in *Sapeornis* (Hu et al., 2019).

While the temporal and palatal regions retain plesiomorphies, the rostrum of *Jeholornis* is heavily modified. The new specimen reveals that its premaxillae corpora are fused while the frontal processes remain separate. Rostral fusion of the premaxillae is also present in extant birds, confuciusornithiforms and several enantiornithines e.g., *Linyiornis* and *Shangyang* (Wang and Zhou, 2019; Wang et al., 2016). Its occurrence in *Jeholornis* indicates that it occurred phylogenetically earlier than previously thought. *Jeholornis* also shows dental reduction, with an edentulous premaxilla, two rostrally restricted maxillary teeth and three extremely tiny teeth in the dentary (Figure 1). N \ c i \ U

Geometric Morphometric Analyses

We digitally reassembled the cranium and mandible of *Jeholornis* STM 3-8, producing 2D cranial and 3D mandible reconstructions (Figure 1). These were included in a 3D GMM analysis of the mandible and a 2D analysis of the cranium of extant birds and select extinct pennaraptorans (for landmark definitions see Figure 2 - figure supplements 1 and Figure 2 - Source data 1&2), to evaluate the similarity of the mandible and cranium of *Jeholornis* to extant birds with different diets. Diets of extant birds were separated into five categories: (1) Seed-crackers (parrots): granivores that de-husk and fragment seeds using the beak prior to ingestion; (2) Seed-crackers (passerines): granivores that de-husk but do not extensively fragment seeds using the beak prior to ingestion; (3) Seed-grinders: granivores that primarily

process seeds using a gastric mill, with minimal beak processing; (4) Fruit eaters; and (5) Other diets (such as folivores, carnivores and omnivores).

Mandibular Morphospace. The principal components analysis (PCA) results reveal that a large portion of mandibular shape variation (PC1: 36%) is related to the relative length of the mandible compared to its rostral depth: positive values of PC1 indicate short, deep mandibles, whereas negative values indicate long, low mandibles. PC2 explains 34% of variation and is also related to the relative depth of the mandible, with positive values indicating low mandibles with coronoid eminence absent or less developed, and negative values indicating deep mandibles with a large coronoid eminence. PC3 (10% of variation) is related to the curvature, with positive values indicating a straight profile in lateral view, and negative values indicating rostroventral curvature of the rostral portion of the mandible (Figure 2A, B).

The results plot *Jeholornis* near the centre of mandibular morphospace. Seed-crackers, especially parrots, are clearly separated from the other diet types including *Jeholornis* in mandibular morphospace. They occupy a distinct region with high, positive values of PC1 and low, negative values of PC2, reflecting their deep and anteroposteriorly short mandibles with a large coronoid process and deep mandibular symphysis, which suits their seed-cracking diet by reducing the beak failure risk during cracking (Soons et al., 2015, 2010). The frugivorous parrot *Psitttrichas fulgidus* (Billerman et al., 2020) has a shallow mandible compared to those seed-cracking parrots, and plots closer to the distribution of non-parrots, consistent with the hypothesis that species can secondarily lose specialisations associated with their ancestral diet.

Seed cracking passerines also occupy an area with negative PC2 values compared to most frugivores and seed-grinders, being closer to seed-cracking parrots. They also show negative values of PC3, indicating that they have more downward inclined mandibles, which

is related to their ability to de-husk seeds (Meij and Bout, 2008). Therefore, finches are also clearly distinct from the position of *Jeholornis* in mandibular morphospace (Figure 2A, B), rejecting the previous hypothesis of *Jeholornis* as a seed cracker (both parrot-type and finch-type) (Zhou and Zhang, 2002).

Jeholornis is plotted within the overlapping range of frugivores, seed-grinders, and birds (Figure 2A, B; Figure 2 - figure supplements 2A, B). Frugivores and seed-grinders show wide and highly overlapping distributions (Figure 2A, B), indicating that *Jeholornis* was a generalist, capable of processing a wide range of foods using the beak, including seeds, fruits, and insects. Therefore, although our results exclude *Jeholornis* from being a seed cracker, they cannot distinguish between the hypotheses that seeds entered the gut of *Jeholornis* due to frugivory, or due to seed-grinding granivory.

