

## Research



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# Reinterpretation of a previously described Jehol bird clarifies early trophic evolution in the Ornithuromorpha

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STM35-3 from the Yixian Formation is the only Early Cretaceous ornithuromorph preserving direct evidence of granivory. The crop contains numerous seeds and the preservation of gastroliths presumably within the ventriculus indicates this diet was paired with the presence of a gastric mill as in living granivorous birds. STM35-3 was originally referred to *Hongshanornis longicresta*, member of a diverse clade of small, basal ornithuromorphs with elongate hindlimbs known as the Hongshanornithidae. Hindlimb proportions suggest that hongshanornithids were wading birds, an ecological inference somewhat in conflict with direct evidence suggesting *Hongshanornis* fed on seeds. However, close inspection of STM35-3 reveals that the specimen represents a new species not closely related to hongshanornithids, distinguished by large forelimbs that exceed the length of the hindlimbs, robust and narrow coracoids, and a delicate edentulous rostrum. By contrast, all hongshanornithids have hindlimbs that far exceed the length of the forelimbs, coracoids with wide sternal margins, and small teeth throughout the upper and lower jaws. Reinterpretation of this new taxon, *Eogranivora edentulata* gen. et sp. nov, helps to clarify trophic driven patterns of tooth loss within the Ornithuromorpha. Apparent loss of the hallux may represent the first such occurrence in a Mesozoic bird and suggests a highly terrestrial lifestyle.

## 1. Introduction

Modern birds have a highly specialized digestive system that is lightweight, efficient and capable of sustaining the energetic demands of powered flight, the most costly form of vertebrate locomotion [1]. Birds possess two features unique among reptiles: the oesophageal crop and the distinctly double-chambered stomach with the caudal portion (the ventriculus) specialized into a grinding gizzard in many taxa [1]. Among living birds the shape and proportions of these two organs vary enormously reflecting the wide range of diets used by different species [1,2]. Normally soft tissues in fossilized organisms can only be studied indirectly but due to extraordinary taphonomic conditions, the Jehol Lagerstätte has produced a large number of exceptionally preserved fossils that provide direct clues as to the architecture of the digestive system in several Early Cretaceous avian lineages [3]. This has produced increased interest into the trophic habits and digestive abilities of early birds and their closest relatives [4]. This information has the potential to reveal if any changes in the digestive system co-occurred with the evolution of flight, and how structural changes of the digestive system may have played a part in the diversification of early avian lineages as well as the eventual extinction of all non-neornithine lineages. Although nearly all evidence of diet and alimentary canal structure comes from the Early Cretaceous Jehol Biota, data are still relatively rare [5]. Owing to the limited available data, every specimen preserving direct evidence is of great interest.

Despite being known from fewer specimens than other groups of Cretaceous birds, the greatest number of specimens preserving evidence of diet are referable to the crown-ward avian clade, the Ornithuromorpha, which includes Neornithes (all living birds) nested within. Fish remains are preserved in the crop and ventriculus of more than a dozen specimens of *Yanornis* indicating the presence of a complex digestive system characterized by bi-directional peristalsis capable of egesting hard to digest items [4]. Gastroliths interpreted as gizzard stones are preserved in a diversity of taxa including both edentulous (*Archaeorhynchus*) and toothed (*Hongshanornis*, *Iteravis*) forms [6–8]. However, only a single reported ornithuromorph preserves ingested seeds—STM35-3, previously referred to *Hongshanornis longicresta*, member of the Hongshanornithidae, a diverse group of small birds with distinct hindlimb proportions that persisted through the entirety of the Jehol [3,9]. All these taxa have an intermembral index ( $\text{ImI} = (\text{humerus} + \text{ulna}) / (\text{femur} + \text{tibiotarsus})$ ) between 0.81 and 0.87, whereas other Early Cretaceous ornithuromorphs typically have forelimbs longer than the hindlimbs ( $\text{ImI} > 1.0$ ) [9]. Owing to their elongate hindlimbs hongshanornithids are commonly interpreted as wading birds [10].

A granivorous diet is not entirely consistent with a wading ecology, which rather suggests a diet of small aquatic invertebrates. No other specimen of hongshanornithid ( $n = 7$ ) preserves seeds and only one preserves gastroliths [7]. However, the presence of gastroliths alone does not allow for the reconstruction of diet; modern birds consuming a variety of hard food items, including molluscs and insects, are also known to use gizzard stones [11]. The presence of seeds in STM35-3 could suggest omnivory, seasonal changes in diet or lineage-specific patterns in diet. However, closer inspection of STM35-3 reveals that this specimen does not belong to the Hongshanornithidae. This specimen is reidentified as a new species, for which we erect the name *Eogranivora edentulata* gen. et sp. nov. We provide a complete anatomical description of STM35-3 and investigate its phylogenetic position within Aves through a cladistic analysis. Reidentification of this specimen helps to clarify our understanding of early avian trophic diversity and patterns of tooth loss among Cretaceous birds.

## 2. Systematic palaeontology

Aves Linnaeus 1758 [12]

Ornithothoraces Chiappe 1995 [13]

Ornithuromorpha Chiappe 2002 [14]

*Eogranivora* gen. nov.

Diagnosis. As for species.

*Eogranivora edentulata* sp. nov.

### (a) Holotype

STM (Shandong Tianyu Museum of Nature, Pingyi, China) 35-3, a nearly complete fully articulated subadult–adult individual preserved in a slab and counterslab with weak feather impressions, crop contents and gastroliths.

### (b) Etymology

'*Eogranivora edentulata*' meaning toothless early granivore. The generic name '*Eogranivora*', *eo-* meaning early and *-granivora* meaning seed-eater, refers to the crop contents preserved in the holotype; the specific name '*edentulata*' means without

teeth and refers to the toothless rostrum that characterizes this taxon.

