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Frugivory in *Sapeornis* Zhou & Zhang, 2002b indicates diverse herbivorous trophic habits

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Frugivory in *Sapeornis* Zhou & Zhang, 2002b indicates diverse herbivorous trophic habits

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ABSTRACT
Emerging evidence regarding the diet of Early Cretaceous birds from the Jehol Biota suggests that herbivory was the dominant feeding strategy among stem-ward taxa. Evidence suggests two different herbivorous diets. Granivory is inferred based on the presence of disseminules within the esophageal crop and accompanied by gastroliths in the gizzard. Frugivory is inferred when the disseminules are preserved in the abdominal cavity with an absence of gastroliths. Direct evidence indicates that herbivory spans the entire phylogeny of Early Cretaceous birds, with frugivory documented in the long boney-tailed *Jeholornis* Zhou & Zhang, 2002a, and the enantiornithine *Longipteryx* Zhang, Zhou, Hou & Gu, 2001, and granivory documented in the basal pygostylian *Sapeornis* Zhou & Zhang, 2002b, and the non-ornithurine ornithuromorph *Eogranivora* Zheng, O'Connor, Wang, Wang & Zhou, 2018. Seasonal changes in diet are inferred for *Jeholornis* based on the presence of a gastric mill in some specimens although not accompanied by direct evidence of ingested food items and suggested for *Longipteryx* based on the absence of obligate avian frugivores in extant temperate climates. Here we provide the first direct evidence of dietary complexity in a Mesozoic bird. Two specimens of *Sapeornis* reveal that this taxon also fed on fruits. While this could reflect seasonal differences in diet, the unusual distribution of gastroliths in specimens of *Sapeornis* may suggest that this taxon was not so specialized. Evidence suggests that phylogenetically disparate members of the Jehol avifauna utilized diverse trophic resources, but *Sapeornis* provides the first direct evidence of this. Dietary complexity and phenotypic plasticity of the digestive tract are likely factors that facilitated the early radiation and success of Aves.

KEY WORDS
Jehol Biota, gastric mill, gymnosperm disseminule, herbivory.

RÉSUMÉ
La frugivorie chez Sapeornis *Zhou & Zhang, 2002b témoigne de la diversité de ses habitudes alimentaires herbivores.*
De nouvelles données concernant le régime alimentaire des oiseaux du Crétacé inférieur issus du biote de Jehol suggèrent que l'herbivorie était la stratégie alimentaire dominante à la base du taxon Avialae. Ces données indiquent l'existence de deux régimes herbivores distincts. La granivorie est inférée grâce à la présence de dissémules dans le jabot œsophagien, accompagnés de gastrolithes dans le gésier. La frugivorie est inférée lorsque les dissémules sont conservés dans la cavité abdominale en l'absence de gastrolithes. Des preuves directes indiquent que l'herbivorie s'étend sur l'ensemble de la phylogénie des oiseaux du Crétacé inférieur, la frugivorie ayant été documentée chez le *Jeholornis* Zhou & Zhang, 2002a à longue queue osseuse et chez l'énantiornithine *Longipteryx* Zhang, Zhou, Hou & Gu, 2001, tandis que la granivorie a été documentée chez le pygostylien basal *Sapeornis* Zhou & Zhang, 2002b, et chez l'ornithuromorphe basal *Eogranivora* Zheng, O'Connor, Wang, Wang & Zhou, 2018. Des variations saisonnières du régime alimentaire sont inférées pour le *Jeholornis* sur la base de la présence d'un moulin gastrique chez certains spécimens, bien qu'elles ne soient pas accompagnées de preuves directes d'aliments ingérés, et suggérées pour le *Longipteryx* en raison de l'absence de frugivores aviaires obligatoires dans les climats tempérés actuels. Nous apportons ici la première preuve directe de la complexité alimentaire chez un oiseau du Mésozoïque. Deux spécimens de *Sapeornis* révèlent que ce taxon se nourrissait également de fruits. Bien que cela puisse refléter des différences saisonnières dans le régime alimentaire, la répartition inhabituelle des gastrolithes chez les spécimens de *Sapeornis* pourrait suggérer que ce taxon n'était pas aussi spécialisé. Certaines données suggèrent que des membres phylogénétiquement disparates de l'avifaune de Jehol exploitaient des ressources trophiques variées, mais *Sapeornis* apporte la première preuve directe de ce phénomène. La complexité alimentaire et la plasticité phénotypique du tube digestif sont probablement des facteurs qui ont favorisé la radiation précoce et le succès du taxon Aves.

MOTS CLÉS
Biote de Jehol, moulin gastrique, dissémule de gymnosperme, herbivorie.

INTRODUCTION

The majority of information pertaining to the Mesozoic evolution of birds (Aves Linnaeus, 1758 *sensu* Haeckel [Haeckel 1866]) comes from the thousands of nearly complete and articulated specimens recovered from the 131-120 Ma (Lower Cretaceous Hauterivian-Barremian) deposits in northeastern China that have produced the celebrated Jehol Biota, famous for its feathered dinosaurs and early mammals and angiosperms (Chang *et al.* 2003; Zheng *et al.* 2011; Wang M. *et al.* 2021). The exceptional preservation of this Lagerstätten often extends beyond the skeleton and a significant portion (*c.* 40%) of recovered specimens preserve feathers revealing the influence of sexual selection on plumage (e.g., Wang X.-L. *et al.* 2014; Wang W. & O'Connor 2017), molt strategies (e.g., O'Connor *et al.* 2020a; Wang X.-L. *et al.* 2024), melanosome

morphology (e.g., Zheng *et al.* 2017; O'Connor *et al.* 2020b), and more. Less common is the preservation of direct traces of diet, which is only known in a handful of taxa (Zhou Z. & Zhang 2002b; Zheng *et al.* 2011; Zhou S. *et al.* 2013b; Zheng *et al.* 2014b; Zheng *et al.* 2018; O'Connor *et al.* 2024). Inferring avian diet from morphological proxies has proved to be problematic due to the lack of suitable analogues (no living toothed birds), complex diets driven by the elevated energetic demands of flight, and possible functions of the rostrum unrelated to diet (Clark *et al.* 2023; O'Connor *et al.* 2024). However, even direct evidence of diet in the form of ingested remains can be difficult to interpret.

The earliest record of avian herbivory comes from *Jeholornis*, Zhou & Zhang, 2002a, and *Sapeornis* Zhou & Zhang, 2002b, both from the Jiufotang Formation – the youngest stage in the Jehol Biota (Pan *et al.* 2013). The first described specimen of *Jeholornis*, a long boney-tailed bird that is crownward of *Archaeopteryx* Von Meyer, 1861, preserved "seeds" in the abdominal region (Zhou Z. & Zhang 2002a). Shortly after, a referred specimen of *Sapeornis*, a basal pygostylian, was described preserving gizzard stones, which are most commonly associated with herbivorous or omnivorous diets in extant taxa (Gionfriddo & Best 1996, 1999; Zhou Z. & Zhang 2003). Since then, additional specimens of both taxa have been described providing further direct evidence of herbivory. Gizzard stones were described in new specimens of *Jeholornis* (O'Connor *et al.* 2018), and large clusters of seeds in the position of the esophageal crop were reported in specimens of *Sapeornis* (Zheng *et al.* 2011). However, interpretation of these ingested remains has been debated.