Cranial Morphospace. Cranial shape distinguishes between our focal diet categories less effectively than mandibular shape (Figure 2C, D, Figure 2 - figure supplements 2C, D). Nevertheless, some separation is still evident, especially between seed-crackers and other dietary groups. This also indicates that *Jeholornis* was not a seed-cracking granivore. Extant seed-crackers occupy positive values of both PC1 and PC2, compared to more centrally-positioned frugivores and seed-grinders. Variation in PC1 (45%) is related to the relative length of the rostrum compared to the jugal bar, with positive values indicating a shorter rostrum. Variation in PC2 (14%) is related to the depth and curvature of the rostrum, with positive values indicating deeper and rostroventrally curved rostra, present in seed-crackers and toucans (*Ramphastos*, which differs from seed-crackers in having a negative PC1 score). Variation in PC3 is related to the relative size of the orbit and naris, with positive values indicating smaller orbits and naris. Because some fossil samples included in our analyses are incomplete, we did not include the skull roof in this analysis. Our results indicate that seed-

crackers have relatively short, deep and rostroventrally curved rostra compared to most other birds, including *Jeholornis*, *Sapeornis* and other Mesozoic taxa.

Mesozoic taxa are mostly separated from modern birds along PC2 and PC3, occupying negative values of PC2 and positive values of PC3 separately (Figure 2C, D). Among them, *Jeholornis* and *Sapeornis* are more similar to extant birds along PC2, which describes rostral morphology. This may reflect the dietary specialization of *Jeholornis* and *Sapeornis* (frugivory-like or granivory) compared to other Mesozoic taxa. Nevertheless, they cluster with other Mesozoic taxa along cranial PC3, indicating conservative aspects shared with non-avian theropods, especially a proportionally small orbit and external naris.

Alimentary Content Analyses

Our morphometric analyses indicate that *Jeholornis* distinguish between frugivorous and seed-grinding granivorous diets. We therefore conducted a comparison of the alimentary contents of *Jeholornis* (Figure 3) with selected modern birds (Figure 4) using high resolution CT scanning. Our modern bird sample includes frugivores (*Manucodia comrii*, Curl-crested manucode; *Bombycilla garrulus*, Bohemian waxwing), seed-cracking parrots (*Conuropsis carolinensis*, Carolina parakeet), seed-cracking passerines (*Geospiza fuliginosa*, Small ground-finch; *Calcarius lapponicus*, Lapland longspur), and seed-grinding granivores (*Ectopistes migratorius*, Passenger pigeon; *Pedionomus torquatus*, Plains-wanderer; *Thinocorus rumicivorus*, Least seedsnipe) (detailed specimen information see Figure 4 - Source data 1; detailed descriptions of their alimentary contents see Methods and Materials).

Comparative evidence from those modern avian gut contents show that granivory is strongly indicated by fragmentation (in seed-crackers) or abrasion (in seed-grinders) of seeds in the alimentary canals, which is likely a prerequisite for nutrient extraction. The seed

remains are highly fragmented in seed-cracking parrots (Figure 4E), whereas in seed-cracking passerines, although the crop contents are almost intact, those in the stomach are also highly fragmentary (Figure 4D, Figure 4 - figure supplements 1E, F). This is consistent with behavioural observations of finches and other granivorous passerines (Billerman et al., 2020), in which seed-cracking passerines use the beak only to remove the outer coats of seeds, and do not fragment the seed before ingestion, differing from parrots that can fragment seeds prior to ingestion (Figure 4E). Fragmentation (in granivorous passerines) is completed later by the gastric mill, showing a similar condition of seed-grinders. Fragmentation of seeds in passerines is primarily achieved through the gastric mill, similar to some seed-grinders e.g. *Ectopistes migratorius* (Passenger pigeon) (Figure 4C, Figure 4 - figure supplements 1B). However, in most seed-grinders the gut contents consist of abraded and partially-damaged, rather than highly-fragmented, seed remains (Figure 4B, Figure 4 - figure supplements 2A-F).

Seed remains in all the sampled granivores were tightly aggregated together, and typically co-occurred with gastroliths (Figure 4B-E). Gastroliths are especially abundant in some seed-grinders and seed-cracking passerines (Figure 4B, D) compared to the parrot (Figure 4E) and pigeon (Figure 4C). In contrast, the seed remains in frugivores are completely intact, often in their original [k] - [z] configurations. They are sparsely dispersed in the alimentary tract, sometimes accompanied by a few tiny gastroliths (Figure 4A, Figure 4 - figure supplements 1A, C, D). The seed remains preserved in currently known *Jeholornis* specimens most closely resemble the condition in frugivores, being completely intact and sparsely dispersed (Figure 3A-C) compared to the gastroliths preserved in other individuals (Figure 3D).