### (c) Diagnosis

Medium-sized ornithuromorph (U-shaped furcula, coracoid with procoracoid process, small plough-shaped pygostyle, caudally expanded and dorsoventrally compressed first phalanx of the major digit, U-shaped pubes) with the unique combination of the following morphological features: upper and lower jaws completely edentulous; well-developed mandibular symphysis occupying the rostral 20% of the mandible; coracoid without distinct sternolateral process; lateral and intermediate sternal trabeculae narrow and extend caudally to the same level; xiphial region of sternum V-shaped; short and robust alular digit; dorsomedially oriented bluntly triangular process present on the pubes located one-third of the length from the proximal end; metatarsal I and hallux absent.

### (d) Locality and horizon

Lower Cretaceous Yixian Formation (125 Ma), Dawangzhangzi, Lingyuan, Western Liaoning Province, China [15].

## 3. Description

The specimen is badly split, preserved primarily in ventral view in the main slab (figures 1 and 2) and dorsal view in the counterslab (electronic supplementary material, figures S1 and S2). The latter primarily preserves the impressions of the seeds and gastroliths although both these features are recorded in both slabs [3].

### (a) Skull

The skull is preserved primarily in right lateral view in the main slab and the rostral half is not preserved in the counterslab (figure 3). The upper and lower jaws are both completely edentulous. Like neornithines, the skull bones are very delicate compared with toothed birds. The perfect lateral view of the right premaxilla makes it impossible to determine if it was fused to its left counterpart, but the lack of disarticulation suggests at least partial fusion. The premaxillary corpus is small, forming less than one-third of the rostrum, and covered in numerous small foramina, suggesting the presence of a horny beak. The maxillary and frontal rami demarcate a 30° angle. The rostral tip of the premaxilla is sharply tapered so that the rostrum is without the small cranial margin present in some Early Cretaceous birds (e.g. *Yanornis*, *Bohaiornis*). The small concavity present on the dorsal margin of the premaxillary corpus just caudal to the tip of the rostrum is interpreted as a preservational artefact. The caudally tapered maxillary ramus is approximately as long as the premaxillary corpus itself. The maxilla is reduced to a simple bar without a nasal (ascending) ramus, whereas this process is present in hongshanornithids. The maxilla tapers rostrally and articulates with the dorsal surface of the premaxilla. The nasals are long and narrow, and appear to have been completely separated medially by the frontal processes of the premaxilla, which are only visibly preserved articulating with the nasals along their cranial halves (figure 3a). The rostral two-fifths form a tapered premaxillary process. A maxillary (descending) process is absent. The caudal quarter of each nasal is weakly deflected laterally and appears to have articulated medially with the



**Figure 1.** Photograph of the main slab of the holotype of *Eogranivora edentulata* STM35-3. Scale bar equals one centimetre. (Online version in colour.)

frontals, although the latter element appears to be somewhat ventrally crushed, preventing confirmation of this morphology. The caudal margins of the nasals are bluntly tapered. Other aspects of the cranial morphology are obscured by overlap and poor preservation. The caudal halves of the palatines are preserved in the counterslab (figure 3*b*). The preserved portions are broad, triangular and taper caudolaterally.

The mandible has been rotated so that it is primarily exposed ventrally (figure 3*a*). The dentaries are rostrally fused forming an extensive mandibular symphysis that has not yet been observed in an Early Cretaceous ornithuromorph, in which the dentaries are unfused (e.g. *Yanornis*, hongshanornithids). The symphysis extends for approximately the rostral fifth of the mandible. The rostral half of the symphysis is formed by the contacting tips of the dentaries and presumably the predentary bone [16]. The caudal half of the symphysis, between the diverging dentaries, is filled by a thin bony floor (figure 3*a*). The dentaries are very thin and delicate relative to other Jehol ornithuromorphs. The caudal half of the mandible is poorly preserved although the absence of strong disarticulation suggests the postdentary bones were at least partially co-ossified. A thin bone located caudal the occiput is identified as a displaced hyoid bone.

### (b) Axial skeleton

The vertebral column is very poorly preserved (figures 1–3; electronic supplementary material, figures S1 and S2). Approximately nine cervical vertebrae are preserved not including the atlas and axis. The cranial four clearly preserved cervicals, are longer than wide with rounded prezygapophyses and tapered postzygapophyses that are approximately one-third the length of the centrum. The postzygapophyses appear to become more elongate caudal within the series.

The thoracics are obscured by the sternum and the synsacral vertebrae by the gastroliths. Four poorly preserved thoracic vertebrae are exposed distal to the sternum revealing no significant anatomical information. The synsacrum is obscured by the gastroliths but appears to have been fully fused.