Initially, the intra-abdominal stomach contents in *Jeholornis* and the extra-abdominal crop contents in *Sapeornis* were both interpreted as evidence of granivory (Zhou Z. & Zhang 2002a; Zheng *et al.* 2011; O'Connor 2019). This was supported by the presence of gastroliths in the abdominal cavity of one specimen of *Sapeornis* preserving seeds in the region of the crop and the very densely packed association of the seeds themselves (Zheng *et al.* 2011). Gizzard stones are often utilized by extant granivores to help triturate this relatively hard food source (Gionfriddo & Best 1996, 1999; Zhou Z. & Zhang 2003). However, the whole preservation of the seeds in the stomach of *Jeholornis* and crop of *Sapeornis* were later suggested as evidence of frugivory – that these birds were feeding on the fleshy coating (not preserved) surrounding the seed rather than the seeds themselves (Ksepka *et al.* 2019). Indeed, in extant frugivores that ingest fruits whole (gulpers), the soft flesh of the fruit is digested without the aid of gizzard stones and the disseminules (seeds) are either egested or defecated (Fukui 2003). This hypothesis was tested using CT data from extant birds, which demonstrated that whole seeds in the stomach is evidence of frugivory, whereas in granivores the seeds are immediately fragmented by the gizzard stones forming the gastric mill (Hu *et al.* 2022). Frugivory was further supported in *Jeholornis* by morphometric analysis of the mandible, which separates this taxon from granivores (Hu *et al.* 2022).

The four specimens of *Jeholornis* preserving whole seeds in the stomach without gastroliths were thus reinterpreted as evidence of frugivory (Hu *et al.* 2022; O'Connor *et al.* 2024). However, the identification of five specimens preserving numerous gastroliths forming a tight cluster in or near the abdominal cavity, providing evidence of a gastric mill (O'Connor *et al.* 2018), suggests that *Jeholornis* periodically switched diet, as in many extant birds, consistent with the hypothesis that fruits would have only been seasonally abundant in the temperate ecosystem of the Jehol Biota (O'Connor *et al.* 2024). Recently, intra-abdominal plant remains were reported in two specimens of the enantiornithine *Longipteryx* Zhang, Zhou, Hou & Gu, 2001. The absence of intra-abdominal gastroliths in all known specimens of this taxon (and all known enantiornithines; O'Connor *et al.* 2025) led to the interpretation that, like *Jeholornis*, *Longipteryx* was frugivorous and the traces were identified as gymnosperm disseminules based on morphological similarity to well-preserved gymnosperms from Lower Cretaceous deposits in Inner Mongolia (Bickner *et al.* 2024; O'Connor *et al.* 2024) and consistent with previous interpretations regarding the disseminules associated with *Jeholornis* (Tiffney 2004).

Diet in *Sapeornis* has never been revisited. The co-occurrence of seeds in the crop and gastroliths in the abdominal cavity is strongly suggestive of granivory (Zheng *et al.* 2011). However, several specimens of *Sapeornis* were reported to preserve intra-abdominal plant traces but these were neither figured nor closely examined (O'Connor 2019; O'Connor & Zhou Z.-H.2019). Furthermore, the separate occurrence between whole stomach contents and gastroliths appears not as clear-cut in this taxon, further obfuscating interpretations (O'Connor 2019). Here we describe two of these specimens and explore the significance of these intra-abdominal traces with regards to *Sapeornis* diet and biology.

MATERIAL AND METHODS

STM15-6 and STM16-20 are housed at the Shandong Tianyu Museum of Nature (Fig. 1). Photographs of both specimens were taken with a Canon 5DM3. Anatomical nomenclature primarily follows Baumel & Witmer (1993) using the English equivalents of the Latin terminology. Measurements of the specimens were taken in ImageJ, utilizing the scale measuring tool calibrated using scales bars included in the photos.

INSTITUTIONAL ABBREVIATION

IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Beijing;
STM	Shandong Tianyu Museum of Nature, Pingyi.

RESULTS

STM15-6

STM15-6 consists of a nearly complete and articulated skeleton preserved mostly in dorsal view in a single slab (Fig. 1A). Faint feather traces are visible associated with the