Discussion

Digital reconstruction of an exceptionally well-preserved new specimen of the early-diverging bird *Jeholornis* reveals a plesiomorphic, diapsid skull, sharing numerous features with non-avian theropods. These features include a complete postorbital bar, unreduced squamosal, and unmodified palate (Hu et al., 2020b, 2020a, 2019; Rauhut et al., 2018), reinforcing evidence for an early-diverging phylogenetic position among birds (Wang et al., 2018; Zhou and Zhang, 2002). Nevertheless, compared to *Archaeopteryx* (Rauhut, 2014; Rauhut et al., 2018), *Jeholornis* also possesses clear diet-related specialisations of the rostrum including partial fusion of the premaxillae and a strongly reduced dentition.

Our GMM analyses reveal that the mandibular and cranial shapes of *Jeholornis* and *Sapeornis* are distinct from those of seed-cracking granivorous birds, consistent with earlier assumptions that the delicate, vestigial dentary teeth of *Jeholornis* would be too prone to damage if used to de-husk hard foods. Our analysis, however, claims that the reportedly deep mandible of *Jeholornis* is suitable for such a behaviour (Zhou and Zhang, 2002). Although their mandibular and cranial shapes occupy the morphospace in which several diets overlap, including frugivory and gastric seed-grinding granivory, these diets can be distinguished through comparing the condition of ingested remains in the alimentary tract in modern birds.

Known stomach contents preserved in *Jeholornis* take two forms in different fossil specimens, which include: (1) individuals with sparsely distributed and entirely intact seeds (Figure 3A-C) (Zhou and Zhang, 2002), and (2) those with a relatively small concentration of gastroliths without any seed remains (Figure 3D). Our comparisons with modern birds indicate that the first group of *Jeholornis* individuals ingested fleshy propagules (frugivory), rather than consuming seeds for nutrient extraction (granivory). We cannot interpret the presence of gastroliths in the second group of individuals, because gastroliths are widespread in extant birds with a wide range of diets e.g. insectivory,

granivory and frugivory (Wings, 2007), making it impossible to infer diet from this evidence alone. Crucially, no *Jeholornis* specimen preserves seeds and gastroliths together (Zhou, 2020) (and preserved seeds within *Jeholornis* are not abraded), which would be required as evidence for seed-grinding granivory.

Variation in alimentary contents among individuals of *Jeholornis* are best interpreted as evidence of seasonal variation in diet, or potentially other intraspecific variation in diet (Wings, 2007). It is possible that *Jeholornis* consumed fleshy propagules during the seasons in which such food sources were available, but fed on other food sources such as invertebrates or foliage using the gastric mill during other seasons. Similar seasonal dietary shifts are quite common in modern birds that feed on fruits as part of their diet such as Ruffed Grouse (*Bonasa umbellus*) and Hoatzin (*Opisthocomus hoazin*) (Billerman et al., 2020). If our inferences regarding *Jeholornis* are correct, this dietary flexibility can be traced back to the earliest stages of bird evolution.

The evidence for frugivory in *Jeholornis* demonstrates that early birds with seeds preserved in the abdominal area cannot be identified as granivores without further evidence from cranial morphology, or the co-occurrence of abraded or fragmented seeds with gastroliths. It was recently suggested that *Sapeornis*, *Eogranivora* and even some enantiornithines may also have been frugivorous (Ksepka et al., 2019; Mayr et al., 2020). However, the evidence for this remains equivocal. *Sapeornis* and *Eogranivora* preserve apparently whole seeds in the crop, but only gastroliths in the abdominal area (Zheng et al., 2018, 2011), consistent with both seed-grinding granivory and passerine-like seed-cracking (Figure 4C, D). Therefore, *Jeholornis* is so far the only Mesozoic bird that provides strong evidence of frugivory. However, this should not be taken as evidence that frugivory was rare. Direct evidence on diet in fossil birds is rare and preserved gut contents are limited to just a

few individuals from a small number of Early Cretaceous fossil deposits in China and Europe (Chen et al., 2018). Given this low level of current knowledge, evidence for at least seasonal frugivory in *Jeholornis* is important in demonstrating that at least some early birds ate fruits.