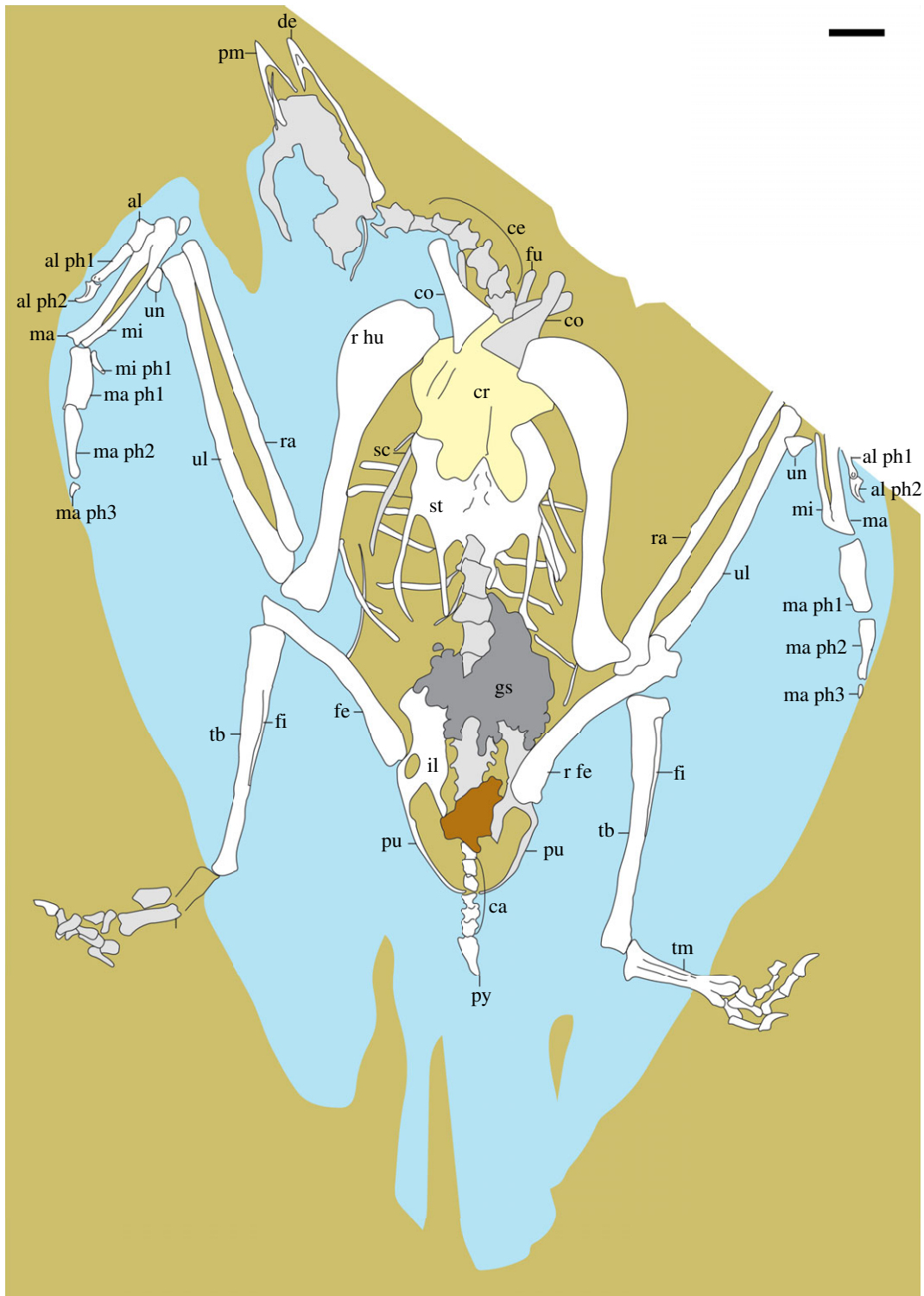
Six free caudal vertebrae are preserved in articulation with a triangular pygostyle (figures 1 and 2; electronic supplementary material, figures S1 and S2). The penultimate caudal may be partially ankylosed to the pygostyle. Even including this caudal, the length of the pygostyle is less than half the cumulative length of the free caudals. The caudals are boxy with short transverse processes, small zygapophyses and large neural canals. The pygostyle is most complete in the counterslab where it is exposed in right dorsolateral view and shares with other ornithuromorphs the typical caudally tapered, ploughshare-shaped condition that also characterizes most neornithines [17].

### (c) Thoracic girdle

The pectoral elements are not well preserved (figure 1; electronic supplementary material, figure S1). The scapulae in particular are unclear. Only the caudal halves are clearly exposed, suggesting the scapulae were long, thin, weakly curved and distally tapered, as in other Jehol ornithuromorphs. The coracoids are sturdy; the neck is robust with a procoracoid process located approximately at its midlength point (visible on the right coracoid in the main slab where the furcula underlies the coracoid). Compared with other ornithuromorphs the sternal margin is weakly expanded, measuring only half of the omal–sternal length of the coracoid (more than half in hongshanornithids). The sternal margin appears to be angled rostromedial–laterocaudally. Although a distinct rectangular lateral process appears to be absent, this corner of the coracoid forms a small laterally tapered projection. The furcula is delicate and U-shaped similar to hongshanornithids. The omal tips are bluntly tapered and a hypocleidium is absent as in most other Early Cretaceous ornithuromorphs although there is a thickening at the furcular apophysis.

### (d) Sternum and ribs

The sternum is craniocaudally elongate and appears to have a rounded rostrum, although this margin is covered by the seeds in the crop (figure 1). The costal margin is weakly angled medially towards a very small lateral process located just cranial to the proximal end of the lateral trabeculae. Two pairs of elongate caudal trabeculae are present. The proximal end of the lateral trabeculae is cranial to the proximal end of the intermediate trabeculae so that the lateral caudal incision demarcated by these trabeculae is much deeper than the medial incision. The lateral trabeculae are caudally oriented and have fan-shaped distal expansions. The intermediate trabeculae are roughly subequal in mediolateral width to the lateral trabeculae and end at the same level. These trabeculae are caudomedially oriented and bluntly tapered throughout their length. The ziphial region appears to be flat although this region is poorly preserved in both slabs. Regardless, the surface area of the sternal body is proportionately smaller in *Eogranivora* relative to some Jehol ornithuromorphs (e.g. *Yanornis*, *Yixianornis*, *Iteravis*), a condition shared with the most basal ornithuromorphs (e.g. *Archaeorhynchus*, *Jiuquanornis*) and the Hongshanornithidae [6,9,18]. The keel is visible through