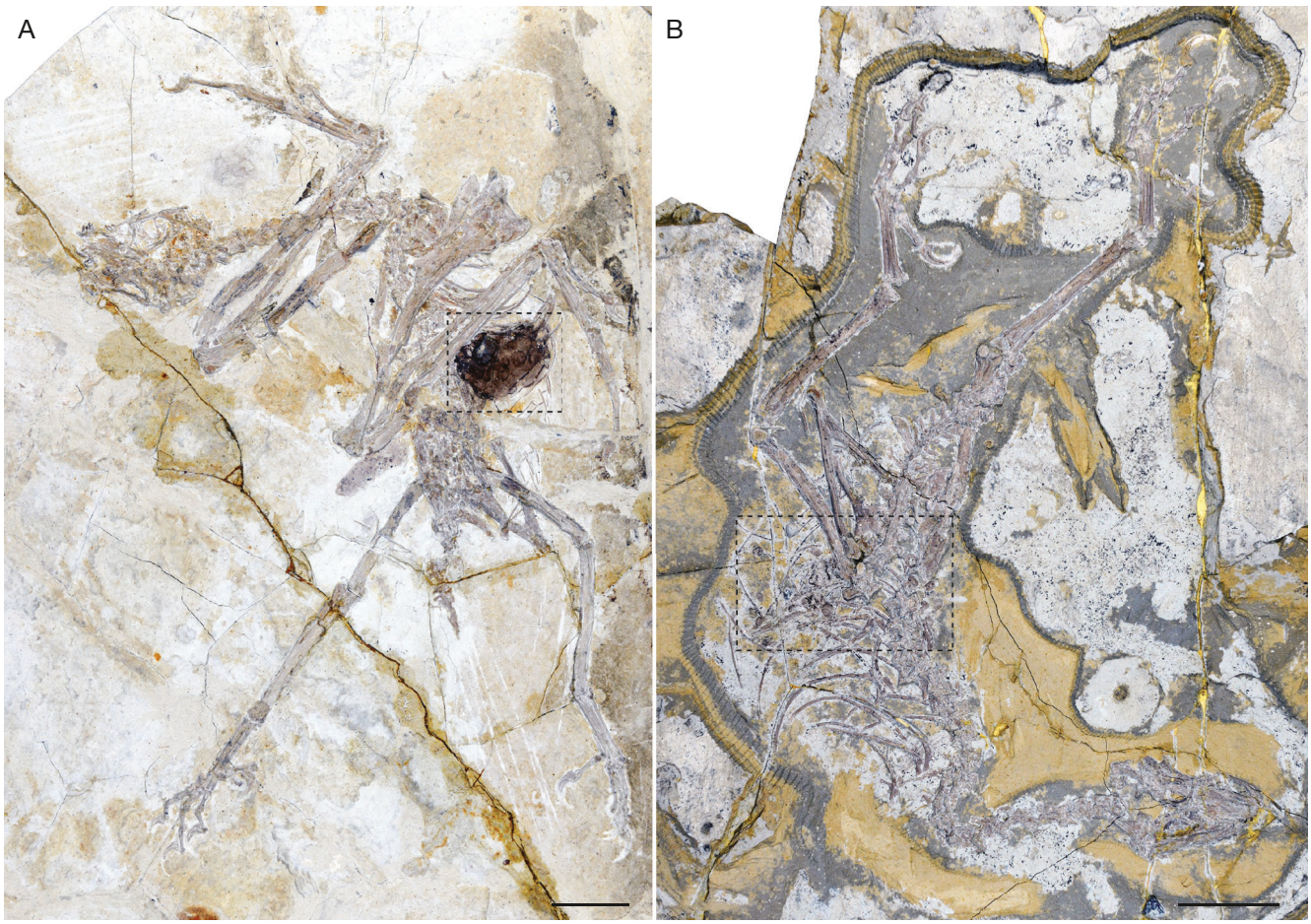


Fig. 1. — *Sapeornis* Zhou & Zhang, 2002 specimens preserving disseminules within the abdominal cavity (**boxed area**): **A**, STM15-6; **B**, STM16-20. Scale bars: 3 cm. Credits: X. Wang.

left wing and tail. This specimen is referrable to *Sapeornis* based on the presence of a short skull with proportionately large premaxillary teeth, triangular pygostyle, narrow deltopectoral crest nearly 1/3 length of the humerus, reduced minor digit without ungual phalanx, ischium with narrow corpus and no dorsal process, and proportionately long and reversed first pedal digit (Zhou Z. & Zhang 2002b, 2003). The femur is approximately 53 mm long.

The intra-abdominal traces consist of a tight, oval cluster of oval to round objects measuring approximately 37 mm long (dorsoventral axis) and 27 mm wide (craniocaudal axis; Figs 1A; 2A, B). The cluster is located just cranial to the pelvic girdle and ventral within the abdomen such that the cranioventral portion of the mass is overlapped by the distal portions of right thoracic (dorsal) ribs and the caudoventral portion is preserved between the right (over) and left (under) gastralia. Embedded within the craniodorsal region of the mass is a single large, rectangular, dark grey gastrolith that measures approximately 7 × 5.2 × 2.5 mm. The oval mass is preserved a rich brown color that contrasts with the pale pink color of the bones and the yellow-beige color of the sediment matrix. Under UV light, the mass becomes a very dark, almost black color; the matrix appears dark brown, the bones glow light pink, and soft tissues fluoresce orange (Fig. 2B). The left gastralia glow faintly through the black mass whereas the overlying right gastralia fluoresce clearly, confirming that the dark traces are preserved between the gastralia and within the abdominal cavity. The dorsal and ventral margins of the mass are more darkly colored and appear to be more three-dimensionally preserved.

The margins of 14 objects can be discerned within the mass, but more were present, obscured by overlap and poor preservation (Fig. 2A). A few traces have longitudinal striations on the surface. The largest object measures 7 × 5.8 mm, whereas the smallest is 4.7 × 3.8 mm. A few of the smaller traces appear to be asymmetrical with one end bluntly tapered. These objects are identified as disseminules based on their consistent size and morphology, oval shape with one tapered pole, and presence of visible surface texture in some traces. Based on their similarity to disseminules preserved in *Longipteryx*, they are identified as gymnosperm (O'Connor *et al.* 2024). A single disseminule along the ventral margin of the mass preserves a cross-section of the testa (seed coat, integument) that is 0.27-0.3 mm thick (Fig. 2A). The location, clearly within the ventral portion of the abdominal cavity, indicates that these disseminules were ingested, preserved within the stomach, and provide evidence of diet.