Flight-related anatomical specialisations suggest that *Jeholornis* was a competent flier in spite of its early-diverging phylogenetic position (Chen et al., 2018; Zhou and Zhang, 2002). Although flight is not an exclusive adaptation to frugivory, compared to non-volant animals, flight allows birds and bats to more easily obtain patchily-distributed but energy-rich food sources in difficult to access and widely dispersed locations, including fruits (Benson et al., 2018, 2014a; Maurer, 1998), and may in part explain the high prevalence of frugivory (and especially the consumption of small fruits such as berries) among extant birds compared to most other tetrapod groups (Tiffney, 2004, 1992).

Although true fruits are only present in angiosperms, seed ferns and gymnosperms evolved functionally analogous fleshy-coated propagules (arils) much earlier (Herendeen et al., 2017). Such structures represent specialisations for animal-mediated seed dispersal. Early fruit-producing angiosperms were present by the Early Cretaceous (Eriksson et al., 2000b), alongside multiple groups of aril-producing gymnosperms including cycadales, ginkgoales and gnetales (Tiffney, 2004, 1986; Wu, 1999) which are also present in Jehol Biota (Leng and Friis, 2003; Sun et al., 2001). The alimentary contents preserved in *Jeholornis* were preliminarily described as ginkgo-like seeds (Zhou and Wu, 2006), but have not been confidently identified with detailed comparisons with all the potential Early Cretaceous fruits/arils. In addition, a diversity of ingested seed morphotypes have been documented among these alimentary contents (Chen et al., 2018). Therefore, considering that early birds such as those from the Jehol Biota would encounter both gymnosperms and angiosperms, we suggest that during the origin of frugivory among birds, early frugivorous

birds were likely to be opportunistic and targeted small, fleshy propagules from both groups, rather than being

Given the importance of frugivorous birds today as agents of seed dispersal (Pejchar et al., 2008; Sekercioglu, 2006; Tiffney, 2004), the ancient origin of frugivory in birds signifies the origin of an important component of modern-like biotic dispersal systems, providing new opportunities for co-evolutionary mutualisms. The occurrence of specialised seed-dispersal by animals during the Early Cretaceous has previously been proposed indirectly, based on the presence of aril-producing gymnosperm and early fruit-producing angiosperms (Eriksson, 2008; Eriksson et al., 2000a). However, the identification of these frugivores has been uncertain and frugivory was almost unmentioned in the recent review of early bird diets (Miller and Pittman, 2021). Strong indications for at least seasonal frugivory in *Jeholornis* provides direct evidence of this for the first time.

Fossil birds have low preservation potential and are known primarily from sites of exceptional preservation. Outside of the Jehol Biota, the fossil record of early birds is poorly-sampled, both in space and time. However, evidence from less complete fossil remains suggests that birds had a wide geographic distribution by the Early Cretaceous (Chiappe and Witmer, 2002; Close et al., 2009), suggesting a and the likely ecological diversity of Mesozoic birds. Diversification of birds therefore may explain, at least in part, the evolutionary expansion of fruit abundance, especially angiosperm fruits, that occurred through the Cretaceous (Eriksson, 2008; Eriksson et al., 2000a). Direct evidence for the diet of extinct species is rare. However, evidence for fruit consumption in *Jeholornis* indicates the potential for either opportunistic or specialised frugivory among early birds in general. It therefore increases support for the hypothesis that bird-plant interactions played a role in the Cretaceous Terrestrial Revolution (Tiffney, 2004). Specifically, the occurrence of frugivory in one of the earliest-diverging bird lineages raises the possibility of synergistic

diversification, with birds enabling seed dispersal for plants, and obtaining a rich energy resource in return. New discoveries and comparative analyses are required to further test this hypothesis, by insights into the ecologies of more early bird species, and the potential role of the birds during the transition from gymnosperm- to angiosperm- dominated floras.

