Fossil evidence of avian crops from the Early Cretaceous of China

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The crop is characteristic of seed-eating birds today, yet little is known about its early history despite remarkable discoveries of many Mesozoic seed-eating birds in the past decade. Here we report the discovery of some early fossil evidence for the presence of a crop in birds. Two Early Cretaceous birds, the basal ornithurine *Hongshanornis* and a basal avian *Sapeornis*, demonstrate that an essentially modern avian digestive system formed early in avian evolution. The discovery of a crop in two phylogenetically remote lineages of Early Cretaceous birds and its absence in most intervening forms indicates that it was independently acquired as a specialized seed-eating adaptation. Finally, the reduction or loss of teeth in the forms showing seed-filled crops suggests that granivory was possibly one of the factors that resulted in the reduction of teeth in early birds.

paleornithology | feeding

Despite the discoveries of more than 30 genera of fossil birds from the Early Cretaceous lacustrine deposits in northeastern China and many examples of dietary adaptations (1), it remains unknown whether a crop was present in these birds. Recently we examined hundreds of Early Cretaceous birds housed at the Tianyu Museum of Nature in Shandong Province, China, and found several specimens belonging to two taxa with unequivocal evidence of crops. One of them is *Sapeornis*, one of the basal birds presumed to have an herbivorous diet (2, 3), and the second taxon is the basal ornithurine *Hongshanornis* (4). Both have preserved seeds in the anatomical location of the crop in extant birds. In some cases, even the soft tissue outline of the crop can be observed and resembles closely the structure in modern birds.

In extant birds a crop is a ventral pouch of the esophagus and is situated anterior to the shoulder girdle just in front of the furcula (5) (Fig. 1). In fossils its position is indicated by a roughly spherical mass of seeds that is easily discriminated from stomach contents by its location outside of the ribcage. The discovery of a crop in two phylogenetically separate avian lineages opens a window for our understanding of dietary adaptation in the early avian radiation and may also help us better understand the great diversity in the Early Cretaceous, which occurred approximately 20 million years after the earliest bird, *Archaeopteryx* (6, 7).

In modern seed-eating birds the crop provides storage, so that a number of seeds can be gathered quickly and then processed later in a more secure location without interference from competitors and/or predators. The mucus in the crop softens hard seeds so that they are more easily ground by the gizzard. The gizzard may be a more basal feature for birds, because it is widely distributed in sister groups, such as modern crocodilians. In recent birds the gizzard is posterior to the proventriculus or glandular part of the stomach. The practice of collecting large numbers of small stones in the gizzard is characteristic of seed eaters among modern birds and is often correlated with a well-developed crop.

A number of other Mesozoic birds and their theropod relatives have recently been reported with gizzard stones (gastroliths), including the basal ornithurines *Yanornis* (8) and *Archaeorhynchus* (9), the oviraptosaur *Caudipteryx*, and the ornithomimosaur *Shenzhousaurus* (10), confirming that the presence of a muscular grinding stomach is primitive for birds. It may well have occurred in most species but is only documented in forms that foraged on the ground and thereby came into contact with small stones. The discovery of crops in combination with stomach stones demonstrates the presence at an early date of an essentially modern avian digestive system.

Description and Comparison

Among the avian specimens we examined at the Tianyu Museum of Nature, at least three preserve clear evidence of a crop. Of these, *Sapeornis chaoyangensis* (2, 3) is the most basal bird that preserves this structure, and we discovered two examples (STM 15-15 and STM 15-29). STM 15-29 (Fig. 2 *A* and *B*) is a semi-articulated skeleton with the neck and head pulled away from the body for ≈5 cm. The skeleton is exposed dorsolaterally, with the wings folded. The right manus has moved away from the body. The sacrum is viewed dorsally, but the legs are laterally exposed. The crop is represented by a roughly circular mass (≈3 cm in diameter) of seeds. The outside was rimmed by a layer of larger seeds ranging from 4 to 6 mm in diameter, and the anterior portion of this layer had floated out, spreading over an area of some 9 × 2.5 cm (Fig. 2*B*). The center of the mass is densely packed with more than 70 smaller seeds showing an individual diameter of ≈2 mm. The seed mass was inset against the front of the furcula as in modern birds. The second specimen, STM 15-15 (Fig. 2 *C* and *D*) shows a cylindrical discoloration (darkening) of the sediments just below the ventral surface of the cervical vertebrae, extending a few centimeters anteriorly. This seems to be a trace of the esophagus, and it is faintly visible around the seed mass. The seeds were closely packed one against the other, indicating that there was little or no fleshy surface around them. The postcranial skeleton is nearly intact, with the ribcage still in its original position. Counting five vertebrae posterior to the end of the neck and within the ribcage there is a small mass of polished stones. A few of the stones are scattered away from the main concentration. The main mass indicates the position of the gizzard. Just posteroventral to this mass is a pocket of coprolitic material in the position of the intestines. The outline of the skeleton and positioning of the crop and gizzard is remarkably similar to that found in modern birds (Fig. 2).