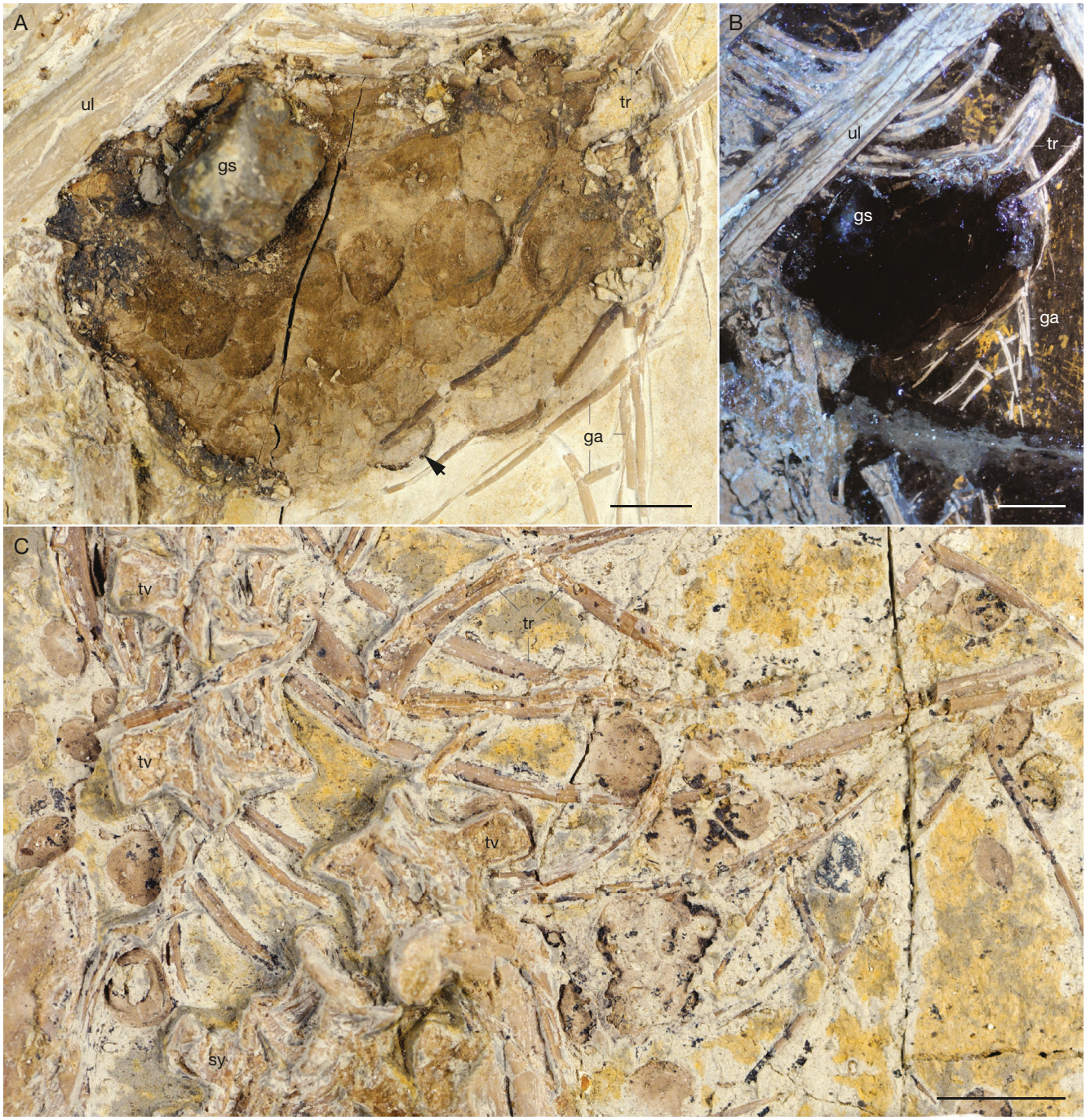


FIG. 2. — Close up of *Sapeornis* Zhou & Zhang, 2002 disseminules: **A**, STM15-6, normal light; **B**, STM15-6, UV light; **C**, STM16-20, normal light. Abbreviations: **ga**, gastralia; **gs**, gastrolith; **sy**, synsacrum; **tr**; thoracic rib; **tv**, thoracic (dorsal) vertebra; **ul**, ulna. Scale bars: A, 5 mm; B, C, 1 cm. Credits: X. Wang.

STM16-20

STM16-20 consists of an articulated skeleton missing the pectoral girdle and the forelimbs, dorsolaterally exposed and preserved in a single slab (Fig. 1B). Soft tissues are not preserved. This specimen can be referred to *Sapeornis* based on its proportionately short skull, triangular pygostyle, narrow ilium with pointed cranial margin, ischium with narrow corpus and no dorsal process, and proportionately long and reversed first pedal digit (Zhou Z. & Zhang 2002b, 2003). It has an estimated femoral length of 65 mm.

The purported ingested remains appear to consist of two morphotypes (Fig. 2C). One type is larger and nearly circular, with the largest well-preserved trace measuring 6.2 × 5.8 mm and the smallest well-preserved trace measuring 4 × 4.6 mm. The second type is smaller with tapered poles, measuring between 4.6-5.1 mm on the long axis and 2.6-3.3 mm on the short axis. These traces form shallow excavations (impressions) in the slab that are lined with a pinkish residue. These are interpreted as disseminules based on the lacriform morphology of the smaller traces and the presence of a micropyle-like

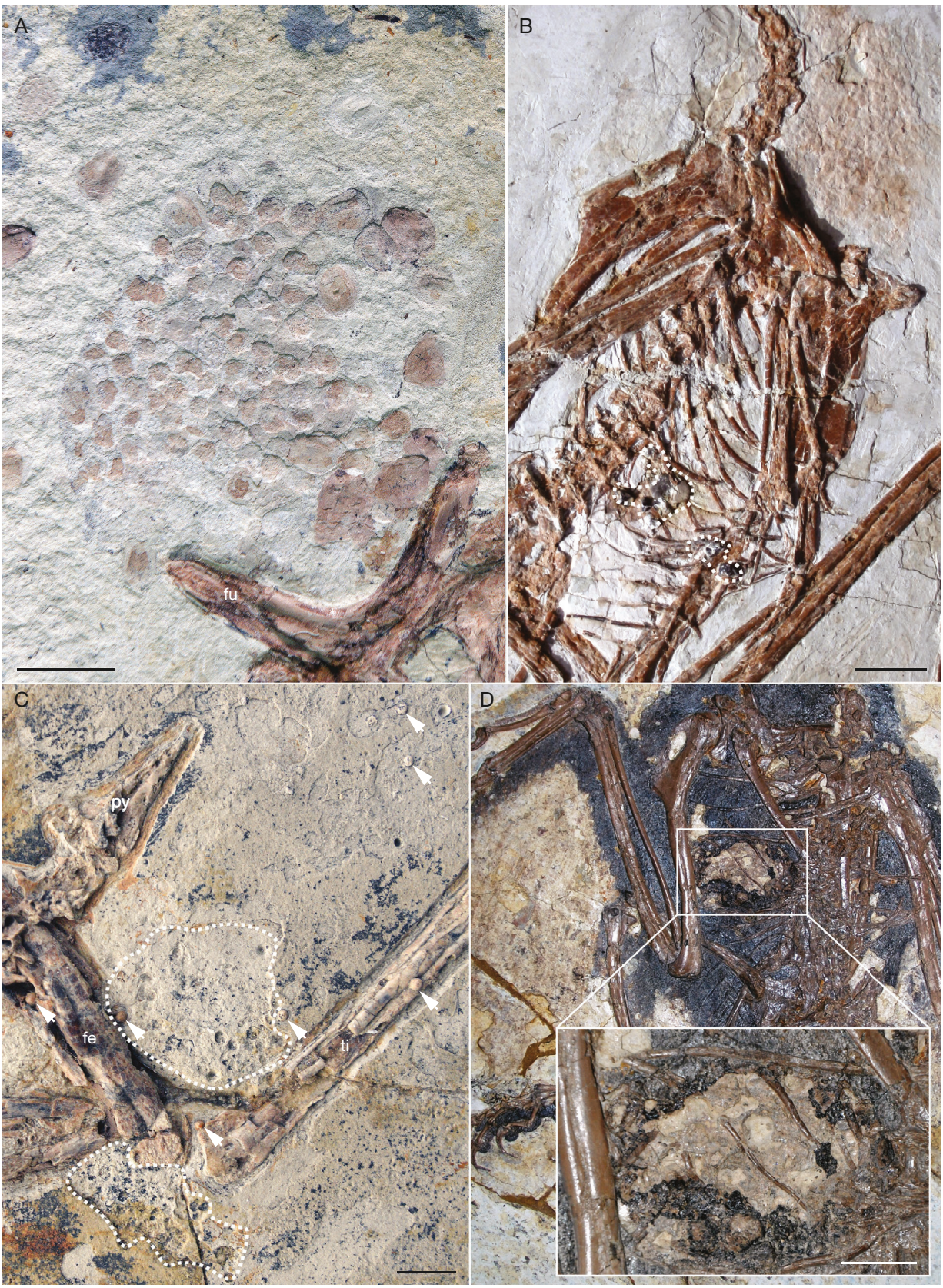


FIG. 3. — Previously reported *Sapeornis* Zhou & Zhang, 2002 digestive traces: **A**, crop contents preserved in STM15-29; **B**, STM15-15 preserving crop contents and gizzard stones (**white outline**) in the ventriculus; **C**, purported gastroliths preserved in IVPP V13275, reinterpreted here as spherules (**white arrows** indicate individual spherules while the **dashed line** indicates region of concentrated and poorly preserved impressions); **D**, 41HIII0405 reportedly preserving gastroliths, reinterpreted here as disseminules, with inset close up of the stomach contents. Abbreviations: **fe**, femur; **fu**, furcula; **py**, pygostyle; **ti**, tibia. Scale bars: A, C, D, 1 cm; B, 2 cm. Credits: A, B, X. Wang; C, L. Chiappe; D, H.-L. Chang.