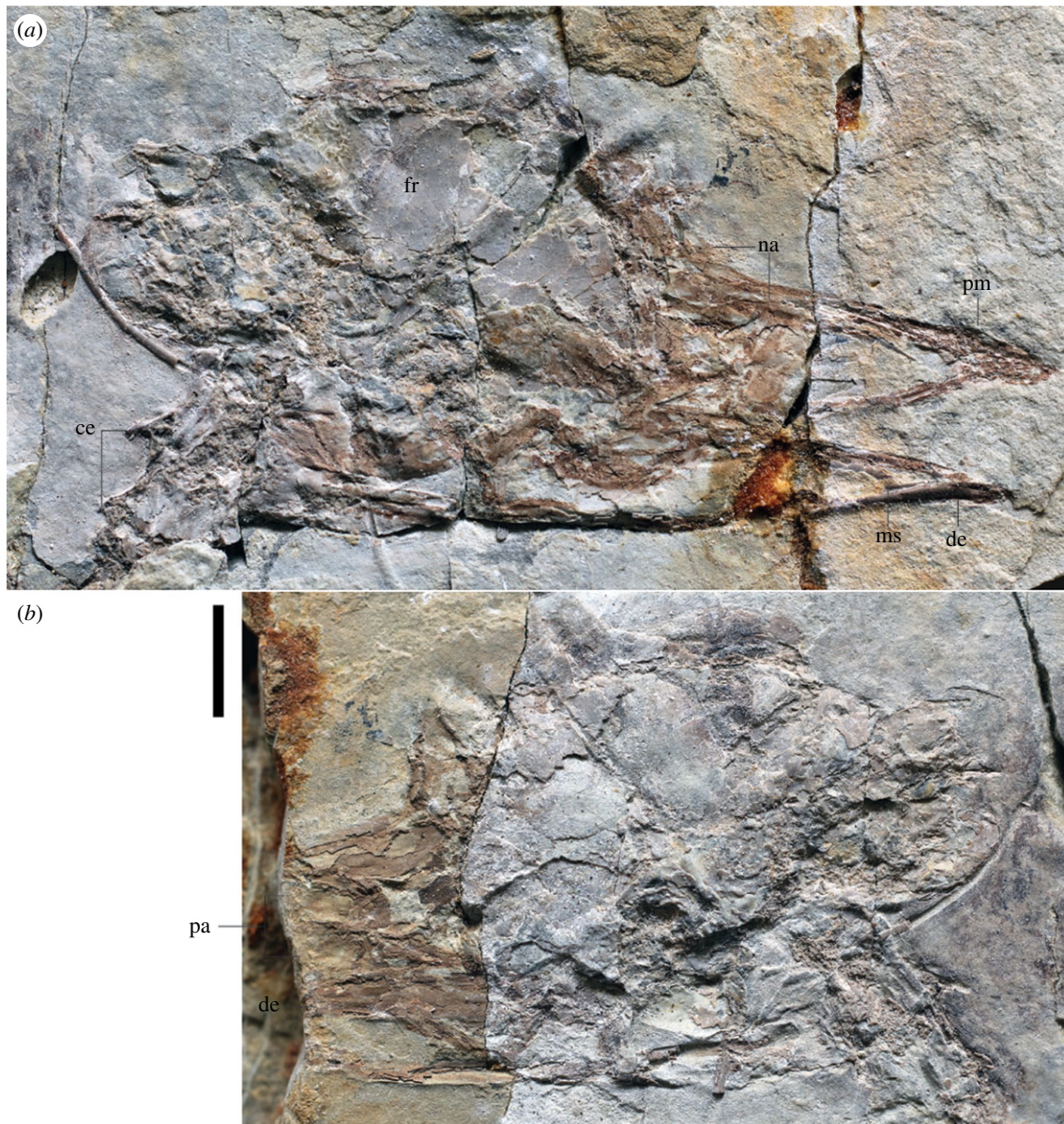
**Figure 2.** Line drawing of the main slab of the holotype of *Eogranivora edentulata* STM35-3. Bones are indicated in white (or light grey if damaged); the crop is indicated in yellow, the gizzard is dark grey, and the unusual material preserved in the pelvis is indicated in brown. Feather impressions are indicated in blue and the matrix is tan. Anatomical abbreviations: al, alular metacarpal; al ph, alular phalanx; ca, caudal vertebrae; ce, cervical vertebrae; co, coracoid; cr, crop; de, dentary; fe, femur; fi, fibula; fu, furcula; hu, humerus; gs, gastroliths; il, ilium; l, left; ma, major metacarpal; ma ph, major digit phalanx; pm, premaxilla; pu, pubes; py, pygostyle; r, right; ra, radius; rd, radiale; sc, scapula; st, sternum; tb, tibiotarsus; tm, tarsometatarsus; ul, ulna; un, ulnare. Scale bar equals one centimetre. (Online version in colour.)

the crop contents and appears to extend the entire length of the sternum though diminishing in ventral height as it approaches the rostrum.

Four to six pairs of sternal ribs articulate with the sternum. Approximately eight pairs of dorsal ribs are preserved. These greatly decrease in proportions caudally. Uncinate processes and gastralria do not appear to be preserved.

### (e) Thoracic limbs

Both forelimbs are fully preserved except for the left wrist but detailed morphologies are obscured by poor preservation in several critical areas (figure 1; electronic supplementary material, figure S1). The ulna is slightly longer than the humerus (electronic supplementary material, table S1). The humerus has



**Figure 3.** Skull of *Eogranivora edentulata* STM35-3. (a) Main slab. (b) Counterslab. Scale bars equal five millimetres. Anatomical abbreviations not listed in the figure 1 caption: de, dentary; fr, frontal; ms, mandibular symphysis; na, nasal; pa, palatine. (Online version in colour.)

a large, rounded deltopectoral crest that exceeds the width of the shaft and extends three-sevenths (0.43) of the humerus, similar to hongshanornithids [9]. Both the proximal and distal articular surfaces are poorly preserved. The distal end of the humerus is expanded relative to the midshaft. The distal margin appears to be weakly angled relative to the shaft, also observed in hongshanornithids. The ulna is proximally bowed, as in other Early Cretaceous birds. The proximal and distal ends are expanded so that at its widest point the ulna is double the width of the radius, but the radius is seven-tenths (0.7) of the width of the ulna at this element's narrowest point on the shaft. A distinct olecranon process does not appear to be present. The radius is straight and weakly expanded at both ends. The ulnare is U-shaped with equal-length rami demarcating an obtuse angle. The radiale is bluntly triangular and less than one-third the size of the ulnare (both visible in the left hand of the counterslab).

The hand is shorter than the humerus. Fusion is obscured by poor preservation. The alular metacarpal is large, nearly equal to the major metacarpal in craniocaudal thickness (figure 4*a,b*). The proximal end is craniocaudally thicker and the proximocranial margin forms a small extensor process.