Materials and Methods

Taxonomy of *Jeholornis* STM 3-8

Jeholornis STM 3-8 was collected from the Jiufotang Formation (~120 Ma) (He et al., 2004) at the Dapingfang locality in Chaoyang, Liaoning province, preserving a complete and mostly articulated skull, and a few postcranial elements. This new specimen is tentatively assigned to *Jeholornis prima* based on the presence of the following features: relatively robust mandible with three rostrally restricted teeth; edentulous and robust premaxilla; maxilla lacking teeth in the caudal portion; long bony tail consisting of more than 20 caudal vertebrae. This specimen could be distinguished from *Jeholornis palmapenis* by its flattened dorsal margin of ilium, compared to the strongly convex condition in *J. palmapenis*. The validity of another recently reported jeholornithiformes, *Kompsornis longicaudus* (Wang et al., 2020) needs more discussions since only one specimen is used to erect it, while no detailed comparisons have been done to the numerous specimens which have been assigned to *Jeholornis* before. In addition, the parts bearing key features listed in (Wang et al., 2020) such as pectoral girdle and sternum, are not preserved in STM 3-8. However, some characters such as the relatively pointed rostral tip of the mandible of *Kompsornis* still tentatively indicate that STM 3-8 may be distinguished different from it.

CT scans and digital reconstructions

Microtomographic measurements of *Jeholornis* STM 3-8 were performed using the Imaging and Medical Beamline (IMBL) at the Australian Nuclear Science and Technology C f [U b] g U h] c b Ð g ´ fl 5 B G H C Ł ´ 5 i g h f U `] U b ´ G m b W \ f c h f c investigation, acquisition parameters included a pixel size of 16.9 x 16.9 µm, monochromatic beam energy of 70 keV, a sample-to-detector distance of 200 mm. As the height of the specimen exceeded the detector field-of-view, the specimen was aligned axially relative to the beam and imaged using seven consecutive scans. The raw 16-bit radiographic series were normalised relative to the beam calibration files and stitched. Reconstruction of the 3D dataset was achieved by the filtered-V U W _ ´ d f c ^ Y W h] c b ´ a Y hTRACT´ i g] b [´ (Gureyev et al., 2011).

The 3D reconstructions (Figure 1A, B) and the fixing of 3D models (Figure 1C, D) were created and completed with the software Mimics and 3-matic (version 16.1). The mandible model of *Jeholornis* STM 3-8 was reconstructed for the GMM analysis (Figure 1H) by the following steps; the crashed left splenial was replaced by the mirrored right splenial; the breakage through the left dentary and surangular was joined together; second left dentary tooth was replaced by the mirrored right counterpart with better preservation; all the left dentary teeth were slightly relocated according to the morphology of the alveoli; the fixed left mandible was then mirrored to create the right half; the two sides were joined together, with the angle between them determined by the width of the braincase. The 3D models of the cranial elements of *Jeholornis* STM 3-8 were reassembled (Figure 1C, D) by the following steps: all the left elements with better preservation were mirrored to create the right half, except for the pterygoid, for which the better-preserved right one was used as the reference; all the elements were relatively relocated to build a complete skull according to their articulations and anatomical geometry. Since most elements are only slightly dislocated with the articulations/articulation facets preserved, this reassembled model is largely reliable, with

the location of the preorbital ossifications being the highest uncertainty. The reassembled cranial model was then used as the reference for the 2D reconstruction of the *Jeholornis* skull in lateral and ventral views (Figure 1E, F).

GMM analyses

The dataset incorporates *Jeholornis* and 160 extant bird species representing 111 families and 36 orders in our 3D mandible analysis, with additional Mesozoic theropods in 2D skull analysis including: *Sinornithosaurus* (Dromaeosauridae) (Xu and Wu, 2001), *Linheraptor* (Dromaeosauridae) (Xu et al., 2015), *Dilong* (Tyrannosauroidae) (Xu et al., 2004), *Archaeopteryx* (non-Ornithothoraces Aves) (Rauhut, 2014), *Sapeornis* (non-Ornithothoraces Aves) (Hu et al., 2019), *Pengornis* (Enantiornithes) (Field et al., 2011) and *Ichthyornis* (Ornithuromorpha) (Field et al., 2018). We note that the 2D cranial reconstruction of *Pengornis* is less reliable among those Mesozoic samples due to the comparatively poor preservation, but we incorporate it here as it is currently the best representative enantiornithine.