structure in some traces (O'Connor *et al.* 2024). The disseminules are not preserved fully *in situ*, consistent with the loss of the forelimb and pectoral girdle that indicates some post-mortem decay of the individual prior to burial, as observed in several specimens of *Jeholornis* and *Longipteryx* STM8-86, which also preserve associated ingested remains (O'Connor *et al.* 2018; O'Connor *et al.* 2024). The disseminules are preserved in two visible regions. Fifteen disseminules are preserved cranioventral to the pelvis and dorsal to the disarticulated gastralia (Figs 1B; 2C). The second cluster of eight disseminules is preserved along the dorsal margin of the caudal thoracic vertebrae where the proximal portions of some of the left thoracic ribs are also visible. Under normal light the bone and disseminules appear light pink, whereas the matrix is beige to yellow. Under UV light the bone fluoresces light pink, the matrix is dark purple and brown, and the disseminules fluoresce a dark reddish-brown.

Comparison

Comparison of the ingested remains between specimens is obscured by poor preservation in most specimens, which is at least partially due to the compression of numerous 3D traces into a nearly 2D plane (Figs 2; 3). The disseminules preserved in STM15-6 are generally similar in morphology and size to those preserved in *Longipteryx* and *Jeholornis* (O'Connor *et al.* 2018, 2024), corresponding to morphotype 1 in *Jeholornis* (IVPP13274, STM2-19, STM2-41, STM2-52). The disseminules preserved in STM16-20 resemble morphotype 1 and 3 preserved in some specimens of *Jeholornis* (morphotype 3: STM2-19; O'Connor *et al.* 2018). Overall, the general morphology of these disseminules is consistent with the interpretation that they are from gymnosperms, as interpreted for those preserved in *Jeholornis* and *Longipteryx*, based on their similarity to known gymnosperms from deposits in China that are similar in age (Tiffney 2004; Bickner *et al.* 2024; O'Connor *et al.* 2024).

More specific information regarding the affinity of these gymnosperm disseminules is currently unavailable. The disseminules preserved in the holotype of *Jeholornis* were referred to *Carpolithus* Wallerius, 1747 (Zhou Z. & Zhang 2002a), a form taxon that includes specimens from the Paleozoic to Pleistocene and provides no phylogenetic information. It has also been suggested some ingested disseminules represent *Strobilites*, Lindley & Hutton, 1835, a taxon not currently referred to any specific plant clade (Mayr *et al.* 2020). Vegetation documented in the Jehol Biota (Zhou Z. *et al.* 2003) supports interpretation that these disseminules, as well as others known to have been ingested by birds, represent gymnosperms (Tiffney 2004). This general identification, and the fact the seeds were "fruit"-like is further supported through morphological similarity with well-preserved gymnosperm disseminules, that preserve evidence that they bore a fleshy outer-coating, recovered from similar aged deposits found not far away in Inner Mongolia (Bickner *et al.* 2024). *Ephedra* Linnaeus, 1753, and ginkoopsids represent possible candidates for consumption, supported by the fact that many of their extant relatives are endozoochoric (McLoughlin & Pott 2019).

The disseminules in the abdomen of STM15-6 and STM16-20 are proportionately larger and less numerous than those preserved in the crop of STM15-29 and STM15-15 (Zheng *et al.* 2011). STM15-29 has the best-preserved crop contents (Fig. 3A). The initial report describes at least 70 circular disseminules with a diameter of *c.* 2 mm preserved ventral to the neck and just cranial to the furcula. The large number and densely compacted preservation of these disseminules was evoked as evidence that they lacked a fleshy outer coating (Zheng *et al.* 2011). These co-occur with a few larger oval disseminules measuring 4-6 mm, scattered around the tighter cluster of smaller disseminules (Zheng *et al.* 2011). Their preserved location is consistent with the location of the well-developed and ventrally positioned esophageal crop in granivorous birds, whereas primarily frugivorous birds typically have a reduced crop (Jordano 2014). Closer inspection reveals at least three if not four morphotypes, all of which are distinct from the intra-abdominal disseminules preserved in *Sapeornis* STM16-20 and STM15-6, *Jeholornis*, and *Longipteryx*. The smaller and more numerous disseminules have a surficial ornamentation consisting of many small bumps. Two larger seeds dispersed from the mass appear to have a similar textured surface. Tentatively, these traces resemble the seeds of the gymnosperm *Carnoconites*, Srivastava, 1944 (McLoughlin & Pott 2019). Five larger disseminules are almost triangular, with a bluntly tapered apex; two of these preserve a fibrous surficial texture. Five large disseminules have an elongate oval shape with sharply tapered poles. Approximately 19 disseminules have a bluntly rectangular profile with one end slightly wider and a midline ridge; these are mostly scattered away from the main mass. Preservation of the crop is less clear in STM15-15, but it appears to consist of a similarly large mass dominated by small (*c.* 2 mm) circular seeds (Fig. 3B).

DISCUSSION

Fifteen specimens of *Sapeornis* reportedly preserve ingested remains that provide direct (ingested food remains) or indirect (gastroliths) evidence of diet (O'Connor & Zhou Z. 2019). Some specimens record numerous, small disseminules outside the abdomen interpreted as located in the crop, whereas others preserve fewer but larger and morphologically distinct disseminules in the abdominal cavity interpreted as within the ventriculus. Together, these traces provide strong evidence that *Sapeornis* was primarily herbivorous. The morphological similarity between the *Sapeornis* intra-abdominal disseminules and those preserved in the sympatric frugivores *Longipteryx* (O'Connor *et al.* 2024) and *Jeholornis* (Zhou Z. & Zhang 2002a; O'Connor *et al.* 2018), their whole morphology, and their preserved location all support the interpretation that *Sapeornis,* like these taxa, periodically fed on the fleshy outer coating of gymnosperm disseminules. The unique size, quantity, and morphology of the disseminules in the crop of other specimens (e.g., STM15-15, STM15-29) suggests that, contra Ksepka *et al.* (2019), these specimens were not feeding on fruits at the time of death. Instead, the original inter-