The robust alular digit is short, ending well proximal to the distal end of the major metacarpal, with a well-developed unguis phalanx larger than that of the major digit. The first phalanx is less than half the length of the major metacarpal but two-thirds of the craniocaudal thickness. The curved and robust claw has a small but distinct flexor process and a well-developed ligamental groove. The major metacarpal is straight and craniocaudally expanded at the distal articular surface. The minor metacarpal is six-tenths of the craniocaudal thickness of the major metacarpal. Distally it weakly bows cranially to meet the major metacarpal to distally enclose an intermetacarpal space that is slightly narrower than the minor metacarpal itself in dorsal and ventral views. The proximal end of this space is level with the distal end of the alular metacarpal. It cannot be determined if the distal ends of the major and minor metacarpals were fused. The first phalanx of the major digit is the longest in the hand. As in other ornithuromorphs this phalanx is dorsoventrally compressed and caudally expanded so that it is craniocaudally thicker than the major metacarpal. The penultimate phalanx is three-quarters of the length of the proximal phalanx and tapered so that the distal end is much smaller than the proximal end.

The unguis phalanx is reduced, one-third the size of the alular unguis, and triangular, lacking curvature. The minor digit consists of two heavily reduced phalanges (figure 4*a,b*). The proximal phalanx is poorly preserved visible in the right hand in the main slab. It measures roughly one-third of the length of the first phalanx of the major digit, and less than half its thickness, and appears to be weakly curved and tapered distally. The second phalanx is well preserved in the left hand in the counterslab. This diminutive phalanx (less than 2 mm long in STM35-3) is proximally expanded but rapidly tapered along the distal three-fourths of its length (spoon-shaped).

The forelimb is much longer than the hindlimb. The intermembral index is 1.35 compared with 0.81–0.87 in hongshanornithids [9].

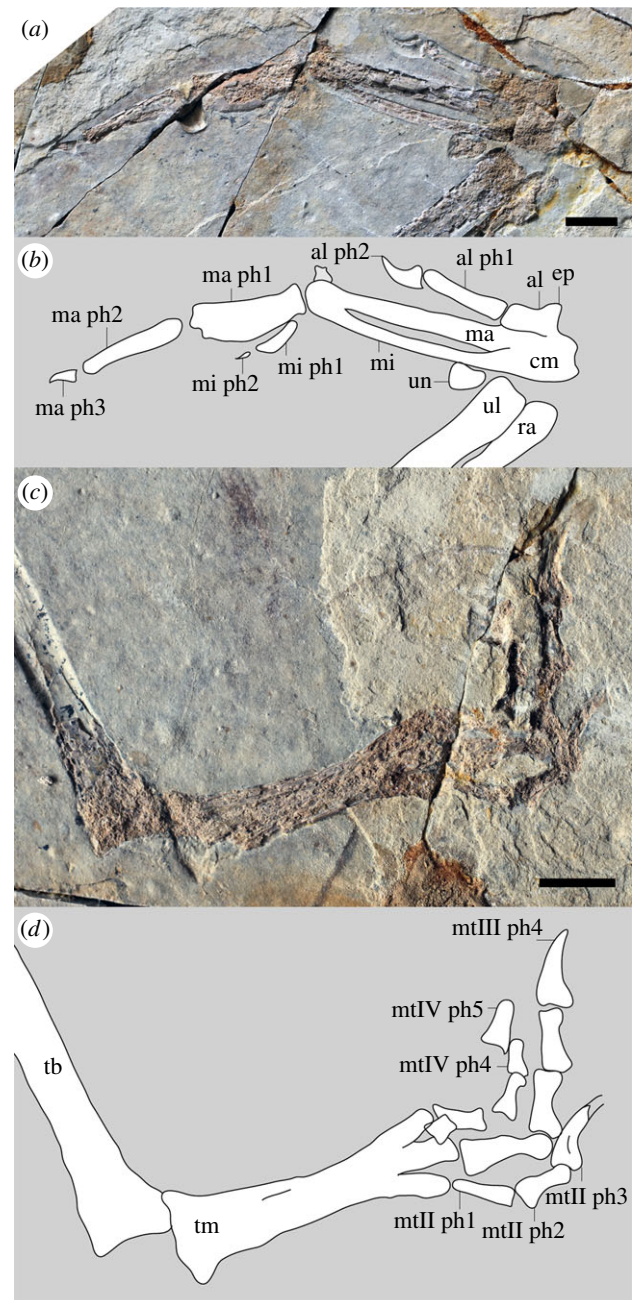
### (f) Pelvic girdle

The pelvic elements appear to be at least partially fused at the level of the acetabulum although the two halves of the pelvic girdle do not appear fused to the synsacrum. The cranial margin of the ilium is broad and convex. The dorsal margin appears straight while the ventral margin of the preacetabular wing is concave, rostrally demarcated by a ventral hook present in some other ornithuromorphs (e.g. *Schizooura*, *Dingavis*). The preacetabular wing of the ilium is 50% longer than the small and sharply tapered postacetabular wing (main slab, left ilium). The ischia are not clearly preserved; only their proximal ends where they contribute to the acetabulum can be discerned. Preservation suggests that these elements were very delicate, presumably not visible appressed to the pubes. The pubes are delicate, tapered distally and strongly curved so that they distally approach each other to demarcate a wide U (figure 1). It cannot be determined if they were in contact distally due to overlap of their distalmost portions by the caudal vertebrae. However, a well-developed pubic symphysis like that present in hongshanornithids is clearly absent. A dorsal or dorsomedially oriented bluntly triangular process is present one-third from the proximal end of the pubes, possibly suggesting the presence of an obturator foramen.

### (g) Pelvic limbs

Both hindlimbs are nearly complete but neither is well preserved (figure 1; electronic supplementary material, figure S1). The femur is robust and weakly bowed, as in other Early Cretaceous birds. The tibiotarsus is 33% longer than the femur. Distally, the proximal tarsals appear fully fused to the tibia. The fibula is slightly more than half the length of the tibiotarsus. The proximal end is well developed but the shaft rapidly tapers and is thin for most of its length. A caudolaterally oriented tubercle is present on the midshaft for attachment of the *m. iliofibularis*.

