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SHORT COMMUNICATION

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Gastroliths in *Yanornis*: an indication of the earliest radical diet-switching and gizzard plasticity in the lineage leading to living birds?

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Abstract *Yanornis martini* is an Early Cretaceous basal ornithurine bird. Its fish-eating diet was previously recognized from a discrete mass of disarticulated fish remains discovered in its abdominal region. A new complete and articulated specimen of *Yanornis martini* preserves abundant in-situ gastroliths such as have been associated with a herbivorous diet. We suggest that the occurrence of gastroliths in this specimen, fish remains in a second, and the lack of gastroliths in three others, is consistent with diet-switching in *Yanornis martini*. Incompatibility of the preserved data with explanations of the grit as an artifact of preservation or result of accidental ingestion is discussed. This discovery indicates the earliest presence of intermittent diet change (and associated gizzard plasticity) observed in extant birds seasonally and in response to changes in available food sources.

Introduction

Yanornis martini is an ornithurine bird species phylogenetically close to the radiation of all living birds (Zhou and Zhang 2001). A specimen of *Yanornis martini* comprised the majority of the infamous composite fossil 'Archaeoraptor' (Zhou et al. 2002). Now represented by five specimens, the species is comparatively well-known for a Mesozoic bird. It is a flying, chicken-sized taxon with an elongated rostrum, a dentary and maxilla filled with small, densely distributed teeth and a foot with elongated toes and relatively small claws. These listed features were originally interpreted as being consistent with a piscivorous, possibly shorebird-like, diet for the species at its original description (Zhou and Zhang 2001). The preservation of fish remains in the abdominal region of one subsequently discovered specimen (IVPP V 13259) supported this inference (Zhou et al. 2002).

A new referred specimen (IVPP V13358) is represented by a complete and articulated skeleton with feather impressions. It was collected from the Early Cretaceous lacustrine Jiufotang Formation at the Dapingfang locality, Chaoyang City, Liaoning Province (Fig. 1). Other birds from this locality in northeast China include the enantiornithine *Longipteryx chaoyangensis* (Zhang et al. 2001)

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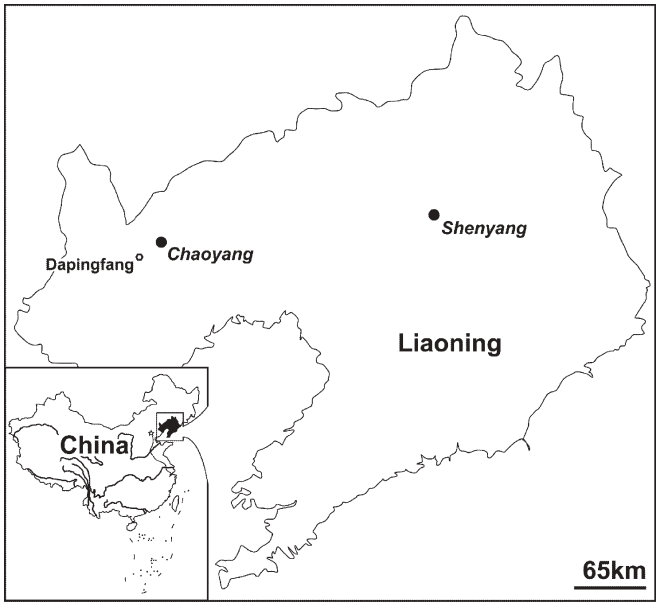

Fig. 1 Map showing the location of the *Yanornis martini* locality Dapingfang near Chaoyang City, Liaoning, in northeast China

Fig. 2 A new specimen (IVPP V13358) of the fish-eating bird *Yanornis martini*, showing the grit mass in the abdominal region

and the basal birds *Sapeornis chaoyangensis* (Zhou and Zhang 2002a) and *Jeholornis prima* (Zhou and Zhang 2002b, 2003a).

The most distinctive feature of the new specimen is the preservation of a large aggregate of grit in the abdominal area (Figs. 2, 3), which is interpreted as a mass of gastroliths. Although hundreds of Early Cretaceous bird specimens have been discovered in the past decade from Liaoning, northeast China, only two of them preserved direct evidence of diet. A large number of seeds are preserved in the abdominal region in one specimen of *Jeholornis prima* (IVPP V13274; Zhou and Zhang 2002b), and macerated fish remains were similarly preserved in the one specimen of *Yanornis martini* mentioned above (IVPP V13259; Zhou et al. 2002). The abundant gastroliths in the new *Yanornis* specimen (IVPP V13358) and a small number of gizzard stones described for one *Sapeornis* specimen (IVPP V13275; Zhou and Zhang 2003b) are the only other specimens of the thousands of exquisitely preserved birds from the Mesozoic of China to preserve direct evidence relevant to the inference of diet.