pretation that these specimens preserve evidence of periodic granivory is supported based on the distinct morphology of the disseminules (being smaller and morphologically different from those preserved within the abdominal cavity), the consistent difference between their quantity, morphology, and preserved location (numerous, small disseminules in the crop vs fewer, larger and morphologically distinct disseminules in the ventriculus), and the variable presence of intra-abdominal gastroliths interpreted as gizzard stones (Zheng *et al.* 2011). Furthermore, primarily frugivorous neornithine birds typically reduce or entirely lose the crop, although they may still store excess fruits in the esophagus when the stomach is full (Jordano 2014). The crop in *Sapeornis* is well-developed, located at the base of the esophagus and resting on the furcula; this is consistent with the morphology in granivorous birds (unreduced; Zheng *et al.* 2011). If the crop contents in *Sapeornis* also represented evidence of fruit consumption, fruit seeds would also be present within the abdominal cavity. The cumulative evidence supports the interpretation that crop contents in *Sapeornis* represents evidence of granivory, whereas recovered stomach contents record periods of frugivory. However, the co-occurrence of intra-abdominal gastroliths with both crop and stomach contents in *Sapeornis* is unusual and the significance of the single large stone in STM15-6 is currently unknown.

Dietary switching

Extant birds utilize an enormous diversity of trophic resources and diets are often complex, utilizing multiple resources beyond their primary diet (e.g., nectivorous hummingbirds also consume insects, piscivorous cormorants will opportunistically prey on terrestrial and aquatic arthropods; Schuchmann 1995; Kiss & Rékási 2002). This complexity is driven by the elevated energetic demands of powered flight and the high metabolic rates associated with avian physiology. To meet these energetic demands birds have evolved a sophisticated feeding apparatus (O'Connor *et al.* 2026) and highly efficient digestive system that is characterized by a high degree of phenotypic plasticity. In some species, the weight of the ventriculus and the total length of the digestive tract varies significantly throughout the year in response to changes in available trophic resources and their differing digestive requirements (Battley & Piersma 2005). Ontogenetic changes in diet are observed in many extant reptiles and inferred in many non-avian dinosaurs based on extreme changes in body size (e.g., sauropods), dentition (e.g., *Limusaurus* Xu, Clark, Mo, Choiniere, Forster, Erickson, Hone, Sullivan, Eberth, Nesbitt, Zhao, Hernandez, Jia, Han & Guo, 2009; Wang S. *et al.* 2017), and isotopes (e.g., *Deinonychus* Ostrom, 1969; Frederickson *et al.* 2020).

Some species, including a very large number of birds, will additionally change diet seasonally in response to shifts in available resources. This was first reported in *Yanornis* Zhou & Zhang, 2001, based on the presence of gastroliths in one referred specimen and teleost fish remains in another (Zhou Z. *et al.* 2004). However, the discovery of a dozen new specimens of *Yanornis* preserving ingested teleost remains, and no new specimens preserving clusters of gastroliths, led to the reinterpretation that the gastroliths in *Yanornis* IVPP V13558 were impacted in the intestines (a typically fatal condition in which a foreign object blocks the digestive tract) and not evidence of a gastric mill (Zheng *et al.* 2014b). While fossilized gastric mills were very rare when the prediction regarding partial herbivory in *Yanornis* was put forth, the subsequent discovery of multiple specimens of several other taxa preserving gastric mills, such as *Archaeorhynchus* Zhou & Zhang, 2006, and *Hongshanornis* Zhou & Zhang, 2005 (Zhou S. *et al.* 2013a; Chiappe *et al.* 2014) revealed key differences between gizzard stones and those gastroliths in *Yanornis* IVPP V13558 that further support this reinterpretation (Zheng *et al.* 2014b). Unlike gizzard stones, the gastroliths in IVPP V13558 are very small, very numerous, caudally located in the position of the intestines, and even form faintly visible folded, narrow, tube-like structures that resemble the intestinal morphology (Zheng *et al.* 2014b). The variable preservation of a gastric mill or whole intra-abdominal disseminules in specimens of *Jeholornis* provides indirect evidence of dietary switching (O'Connor *et al.* 2018). However, there is no direct evidence indicating the trophic resources consumed in addition to fruits. Similarly, dietary switching is tentatively suggested for *Longipteryx* based only on the seasonality of fruits in temperate ecosystems like the Jehol. However, in the absence of even indirect evidence such as gizzard stones, this is very weakly supported given that fruits are an important winter resource for many birds in many modern temperate forests (McCarty *et al.* 2002).

Sapeornis specimens preserve clear evidence of two distinct diets: granivory and frugivory. The clear distinction in seed type and preserved location in all known specimens indicates these two distinct food sources were not consumed at the same time as part of a single foraging bout, which is consistent with the different digestive needs of these two resources. These specimens range in femoral length from 50-93 mm with both granivory and frugivory documented throughout the size range, indicating that different diets are unlikely to be related to ontogeny (Table 1). Although all evidence indicates this taxon was herbivorous (Zheng *et al.* 2011), this provides the first direct evidence in the Mesozoic of an adult dinosaur consuming diverse food resources consisting of two distinct diets associated with phenotypic changes in the digestive tract, i.e., the variable use of gizzard stones in the ventriculus. We tentatively interpret this as evidence of dietary seasonality because fruits are typically considered seasonally abundant resources in temperate ecosystems. However, the co-occurrence of gastroliths with crop and stomach contents may suggest that the food resources utilized by *Sapeornis* were less affected by seasonality and it also possible that *Sapeornis* utilized seeds and fruits during overlapping intervals. Indeed, contra expectations, fruits are an important winter resource in many modern temperate forest ecosystems (McCarty *et al.* 2002). This dietary switching found in the same deposits may indicate that *Sapeornis* was a year-round resident of the Jehol ecosystem. This is consistent with aspects of *Sapeornis*' flight apparatus (e.g., absence of an ossified sternum; Zhou Z. & Zhang 2002b, 2003; Zheng *et al.* 2014a) that suggest limited flight capabilities inconsistent with migratory flights.

TABLE 1. — Currently known specimens of *Sapeornis* Zhou & Zhang, 2002 preserving ingested remains. Updated from O'Connor & Zhou Z. (2019).