The skeleton of *Sapeornis*, as in *Archaeopteryx*, lacks an ossified sternum, but the maxilla was edentulous, whereas the premaxilla has a small number of teeth that are elongated anteroposteriorly. The mandible was toothless and covered by a horny bill, as was

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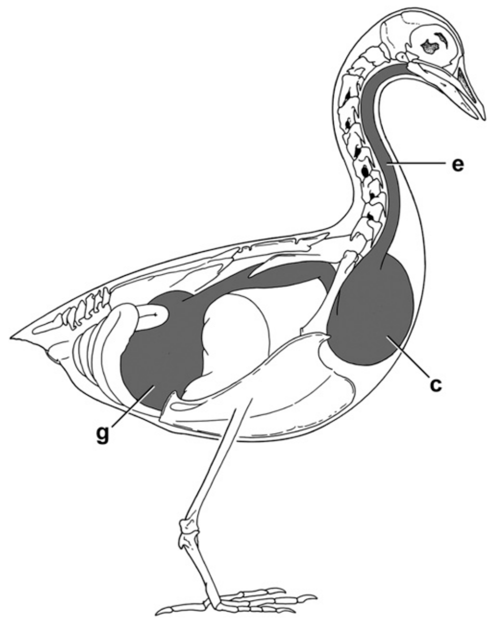

Fig. 1. Relative position of the crop (c) and gizzard (g) in a modern bird (some skeletal elements removed for clarity). e, esophagus.

probably also the case with the maxilla. It seems that the premaxillary teeth in *Sapeornis* were suitable for cutting fibrous material, such as stems attached to seeds, and this was likely the use of the horny bill as well.

One specimen of the basal ornithurine bird *Hongshanornis longicresta* (4) (STM 35-3; Fig. 3) shows a seed mass in front of the furcula that extends under the anterior sternum, a position similar to that for the crop in the modern hoatzin. *Hongshanornis* is a small ornithurine characterized by a short wing and the total loss of teeth. It was thought in some ways to be more basal than *Yanornis* (9). There are more than 20 seeds in STM 35-3, and they are all of one type, being oval and approximately 4 mm long and 2 mm wide (Fig. 3*B*). Posteriorly, below the position of the fifth dorsal vertebra, there is a mass of more than 50 small (1-mm) gastroliths, indicating a muscular gizzard at approximately the usual position in birds.

Discussion

Most modern birds with crops are seed eaters and use crops to store and soften foods and regulate their flow through the digestive tract before they pass to a powerfully muscled portion of the stomach, the gizzard (5). The gizzard is usually full of small stones for grinding seeds because birds lack the teeth and jaw musculature to do this by chewing. The gizzard is usually indicated in fossils by masses of small stones that show a distinctive polish.

It seems likely that the earliest birds were insect eaters and that the pointed snout so characteristic of the avian skull resulted from selective feeding on small prey in a complex environment (11). Larger prey requires deeper and more massive snouts, such as those in the dromaeosaurid *Microraptor* (12) and the troodontid *Anchiornis* (13), who have pointed teeth that are flattened and serrated. Such teeth are of no use for mastication but instead serve to catch, kill, and dismember prey. Small prey, like insects, can usually be swallowed whole without any special manipulation by the teeth, and the teeth of insectivorous forms are often simple cones.

The reduction or complete loss of teeth had occurred independently many times in vertebrate evolution, particularly in various lineages of dinosaurs. Teeth have been reduced or lost

Fig. 2. Photographs of two specimens of *Sapeornis chaoyangensis* housed at the Tianyu Museum of Nature with preservation of a crop. (*A*) STM 15-29, a partially articulated skeleton. (*B*) Close-up view of the crop region anterior to the furcula on the counterslab of STM 15-29. (*C*) STM 15-15, a nearly complete articulated skeleton. (*D*) Close-up view of the crop region anterior to the furcula in STM 15-15. Arrows point to seeds in the crop. c, crop; cv, cervical vertebrae; f, furcula; gs, gizzard stone; se, seed.

independently several times in various lineages of early avian evolution [e.g., *Sapeornis*, *Zhongjianornis* (14), Confuciusornithidae (15), Enantiornithes (16) and Ornithurae (4, 9)]. All birds from the beginning of the Cenozoic are toothless. Although reduction of body weight has often been cited as an important factor for reduction or loss of teeth in birds, we believe the dietary adaptation was probably an equally if not more important factor in early avian evolution. Both avian taxa that preserved the evidence of a crop have either largely reduced teeth or have completely lost their teeth. The basal avian *Sapeornis* has partially reduced teeth, whereas the early ornithurine *Hongshanornis* has completely lost its teeth and is one of only few known toothless genera among Mesozoic ornithurine birds. Most ornithurine birds from this period seemed to have been water marginal and used small pointed teeth to capture small arthropods and fish (17, 18).