One anatomical landmark and four curves (semi-landmarks) were placed in each mandible in 3D, and five anatomical landmarks and five curves were placed in each cranium in 2D, using Avizo Lite (version 9.2.0). Landmark definitions and descriptions are modified from Bjarnason and Benson, 2021 (Bjarnason and Benson, 2021) (details see Figure 2 - figure supplements 1 and Figure 2 - Source data 1&2). All the digital landmarks and semi-landmarks were imported into R (version 3.6.0) for further analyses. A GPA was performed to translate, and scale landmark configurations to unit centroid size. To visualize the multivariate ordination of the aligned Procrustes coordinates, a PCA was performed afterward using plotTangentSpace()

The ecological information including diet categories and foraging strategies of modern birds were modified from Wilman et al., 2014 (Wilman et al., 2014). The diets of birds were originally assigned to five categories in: (1) Plant and Seeds; (2) Fruits and Nectar; (3) Invertebrates; (4) Vertebrates and Fish and Carrion; and (5) Omnivore (Wilman et al., 2014). Based on our focal goal and information from *Birds of the World* (BOW) (Billerman et al., 2020), those categories were either split or merged to form five new categories: (1) Seed-crackers (parrots): Psittaciformes; (2) Seed-crackers (passerines): mostly finches including Fringillidae, Thraupidae and Sylviidae, and some other granivorous passerines; (3) Seed-grinders: galliforms and members of Columbidae, Anatidae, Alaudidae, Odontophoridae, Tinamidae, Pedionomidae and Pteroclididae; (4) Fruit eaters: members of Paradisaeidae, Phasianidae, Calyptomenidae, Capitonidae, Coliidae, Musophagidae, Cracidae, Megalaimidae, Opisthocomidae, Pipridae, Psophiidae, Columbidae, Ramphastidae, Cotingidae, Tityridae and Trogonidae, as well as the frugivorous parrot *Psittirichas fulgidus* (Pesquet's Parrot); (5) Other diets (such as other herbivores, carnivores and omnivores). Among them, the diets of three modern species were modified according to BOW (Billerman et al., 2020): *Anas discors* modified to be [Seed-grinders] from [Omnivore] since it is consistent with other anatids; *Psittacus erithacus* modified to be [Seed-crackers (parrots)] from [fruit] since it has the ability and occasionally does crack and eat seeds; *Pedionomus torquatus* modified to be [Seed-grinders] from [Seed-crackers] since it includes 30% of seeds and its complexity is discussed in the Results part. The modified diet categories were used to group the samples in the PCA results (Figure 2).

Detailed descriptions of the alimentary contents in modern birds

1. Frugivores: *Manucodia comrii* (Curl-crested manucode, Figure 4A, Figure 4 - figure supplements 1A), is a specialized fruit eater (Billerman et al., 2020). Several whole fruits are revealed along the alimentary tract of our sample, each including four intact, unabraded seeds in a regular configuration, as well as another kind of disc-shaped seeds, and no gastroliths are preserved (Figure 4A; Figure 4 - figure supplements 1A). Another frugivore *Bombycilla garrulus* (Bohemian waxwing, Figure 4 - figure supplements 1C, D) was also sampled, and the same situation of the contents is revealed as in *M. comrii*. All the seeds preserved through its alimentary tract including crop, stomach and intestines are intact, and more sparsely located than in the seed-grinders and seed-crackers that we sampled.

2. Seed-cracking parrots: *Conuropsis carolinensis* (Carolina parakeet, Figure 4E), a parrot, is a specialized seed-cracker using beak to de-husk the seeds (Billerman et al., 2020). The alimentary tract of this sample contains a proportionally small bolus of highly fragmented seeds with original shapes impossible to determine, and very few small and sparse stones.

3. Seed-cracking passerines: *Geospiza fuliginosa* (Small ground-finch, Figure 4D, Figure 4 - figure supplements 1E) is half a seed-cracker and half a seed-grinder, and has a diet mostly consisting of small seeds (Billerman et al., 2020). The crop contents of this sample consist of seeds with almost intact configuration, whereas those in the stomach are highly fragmentary along with lots of large gastroliths. We then sampled another seed cracking passerine *Calcarius lapponicus* (Lapland longspur, Figure 4 - figure supplements 1F), and found the same situation of the contents as in *G. fuliginosa*.