The tarsometatarsus is less than half the length of the tibiotarsus and proximally fused although the individual metatarsals can easily be distinguished throughout their lengths indicating that fusion between these elements was incomplete. The proximal articular surface is expanded so that it is approximately 50% wider than the tarsometatarsal shaft (figure 4*c,d*). The body of the tarsometatarsus is waisted with the narrowest point located two-thirds of the length from the proximal end (medial margin of metatarsal II and lateral margin of metatarsal IV concave). Metatarsals II and IV are subequal in width and slightly narrower than metatarsal III. The trochlea are not well preserved; it appears metatarsal III



**Figure 4.** Detail photographs of *Eogranivora edentulata* STM35-3. (a) The right hand in the main slab; (b) line drawing of the hand; (c) the left foot of the main slab; (d) line drawing of the foot. Scale bars equal five millimetres. Anatomical abbreviation not listed in figure 1 caption: ep, extensor process. (Online version in colour.)

is the longest and metatarsals II and IV are subequal, roughly ending just proximal to the metatarsal III trochlea. Deep intertrochlear incisions appear to be present between metatarsals II and III and III and IV.

The first metatarsal and digit are not preserved on either side. These elements are at least partially preserved in other articulated Jehol bird specimens. Thus, we interpret this as a true absent and reconstruct the pedal phalangeal formula as x-3-4-5-x (figure 4*c,d*). The pedal digits are short and robust with large weakly curved unguis. The first phalanx of digit II is longer than the penultimate phalanx but shorter than the unguis phalanx. The third digit is the longest. The first phalanx is the longest followed by two subequal phalanges and the largest claw in the foot (only slightly longer than that of the second digit). The first phalanx of the fourth digit is the longest in the

digit, followed by two shorter but subequal phalanges. The penultimate phalanx is slightly larger than the two preceding phalanges. The ungual is not preserved on either side.

### (h) Soft tissue traces

Faint traces of feathers are preserved including impressions of the wings and tail (figure 1; electronic supplementary material, figure S1). Body feathers measuring 12–14 mm are preserved along the ventral margin of the neck. We estimate that the remiges had a maximum length of 98–108 mm. A faint layer of short secondary wing coverts is visible on the right ulna. The wing impressions suggest the presence of an alula. The rectrices are not complete, missing their distal ends, but they appear to form a long narrow fan with a minimum length of 55 mm. Traces of short rectricial coverts are also visible.

An unusual dark mineral is preserved between the pubes primarily in the ventral counterslab (figures 1 and 2; electronic supplementary material, figure S1). This substance differs from the bone, being thin, darker and amorphous. This impression is large and oval (21 × 12 mm). Its shape and anatomical position suggest that it may be the remains of an egg preserved in the oviduct, possibly remains of the eggshell.

### (i) Ingested remains

STM35-3 preserves ingested remains in two places: seeds that are overlapping the rostral half of the sternum and presumably preserved within the crop, and gastroliths overlapping the cranial half of the pelvis, both briefly described by Zheng *et al.* [3]. These traces are best preserved in the counterslab but can be observed in both (figures 1 and 5). At least 15 seeds are preserved in the counterslab. The seeds are generally oval, measuring 4.3 mm by 2.6 mm (figure 5). One of the narrow poles is tapered sharply. Although faint, the surface bears longitudinal grooves or ridges that extend from pole to pole similar to seeds described in some specimens of *Jeholornis* [5].

The gastrolith mass is slightly displaced caudally from its natural position so that it partially overlies the pelvic girdle. The stones, primarily in the counterslab, form a large cluster still mostly embedded in matrix. The gastroliths, where exposed, are proportionately small and numerous (12 in main slab; approximately 100 in counterslab), similar to *Archaeorhynchus* [6]. The stones are all similar in size, ranging from 1 to 2 mm (longitudinal axis), fairly rounded and polished, and appear to constitute a number of lithologies.

## 4. Cladistic analysis

In order to test existing hypotheses regarding the phylogenetic affinity of *Eogranivora edentulata* we added STM35-3 to the O'Connor & Zhou [19] matrix (see electronic supplementary material). The modified matrix consists of 63 taxa (32 belonging to the Ornithuromorpha) scored across 245 morphological characters. Thirty-one characters were treated as ordered; all characters were weighted equally. The data were analysed using TNT software [20]. We conducted a heuristic search using tree-bisection reconnection (TBR) retaining the single shortest tree from every 1000 replications. This produced three most parsimonious tree with 904 steps. In the strict consensus tree *Eogranivora* is resolved in a polytomy of basal ornithuromorphs more derived than *Archaeorhynchus* but

less derived than the Hongshanornithidae (reduced strict consensus; consistency index = 0.363; retention index = 0.647; figure 6). Using implied weights ( $k = 1-3$ ) [20] caused the fragmentary ornithuromorph *Chaoyangia* (based on a single partial specimen) to fall outside the Pygostylia [19].

## 5. Discussion

Although still dwarfed by the species of known enantiornithines, *Eogranivora edentulata* contributes to the growing diversity of Early Cretaceous ornithuromorphs recognized in the Jehol avifauna. *Eogranivora* is distinct from hongshanornithids with respect to limb proportions but shares with this clade a similar sternal morphology that may have resulted in the original misidentification [3]. This morphology strongly suggests that *Eogranivora* is a relatively basal ornithuromorph, consistent with the results of our phylogenetic analysis (figure 6), which places this taxon in a polytomy of basal Jehol ornithuromorphs less derived than the Hongshanornithidae confirming that STM35-3 is not referable to this clade.