Taxon	Specimen no.	Crop	Ventriculus	Additional traces	Reference(s)	Preserved diet	Femur length (mm)
Sapeornis chaoyangensis Zhou & Zhang, 2002	IVPP V13275	–	–	spherules	Zhou Z. & Zhang 2003; this paper	?	74
Sapeornis chaoyangensis	STM15-15	disseminules	gastroliths	-	Zheng *et al.* 2011	Granivory	76
Sapeornis chaoyangensis	STM15-29	disseminules	–	corprolite in intestines	Zheng *et al.* 2011	Granivory	93
Sapeornis chaoyangensis	STM15-30	disseminules, poor preservation	–	–	Zheng *et al.* 2014a	Granivory	55
Sapeornis chaoyangensis	STM15-6	–	disseminules; gastrolith	–	Zheng *et al.* 2014a; this paper	Frugivory	53
Sapeornis chaoyangensis	STM15-42	–	disseminules; two size classes	–	Zheng *et al.* 2014a	Frugivory	63
Sapeornis chaoyangensis	STM15-44	–	gastroliths	–	Zheng *et al.* 2014a	Granivory?	63
Sapeornis chaoyangensis	STM15-60	weak impression, disseminules?	gastrolith	–	Zheng *et al.* 2014a	Granivory	68
Sapeornis chaoyangensis	STM15-64	–	disseminules; gastroliths	–	Zheng *et al.* 2014a	?	70
Sapeornis chaoyangensis	STM15-28	–	gastroliths	–	Zheng *et al.* 2014a	Granivore	75
Sapeornis chaoyangensis	STM15-53	–	gastrolith	–	Zheng *et al.* 2014a	Granivore	no femur
Sapeornis chaoyangensis	STM15-31	poorly preserved, disseminules?	–	–	Zheng *et al.* 2014a	Granivory	no femur
Sapeornis chaoyangensis	STM16-20	–	disseminules	–	Zheng *et al.* 2014a; this paper	Frugivory	65
Sapeornis chaoyangensis	41HIII0405	–	disseminules	–	Pu *et al.* 2013; this paper	Frugivory	65
Sapeornis chaoyangensis	BMNHC-PH 1067	disseminules	gastroliths	–	Chiappe & Meng 2016	Granivory	no scale

SAPEORNIS GIZZARD

Although limited information is available, the gastroliths in *Sapeornis* are unusual. They are reportedly present in four previously figured specimens: STM15-15, IVPP V13275, 41HIII0405, and BMNHC-PH1067 (Zhou Z. & Zhang 2003; Zheng *et al.* 2011; Pu *et al.* 2013; Chiappe & Meng 2016), and are mentioned as present in five others (O'Connor 2019; O'Connor & Zhou Z. 2019; Table 1). STM15-15 preserves 9-10 gastroliths within the abdominal cavity that do not form a single, tight cluster (Zheng *et al.* 2011). BMNHC-PH1067, which preserves disseminules in the crop (Chiappe & Meng 2016), and STM15-6, which preserves disseminules in the stomach (reported here), both preserve only a single, large intra-abdominal gastrolith.

Gastroliths are also reportedly present in IVPP V13275 (Zhou Z. & Zhang 2003) and a referred immature individual, 41HIII0405 (Pu *et al.* 2013). However, the traces in IVPP V13275 differ from gastroliths in their position (preserved ventral to the tail and near the hindlimb as opposed to in the abdominal cavity) and shape, being small, spherical, almost identical in size, whereas gizzard stones are irregular in size, shape, and mineralogy (Fig. 3C). This unusual morphology suggests they are not gastroliths but a sedimentological feature (i.e., ooid, spherule). The purported gastroliths in 41HIII0405 were also misidentified and appear to be disseminules, providing further evidence of *Sapeornis* frugivory (Fig. 3D). In contrast to gastroliths, the traces in 41HIII0405 are flattened, circular, consistent in size, and mostly preserved as impressions (Pu *et al.* 2013). The mass of disseminules is nearly identical to those in STM15-6 in size, shape, and preserved location, with the entire mass measuring 39 × 27 mm with the long axis oriented dorsoventrally. The disseminules are similar in size to the circular traces preserved with STM16-20 and STM15-6. No gastroliths are present.

The gastroliths preserved in *Sapeornis* are unusual compared to those of other Early Cretaceous birds for several reasons, which may suggest they do not actually represent a gastric mill. First, the number of gastroliths is low, ranging from one to ten, whereas the average number of gizzard stones reported in the smaller-bodied ornithuromorphs *Iteravis* Zhou S., O'Connor J. K. & Wang M., 2014, and *Archaeorhynchus* is 22 and 134, respectively (Liu S.-M. *et al.* 2023). *Sapeornis* is also the only known Mesozoic bird to preserve abdominal gastroliths with both crop contents and stomach contents. The co-occurrence of these features is not consistent, as they are in *Jeholornis* in which stomach contents either consist of whole disseminules (frugivory) or a gastral mass (diet unknown; O'Connor *et al.* 2018). Not all specimens of *Sapeornis* preserving disseminules in the position of the crop (n = 6) preserve gastroliths – only

three specimens are known to preserve both. Similarly, of the five reported specimens preserving disseminules in the stomach, only two also preserve gastroliths (or gastrolith). In contrast, all known specimens of *Archaeorhynchus* and *Iteravis* preserve gastroliths. No other Mesozoic bird preserves only a single gastrolith, which is documented in three *Sapeornis*. Lastly, the single gastrolith in STM15-6 is proportionately large. Measuring 7.3 × 5.2 mm, it far exceeds the average grit size of 2.02 × 1.52 mm in the much larger extant *Branta* Scopoli, 1769 (VerCauteren *et al.* 2003); the body size in *Branta* varies from 2.7-6.4 kg compared to estimates between 400-900 g for *Sapeornis* (Liu D. *et al.* 2012; Field *et al.* 2013). The large size of the stone and its singular nature are both at odds with a digestive function and its size makes accidental ingestion unlikely.

The significance of the unusual gastrolith proportions and distribution in *Sapeornis* is unclear. Perhaps it indicates that *Sapeornis* did not require gastroliths for digestion of the disseminules preserved in the crop of some specimens, even if they were beneficial, explaining their occasional presence. This is supported by experiments on extant birds that demonstrate birds can survive when deprived of gizzard stones (Waugh *et al.* 2007; Erener *et al.* 2016). Additional information is required to better understand the unique gastroliths of *Sapeornis*, which may be elucidated by more precise identification of the ingested disseminules and their digestive properties and a better understanding of the *Sapeornis* gastroliths itself through the exploration of reported but undescribed specimens.

Adaptations for diverse plant resources

Recently, the discrepancy between predicted diet and direct evidence in *Longipteryx* suggested that traditional morphological proxies of diet may have limited utility in predicting diet in toothed birds (O'Connor *et al.* 2024). However, geometric morphometric analysis of avian cranial shape places *Sapeornis* in the morphospace occupied by extant frugivores and seed grinders (Hu *et al.* 2022), granivores that break up seeds in the gastric mill through the aid of gizzard stones. This is consistent with the interpretation that the large teeth in the premaxilla and slightly smaller teeth in the maxilla, would represent an impediment to the seed-cracking behaviors in some extant granivores. This morphospace-based prediction is now fully supported by direct evidence in *Sapeornis* in the form of ingested disseminules in the crop and stomach and gizzard stones in the stomach (ventriculus). This suggests that cranial shape comparison with extant birds still has some predictive power with regards to Mesozoic bird diet when based on accurate CT data derived skull reconstructions (Hu *et al.* 2022).