4. Seed-grinding granivores: *Ectopistes migratorius* (Passenger pigeon, Figure 4C, Figure 4 - figure supplements 1B), a seed-specialist pigeon, is a seed-grinder that entirely uses gastroliths to crack the seeds (Billerman et al., 2020). Its crop contains numerous, well-defined and intact seeds, whereas seeds are highly fragmented in the stomach, similar to those

in *C. carolinensis* and *G. fuliginosa*, together with two large, round gastroliths. Another representative, *Pedionomus torquatus* (Plains-wanderer, Figure 4B, Figure 4 - figure supplements 2A-D) is a general, small-sized seed-grinder. The seeds preserved in the alimentary tract of *P. torquatus* are comparatively more intact than those in other seed specialists such as parrots, pigeons and finches, but many seeds show partial breakages and the gastroliths they contained are much smaller. This indicates that *P. torquatus* might utilize another strategy of abrasion to digest the seeds rather than entirely fragmentation. To test this interpretation, we sampled another seed generalist, *Thinocorus rumicivorus* (Least seedsnipe, Figure 4 - figure supplements 2E, F). The seed remains are in the same condition as in *P. torquatus* – not fragmentary but abraded with partial breakages, along with small gastroliths, confirming the strategy used by those general seed-grinders.

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Data and materials availability

The new specimen reported here (*Jeholornis* STM 3-8) is housed and available for future researchers to check at Shandong Tianyu Museum of Nature, China. The original CT scanning slices and segmented STL files of *Jeholornis* STM 3-8 and involved modern birds, and the alimentary contents of selected modern birds are available in Morphosource (<https://www.morphosource.org/projects/0000C1212?locale=en>; <https://www.morphosource.org/projects/00000C420>; <https://www.morphosource.org/projects/0000C1080?locale=en>). Other data that support this study are available in Figshare (<https://figshare.com/s/6a96e1338cadd70f9723>), including the rotating videos of the original/reassembled cranial 3D models of *Jeholornis* STM 3-8 and the 3D models of the alimentary contents of selected modern birds, and the landmark data and taxa lists used in GMM analyses. Further information and requests for resources should be directed to Yixian Zhang (zhangyixian6696@jlu.edu.cn) @ Y U X ' 7 and Han Hu (han.hu@earth.ox.ac.uk).

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698 Figures

Figure 1. *Jeholornis* STM 3-8. (A) Left and (B) right view of the 3D reconstructed model of the skull. (C) Left and (D) ventral view of the reassembled 3D model of the skull. (E) Left and (F) ventral view of the 2D cranial reconstruction. (G) Photograph of the skull. (H) Dorsal view of the reassembled 3D model of the mandible. Abbreviations: 1. premaxilla; 2. nasal; 3. preorbital ossification; 4. lacrimal; 5. maxilla; 6. jugal; 7. quadratojugal; 8. frontal; 9. braincase; 10. squamosal; 11. postorbital; 12. scleral ring; 13. quadrate; 14. dentary; 15. surangular; 16. angular; 17. splenial; 18. vomer; 19. palatine; 20. pterygoid; 21. potential ectopterygoid. Different bones are indicated by different colours. Scale bar equals 5mm.

Figure 2. PCA result of 3D mandible shape (A, B) and 2D skull shape (C, D). Different diet categories are indicated by different colours, and key samples are labelled with generic names.

Figure 3. Seeds preserved in the abdominal area of selected *J. prima* specimens. (A) IVPP V13274 (holotype). (B) STM 2-41. (C) Close up image of seeds in IVPP V13274 (A). (D) Gastrolith mass in *J. prima* STM 2-15. Photos in A-D followed Figures in C D 7 c b b c f ' Y h ' al., 2018 fl C D 7 c b b c f '. Scale bars equal 5mm.

Figure 4. 3D reconstructed seed models preserved in alimentary tract of selected modern birds. (A) *Manucodia comrii* (fruit eater). (B) *Pedionomus torquatus* (seed-grinder). (C) *Ectopistes migratorius* (seed-grinder). (D) *Geospiza fuliginosa* (use both seed-cracking and seed-grinding strategies). (E) *Conuropsis carolinensis* (seed-cracker). Dash-lined boxes indicate local magnifications. Gastroliths are remarkably brighter than other contents in the slices. Red arrows indicate the breakages of seeds in slices, which are difficult to show in the

reconstructed models. Scale bars equal 5mm for the whole models and slices, and 1mm for the magnification boxes.

Figure 2 - figure supplements 1. Landmark and semi-landmark locations in *Menura novaehollandiae* as an example of modern taxa used in GMM analyses (following Bjarnason and Benson, 2021). Black labels indicate the description names, and blue labels below indicate the names in R.