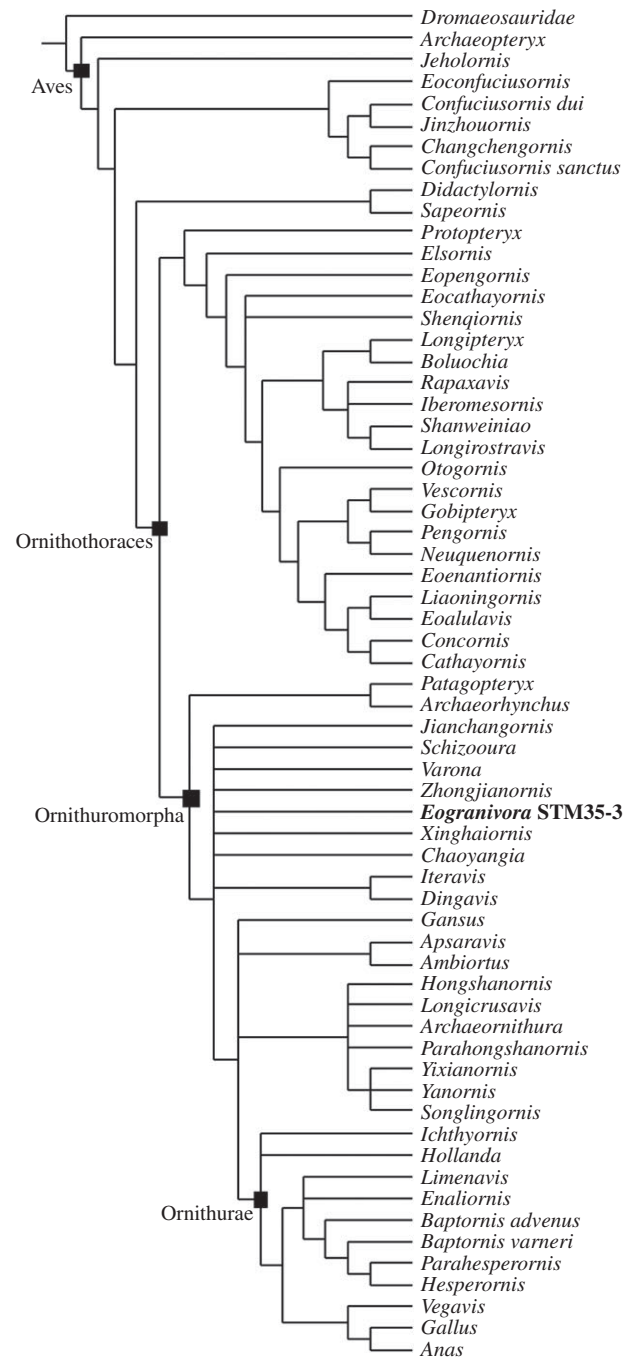
Mounting evidence indicates that seeds constituted an important part of the diet of Early Cretaceous birds and that granivory was fairly common among basal birds in the Jehol. Both the long bony-tailed *Jeholornis*, crown-ward only to *Archaeopteryx*, and the basal pygostylian *Sapeornis* preserve direct evidence that they fed primarily on seeds [3,21]. However, STM35-3 is the only known specimen of Cretaceous ornithuromorph preserving ingested seeds, and thus *Eogranivora* is the only species of this crown-ward clade that may unequivocally be considered at least a partial granivore or herbivore at this time. Although numerous species of Jehol ornithuromorphs preserve gastroliths, living birds that consume other hard-to-digest food items such as insects and molluscs are also known to use gizzard stones to aid in trituration, and thus the presence of gastroliths in fossil birds should not strictly be considered evidence of herbivory [11]. Despite the large numbers of available specimens ( $n = 100$  specimens), the preservation of ingested remains in the form of either seeds and or gastroliths in *Sapeornis* and *Jeholornis* is still a relatively rare occurrence (present in less than 10%) [5]. Thus, the absence of preserved seeds in ornithuromorphs preserving gastroliths but known only from a small number of specimens cannot be taken as evidence that seeds were not being consumed.

In the absence of direct evidence, further clues as to the diet of early ornithuromorphs can be derived from rostral morphology. Tooth loss is considered to correlate strongly with herbivory among theropod dinosaurs [22]. However, there is no direct evidence of herbivory in these non-avian dinosaurs, although the presence of large masses of gastroliths inferred to represent gizzard stones are interpreted as evidence of a herbivorous diet [22]. Gastroliths are present in taxa belonging to the Ornithomimosauria [23] and the Oviraptorosauria [24] and teeth are only present in basal members of each clade. In the basal ceratopsian *Limusaurus* teeth are lost and replaced by a grinding gizzard during ontogeny [25]. Although ultimately lost, teeth persist during the first 80 Myr of avian evolution and are even present in forms that also preserve gastroliths (basal birds *Jeholornis* and *Sapeornis* and ornithuromorphs *Iteravis*, and the Hongshanornithidae), indicating the relationship between tooth loss, the use of gastroliths to aid in digestion and herbivory is not as straightforward in Cretaceous



**Figure 5.** Close-up of the crop and gizzard preserved in STM35-3, the holotype of *Eo granivora edentulata*. (a) Main slab. (b) Counterslab, close-up of seeds in crop. Scale bars equal five millimetres. Dashed lines demarcate location of crop and gizzard. (Online version in colour.)

birds as that observed in non-avian theropod lineages. The piscivorous *Yanornis*, specimens of which commonly preserve ingested fish remains (gastroliths absent), has more teeth than any other Early Cretaceous taxon, and numerous teeth are present in the Late Cretaceous *Ichthyornis* and *Hesperornis*, the latter almost undoubtedly a piscivore given its post-cranial morphology [4,26]. *Eo granivora* is the only ornithuromorph unequivocally known to have fed on plant material and notably this taxon is also completely edentulous. Comparison of the gastral masses in toothless ornithuromorphs (*Eo granivora*,



**Figure 6.** Strict consensus cladogram depicting the phylogenetic position of *Eo granivora edentulata* (tree length equals 904 steps; consistency index 0.363; retention index 0.647).

*Archaeorhynchus*) and toothed forms suggest that diet can be inferred by the morphology of the gastral mass, with the largest aggregates of the proportionately smallest gastroliths occurring in toothless taxa that were presumably herbivorous. Toothed ornithuromorphs typically preserve fewer but larger stones forming the gastral mass (e.g. *Iteravis*). Thus, it appears that although the presence of gizzard stones does not indicate herbivory or directly correlate with tooth loss, herbivory and tooth loss do seem correlated in the Ornithuromorpha. This relationship is absent in basal lineages in which teeth are present despite direct evidence of a granivorous diet. The presence of teeth in the more stem-ward granivores *Sapeornis* and *Jeholornis* supports hypotheses suggesting the presence of a primitive digestive system despite the presence of a gastric mill in both taxa [5]. Although currently there is no available direct evidence, we suggest



toothed ornithuromorphs were omnivorous or may have fed on insects or aquatic invertebrates.