Jeholornis is also predicted to have seasonally changed diet but there exists no direct evidence of what *Jeholornis* consumed when it utilized a gastric mill. The absence of evidence in contrast to *Sapeornis* is intriguing. Tentatively, it may suggest that while both taxa were partially frugivorous and relied on similar gymnosperm resources, *Jeholornis* switched to a different diet than the granivory documented in *Sapeornis*. This hypothesis is supported by differences in dentition between these two taxa (see below). However, a crop has also been hypothesized to be absent in *Jeholornis*, based on the absence of preserved evidence of this feature (O'Connor *et al.* 2018). This suggests an alternative hypothesis – that ingested seeds went directly into the proventriculus and ventriculus and were rapidly triturated, possibly explaining the absence of preserved evidence of ingested grains in *Jeholornis*. Indeed, *Jeholornis*, like *Sapeornis*, occupies the morphospace that suggests frugivory and seed-grinding (Hu *et al.* 2022), which tentatively suggests it was also a granivore. However, there are too many unknowns to draw any conclusions from the currently available data. For example, differences in seed properties might lead to differential preservation and explain differences in the morphology of the gastric mill in these two taxa.

Although *Jeholornis* and *Sapeornis* share several skull traits that are associated with herbivory (Zanno & Makovicky 2011), there are also major differences in the morphology of these two taxa that are consistent with the interpretation that they did not feed entirely on the same resources. At the very least, these differences suggest that they acquired food through different means. Both *Jeholornis* and *Sapeornis* have proportionately short and deep skulls relative to other Early Cretaceous birds. Their morphology somewhat resembles the skull of basal oviraptorosaurs, which are also hypothesized to be herbivorous based on cranial morphology (Zanno & Makovicky 2011) and the presence of large clusters of gastroliths preserved in the abdominal cavity, which have been interpreted as gizzard stones (Ji *et al.* 1998; Zhou Z. & Wang X. 2000; Zhou Z. *et al.* 2000). The number of teeth is also reduced in both taxa, another feature associated with herbivory. However, their dentitions are otherwise quite distinct from one another. Reduction of the dentition is more extreme in *Jeholornis*, in which the premaxilla is edentulous and only two and three very small, peg-like teeth are present in the maxilla and dentary, respectively (total 10 teeth compared to 50-52 in the more stemward *Archaeopteryx*; Rauhut *et al.* 2018; Hu *et al.* 2022; Hu *et al.* 2023). The dentition in *Sapeornis* is also relatively reduced with regards to the total number of teeth, although not to the extreme in *Jeholornis*. It retains the plesiomorphic four premaxillary teeth but has only three smaller maxillary teeth and two small, peg-like dentary teeth, for a total of 18 teeth (Wang Y. *et al.* 2017). Thus, only the dentary dentition is similar in these two taxa. In *Sapeornis*, the upper dentition is very robust compared to most other stemward birds, resembling the bulky teeth characteristic of bohaiornithid enantiornithines (O'Connor *et al.* 2013; Wang M. *et al.* 2014). While the robust teeth of bohaiornithids have longitudinal grooves in at least one taxon (*Sulcavis* O'Connor, Zhang, Chiappe, Meng, Li & Liu, 2013), the teeth of *Sapeornis* are associated with basal tubercles (Wang Y. *et al.* 2017). Both features have been interpreted as evidence of a durophagous diet (O'Connor *et al.* 2013). If predictions are correct and *Sapeornis* was a seed-grinder that processed these hard foods using its gastric mill, then it consumed both seeds and fruits whole. The robust teeth may have aided in plucking fruits and seeds, similar to the serrated beak in some extant frugivorous birds (Galetti *et al.* 2000).

Both *Jeholornis* and *Sapeornis* also preserve evidence of a primitive bill-tip organ (a feature present in many extant birds) which indicates increased rostral sensitivity and sensory discrimination beneficial for feeding (O'Connor *et al.* 2026). This feature is indicated by the presence of a large neurovascular foramen at the tip of the premaxilla and/or dentary indicative of distally exiting branches of the trigeminal nerve (Bailleul *et al.* 2019; O'Connor *et al.* 2026). This feature, first identified in *Yanornis* and then in *Archaeopteryx*, appears to be widespread in early toothed birds (Bailleul *et al.* 2019; O'Connor *et al.* 2026). Given that *Yanornis* is a piscivore (Zhou Z. *et al.* 2002; Zheng *et al.* 2014b) and *Sapeornis* and *Jeholornis* are herbivores, this feature is clearly adapted for diverse diets and foraging behaviors, as it in extant birds (O'Connor *et al.* 2026). Although the bill-tip organ is documented in both the upper and lower jaws in *Archaeopteryx*, *Yanornis*, and *Sapeornis*, it appears to be only present in the lower jaw of *Jeholornis*, with a distinct opening in the upper jaw being absent (O'Connor *et al.* 2026). This is inferred to be related to the absence of teeth in the premaxilla of *Jeholornis*. However, we cannot rule out the presence of a neornithine-like bill tip organ in which the sensory cells were present in the rhamphotheca and osteological correlates are absent, such as in psittaciforms (du Toit *et al.* 2020; O'Connor *et al.* 2026). The absence of teeth in the premaxilla and the presence of a bill-tip organ indicate the presence of a rhamphotheca covering the premaxillae and distal tip of the dentaries in *Jeholornis* and tips of the premaxillae and dentaries in *Sapeornis*. These beaks would have not only protected the bill-tip organ but also may have facilitated the precision feeding necessary for these herbivorous diets, especially in *Jeholornis*.

CONCLUSIONS

Specimens of *Sapeornis* preserving morphologically distinct disseminules in the crop and ventriculus provide the first evidence of dietary switching in an adult dinosaur in the Mesozoic. This evidence of dietary switching from the same deposits suggests that *Sapeornis* was a year-round resident in the Jehol ecosystem. We tentatively suggest that changes in diet are due to the seasonality of these trophic resources. However, the small number and uneven distribution of gastroliths among known specimens of *Sapeornis* may suggest that both food resources were consumed during overlapping periods, although there is no evidence both were consumed in a single foraging bout. As more direct evidence of diet is uncovered from the Lower Cretaceous Jehol deposits, the apparent distinction between various lines of evidence used to discriminate between diets has blurred. While previously the presence of intra-abdominal gastroliths was thought to rule out frugivory, the discovery of specimens of *Sapeornis* preserving both evidence of frugivory and a gastrolith weakens this hypothesis. Closer examination reveals that *Sapeornis* gastroliths are unusual and require further investigation in the future.

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