Figure 2 - figure supplements 2. PCA result of 3D mandible (A, B) and 2D skull shape (C, D) with labels of generic names. Some points in green overlap the points in other colours.

Figure 4 - figure supplements 1. Scanning slices of the alimentary contents in involved modern bird samples.

Figure 4 - figure supplements 2. Scanning slices of the alimentary contents in involved modern bird samples. Red arrows indicate the breakages of seeds.

Figure 2 - Source data 1. Descriptions of cranial and upper jaw landmarks and semi-landmarks (following Bjarnason and Benson, 2021).

Figure 2 - Source data 2. Descriptions of mandible landmarks and semi-landmarks (following Bjarnason and Benson, 2021).

Figure 4 - Source data 1. Specimens used in the alimentary content analyses.

Figure 1

Figure 2

Figure 3

A *Manucodia cornii* B *Pedionomus torquatus* C *Ectopistes migratorius* D *Geospiza fuliginosa* E *Conuropsis carolinensis*

Menura novaehollandiae

Upper jaw beak tip

Skull_LM_Sphenoid_bone_tip

Craniofacial hinge

Skull_LM_Cranio_Facial_hinge

End of jugal bar semi-landmarks (jugal bar end)

Skull_LM_jugal_bar_end

Start of jugal bar semi-landmarks (jugal bar start)

Skull_LM_jugal_bar_start

Jugal bar semi-landmarks

Skull_semi_LM_jugal_bar

Upper jaw ventral bar semi-landmarks

Skull_semi_LM_Mandible_ventral_bar

Start of upper jaw ventral bar semi-landmarks

Skull_LM_Mandible_ventral_bar_start

End of upper jaw ventral bar semi-landmarks (upper jaw beak tip)

Skull_LM_Mandible_jaw_beak_tip

End of upper jaw dorsal bar semi-landmarks (craniofacial hinge)

Skull_LM_Cranio_Facial_hinge

Upper jaw dorsal bar semi-landmarks

Skull_semi_LM_Mandible_dorsal_bar

Start of upper jaw dorsal bar semi-landmarks (upper jaw beak tip)

Skull_LM_Mandible_jaw_beak_tip

Start of nasal aperture semi-landmarks

First landmark in Skull_Semi_LM_Nasal_Aperture

End of nasal aperture semi-landmarks

Skull_Semi_LM_Nasal_Aperture

Nasal aperture semi-landmarks

Skull_Semi_LM_Nasal_Aperture

Orbit semi-landmarks

Skull_Semi_LM_Orbit

Start of orbit semi-landmarks

First landmark in Skull_Semi_LM_Orbit

End of orbit semi-landmarks

First landmark in Skull_Semi_LM_Orbit

Dorsal mandible semi-landmarks

Mandible_Semi_LM_dorsal_mandible

Start of dorsal mandible semi-landmarks (craniodorsal dentary)

Mandible_LM_anterior_precondylar_dentary

End of dorsal mandible semi-landmarks

First landmark in Mandible_Semi_LM_dorsal_mandible

Mandibular symphysis semi-landmarks

Mandible_Semi_LM_mandibular_symphysis

End of mandibular symphysis semi-landmarks

First landmark in Mandible_Semi_LM_mandibular_symphysis

Start of mandibular symphysis semi-landmarks (craniodorsal dentary)

Mandible_LM_anterior_precondylar_dentary

Start of ventral mandible semi-landmarks (end of mandibular symphysis semi-landmarks)

First landmark in Mandible_Semi_LM_mandibular_symphysis

Ventral mandible semi-landmarks

Mandible_Semi_LM_dorsal_mandible

End of ventral mandible semi-landmarks

First landmark in Mandible_Semi_LM_dorsal_mandible

Start of the caudal mandible semi-landmarks

First landmark in Mandible_Semi_LM_posterior_mandible

Caudal mandible semi-landmarks

Mandible_Semi_LM_posterior_mandible

End of the caudal mandible semi-landmarks

First landmark in Mandible_Semi_LM_posterior_mandible

A *Manucodia cornii* (crop&stomach)

B *Ectopistes migratorius* (crop)

C *Bombycilla garrulus* (stomach&intestine)

D *Bombycilla garrulus* (intestine)

E *Geospiza fuliginosa* (crop)

F *Calcarius lapponicus* (stomach)