Description

The mass of fine gravel-sized particles in the new *Yanornis* specimen is necessarily within the articulated body cavity (Fig. 2), as it is posteroventral to the sternum, under-wrapped by articulated gastralia and between the left and right distal pubes (Figs. 1, 2). The mass is in the same position as a gizzard in extant birds (Proctor and Lynch 1993) and there is no evidence of postmortem disarticulation of the specimen; a feathered outline consistent with tracing the torso is preserved (Fig. 2). Such exceptional preservation is germane to the Jiufotang Formation (Zhou et al. 2003). The agglomeration is large relative to body size, extending across most of the posterior abdominal region in a bolus measuring approximately 60×24×3 mm (Figs. 2, 3). It is comprised of quartz grains varying in diameter from 2.7 mm to less than 0.2 mm and in angularity from subrounded to subangular.

The other four specimens of *Yanornis martini* including the holotype (IVPP V12558), one with fish remains (IVPP V 13259, Zhou et al. 2002) and two others (IVPP V10996, V13278) are all completely, or partially, articulated specimens with minimal or no evidence of postmortem disturbance. No gastroliths are known from any of these specimens.

Discussion

In extant birds, the trituration and mixing of foodstuff in the gizzard is the only confirmed function for large quantities of quartz gravel similar to the *Yanornis* grit (Gionfriddo and Best 1999). Small amounts of sediment may get into the gizzards of living birds by accidental ingestion (e.g., Reeders 1951) or intake within prey (gastroliths within fish are reported; e.g., McKeown 1937), but not the large quantities seen in the *Yanornis* fossil or in extant herbivorous birds (Wings 2003). The large number of gastroliths in *Yanornis* is, however, within the range of variation for these extant herbivorous avian taxa (Wings 2003). A large quantity of grit and a high percentage of same-species individuals with grit-containing gizzards correlate with an increased frequency of seeds or other hard materials in the diet (Gionfriddo and Best 1996).

Gastroliths have been proposed to help regulate buoyancy and balance while swimming and diving in specialized aquatic tetrapods including crocodilians and pinnipeds (Cott 1961; Taylor 1993; though see Henderson 2003); but only very small amounts are known from specialized diving birds such as penguins and some cormorants (e.g., Siegel-Causey 1990). Because of the large amount of grit preserved in the new *Yanornis* specimen and its conspicuous lack of diving specializations, this explanation of the grit in *Yanornis* is not supported.

The best explanation for the distribution of gastroliths and macerated fish remains among *Yanornis* specimens appears to be intermittent change in diet from one high in non-digestible fiber, such as seed eating, to a fish-based diet. In many avian species, changes in gizzard structure