The removal of STM35-3 from the Hongshanornithidae means that previous hypotheses regarding trophic evolution within this clade should be reassessed. *Hongshanornis* was previously considered a granivorous herbivore, which is inconsistent with the wading ecology commonly inferred for the Hongshanornithidae [3,9]. Only one hongshanornithid preserves gastroliths, a referred specimen of *Hongshanornis* [7]. This is unusual considering that gastroliths, when present, are relatively commonly preserved in Jehol ornithuromorphs known from fairly complete specimens (gastroliths are preserved in all four known specimens of *Archaeorhynchus*) [6,27,28] and the hongshanornithid *Archaeornithura* is known from two well-preserved specimens [9]. Given the presence of teeth in all hongshanornithids and diet-related patterns of tooth loss in the Ornithuromorpha, it is most likely that this clade was at least not entirely herbivorous. The presence of gastroliths in one specimen of *Hongshanornis* could be due to a number of factors that are impossible to separate with the available data. This could reflect seasonal changes in diet, individual variation or lineage-specific changes in diet (*Hongshanornis* is the basal-most hongshanornithid) [9].

Despite its basal position within the Ornithuromorpha, *Eogranivora* preserves several highly specialized features including the potential absence of pedal digit I. Although represented only by a single specimen in which the foot is admittedly less than perfectly preserved, the specimen is nearly complete and fully articulated, and smaller elements (e.g. minor digit phalanges) are preserved intact. In the authors' experience, the hallux is at least partially preserved in articulated specimens even when highly reduced (e.g. *Archaeorhynchus*). Therefore, at this time we consider *Eogranivora* to have only three pedal digits, although this conclusion may potentially be affected by new material. If correct, this is the first documented occurrence of the loss of a pedal digit in an Early Cretaceous bird, although, notably, this digit is also highly reduced in the basal ornithuromorph *Archaeorhynchus spathula* [6]. All known Jehol ornithuromorphs tend to have a short and elevated hallux similar to most terrestrial neornithines (e.g. Galliformes, Charadriiformes), whereas in enantiornithines this digit is elongate and articulates approximately at the same level as the other digits forming the grasping morphology necessary for perching (similar to passerines) [29]. The two ornithothoracine clades can also be distinguished by differences in pedal proportions, with individual phalanges becoming proportionately shorter distal in each digit in the Ornithuromorpha and elongated in enantiornithines. In living birds these proportions are indicative of terrestrial and arboreal ecologies, respectively [30], and these data suggest that Jehol ornithothoracines occupied distinct niches, with the arboreal niche primarily occupied by enantiornithines whereas ornithuromorphs were apparently terrestrial [29]. Given the total number of extant species, loss of pedal digits is relatively uncommon in Neornithes, but has occurred several times, spanning much of the phylogeny. During the evolution of non-avian theropods the first metatarsal and its corresponding digit were strongly reduced but is maintained through selective pressures related to its perching function [31]. Thus, it may not be surprising that this digit I is most commonly lost as it is considered to be under less developmental constraint than other digits [31].

Pedal digit I is absent in all the flightless paleognaths (emu, cassowary and rhea) and digit II is additionally lost in the ostrich [2]. Digit loss in the ratites is considered an adaptation for running [32]. The volant tinamous have a hallux, which is fully absent in the elegant crested tinamou (*Eudromia elegans*). The hallux is also independently lost in several lineages of volant *Neognathus* birds, occurring twice in the Piciformes (e.g. three-toed woodpeckers *Picoides*; three-toed jacamar *Jacamaralcyon tridactyla*), although perching capabilities are retained through the presence of a reversed fourth digit [33]. Among terrestrial volant *Neognathus* birds loss of the hallux occurs in bustards (Otidiformes), Pala's sandgrouse (*Syrrhaptes paradoxus*, Pteroclidiformes), and numerous lineages of the Charadriiformes including stone-curlews (Burhinidae), button quails (Turnicidae), coursers (Glareolidae), oystercatchers (Haematopodidae), plovers (Charadriidae), the Egyptian plover (*Pluvianus*, Pluvianidae), and the sanderling (*Calidris alba*, Scopolidae) [34]. These birds are fast runners, spending almost all their time on the ground. This suggests that *Eogranivora* was also primarily terrestrial, and may be indicative of other behaviours such as ground nesting. Early ornithuromorphs often display semi-aquatic and aquatic specializations, and are interpreted to have occupied niches similar to extant charadriiforms [35]. The hallux is very much reduced in most charadriiforms and lost more times than in any other clade. The pedal morphology observed in *Eogranivora* and other Early Cretaceous ornithuromorphs indicates that these early 'shorebirds' evolved similar adaptations in parallel with extant lineages living in similar ecologies.

## 6. Conclusion

STM35-3 is redescribed as a new species, *Eogranivora edentulata*, and resolved through cladistic analysis as basal to the Hongshanornithidae. *Eogranivora* contributes to the growing number of occurrences of tooth loss observed among Early Cretaceous ornithuromorphs. The clear evidence of granivory preserved only in this specimen among all known Jehol ornithuromorphs supports an emergent trend observed in this group in which tooth loss correlates specifically with herbivory (so far only granivory recognized) but not with the presence of gastroliths. As in living birds, the presence of gastroliths in Cretaceous ornithuromorphs is not necessarily indicative of herbivory. *Eogranivora* is the first documented occurrence of pedal digit loss in a Cretaceous bird. The hallux is absent in several terrestrial neornithines and strongly suggests *Eogranivora* was a ground-dweller, although its elongate forelimbs indicate strong flight capabilities. Pedal morphology parallels adaptations observed in living charadriiforms.

**Data accessibility.** Data are available from Dryad Digital Repository [36].

**Authors' contributions.** X.Z., J.K.O., X.W., Y.W. and Z.Z. designed the research. J.K.O. wrote the manuscript.

**Competing interests.** We declare we have no competing interests.

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