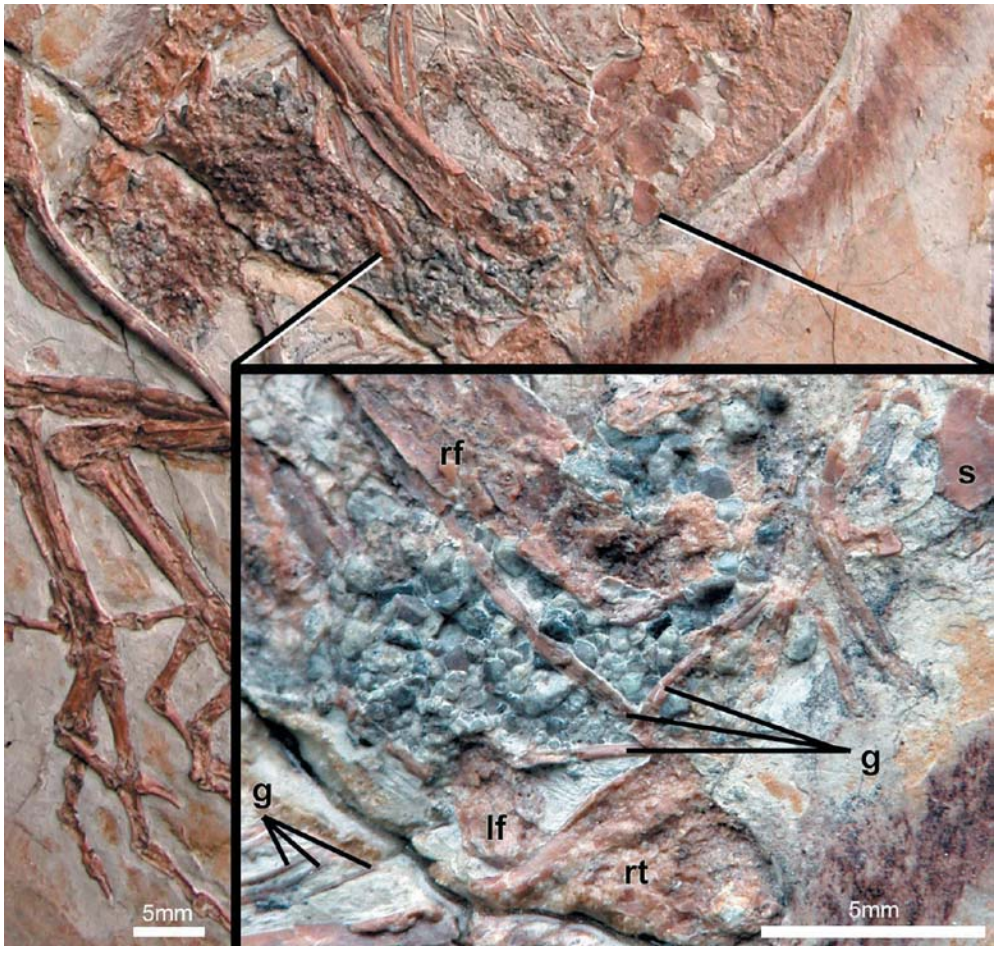

Fig. 3 The grit mass in IVPP V 13358. Abbreviations: *g* gastralia, *lf* left femur, *rf* right femur, *rt* right tibiotarsus, *s* sternum

and function reflect intermittent, usually seasonal, changes in diet (Gionfriddo and Best 1996; Starck 1999). One example of seasonal changes in gizzard size and gastrolith use in extant taxa is found in the bearded tit (*Panurus biarmicus*). In the winter season, bearded tits are granivorous and have grit-filled gizzards, while in summer they are insectivorous and their gizzards are smaller and normally do not contain any grit (Spitzer 1972). Other passeriform species with an extreme seasonal change in diet are the bramling *Fringilla montifringilla* (Thomson 1964) and several titmouse species (*Parus*; Betts 1955).

More relevant to *Yanornis*, seasonal and migration-related diet-switching is common in a variety of shorebirds (Charadriiformes). For example, the diet of the sanderling, *Calidris alba* (Charadriiformes, Scolopacidae), in the breeding area is composed of seeds, arthropods, plant buds, algae, and mosses (Richards 1988). By contrast, in wintering areas, small fish, mollusks, polychaetes, and crustaceans are the dominant food items (Myers et al. 1980; Canevari et al. 2001).

Diet-switching in *Yanornis* is consistent with evidence for seasonality during the Early Cretaceous of northern China (Zhou et al. 2003). The absence of recognizable preserved plant matter within the stomach contents may be a taphonomic artifact or explained by the fact that old or sick birds may not have plant matter in the digestive tract, while the gastroliths are still present (O. Wings, personal observation on ostriches, 2003).

The evidence from the new *Yanornis martini* specimen may indicate that plasticity in gizzard structure arose earlier in bird evolution than the origin of extant lineages. Such an origin for gizzard plasticity (minimally inferred for the most recent common ancestor of *Yanornis* and crown clade Aves) is the most parsimonious explanation of the present data. In extant taxa, gizzard plasticity is present even when radical diet-switching behavior is not exhibited (Starck 1999) and no gastroliths from the outgroup of Dinosauria, Crocodilia, are known to function analogously to birds in food digestion nor are their stomachs known to show such functional plasticity. The rarity of relevant data on Mesozoic outgroups of the avian crown clade due to a paucity of well-preserved specimens necessarily limits the strength of this form of inference, however.

There are similarities between the gastrolith-bearing *Yanornis* and the Early Tertiary pelicaniform bird *Protoplotus beauforti*. The *Protoplotus* holotype also contains a compact mass of quartz pebbles in the abdominal area (Lambrecht 1931). This mass was interpreted as an indicator for a seed/grain diet unlike all related extant taxa, which are fish-eating birds (Lambrecht 1931). Reconsidering the *Protoplotus* gastroliths in light of the present

review of data from extant taxa and *Yanornis* suggests that a possible seasonal diet-switching from fish to seeds or other plant material should also be considered for this taxon.

Gizzard stones are traditionally inferred to indicate a herbivorous diet within non-avian parts of the Dinosauria (e.g., Proctor and Lynch 1993; Xu 1997; Kobayashi et al. 1999), where they are present in an array of lineages. Several dinosaur species have abundant gastroliths, such as Ceratopsians (e.g., *Psittacosaurus*; Xu 1997), Ornithomimosauria (Kobayashi et al. 1999; Ji et al. 2003), and Oviraptorosauria (e.g., *Caudipteryx*, Zhou et al. 2000), and some of them have also been inferred to have a herbivorous diet on the basis of other anatomical features (e.g., toothlessness or tooth reduction; Xu 1997; Kobayashi et al. 1999; Zhou et al. 2000; Ji et al. 2003). However, a few non-avian theropod taxa with gastroliths have not been inferred to be herbivores, and these bear a full complement of teeth like *Yanornis martini* (e.g., *Nqwebasaurus*, de Klerk et al. 2000; *Lourinhanosaurus*, Mateus 1998). We suggest that intermittent dietary switching should be explored for these theropod taxa. Such data are necessary in order to investigate the origin of extant avian gizzard function and digestion generally.

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