Dilger's suggestion that a muscular crop may have led to the loss of teeth (19) in birds, although not entirely correct, is probably at least partially true and seems to be corroborated by our discovery of the crop, along with stone-filled gizzards, in two genera of Early Cretaceous seed-eating birds. The apparent link between the appearance of crops or gizzards or both and the loss of teeth across phylogenetic lineages suggests that granivory was probably one of the factors in the reduction of teeth in early birds.

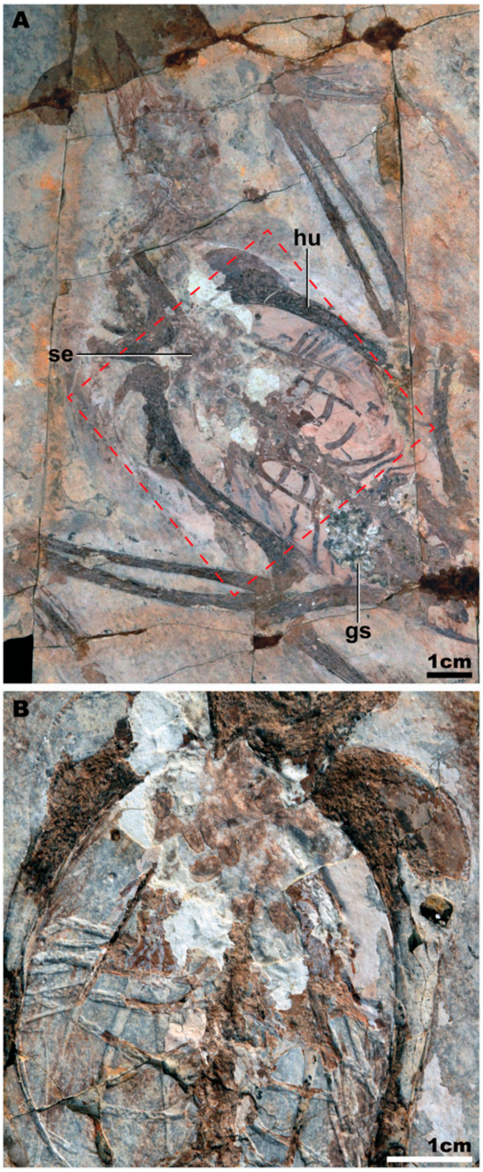

Fig. 3. Photographs of an ornithurine *Hongshanornis longicresta* (STM 35-3). (*A*) Incomplete skeleton; (*B*) close-up view of the seeds belonging to crop and the gizzard stones on the counterslab. hu, humerus; gs, gizzard stone; se, seed.

In a few cases, including the basal bird *Jeholornis* (20), there is evidence for seed-eating from stomach contents, but no crop has been reported despite the presence of more than 100 specimens. One possibility is that a crop was not a feature of all early seed-eating birds; however, it is more likely that it is simply a preservational or taphonomic artifact. Among nearly 100 *Sapeornis* specimens we have examined, there are only two examples with crop preserved. *Hongshanornis* is now represented by more than two dozen specimens, and we have recognized only one example with crop. It may be interesting to note that among extant birds, the leaf-eating hoatzin is unique in having extensive foregut fermentation in a voluminous crop as the fermentation chamber, analogous to the rumen of some mammals (21).

The Early Cretaceous is a critical interval in earth history and lies at the point of appearance and diversification of metatherian and eutherian mammals, as well as the diversification of enantiorithine and ornithurine birds (1). The dominant terrestrial birds in this radiation are enantiornithines (22), and they probably include several herbivorous forms, yet we have not recognized any example with a crop. The dominant plants in the modern flora, angiosperms, also appeared during this interval. At this time, however, early angiosperms were probably mostly herbaceous or shrubby and of low stature, with some aquatics (23, 24), and fruits would not have been widely available. Seed eating would have likely been an important dietary adaptation for arboreal forms. It is interesting to note, however, that angiosperms with fleshy fruits were already diverse in the Early Cretaceous, probably as an adaptation for animal dispersal in which birds may also have played a role (23). There are only two angiosperms taxa (*Archaefructus* and *Sinocarpus*) known with seeds from the Jehol Flora. The seeds in the crops of *Sapeornis* and *Hongshanornis* vary in size but are larger than those of *Archaefructus* and *Sinocarpus*, as well as most other early angiosperm seeds (23, 25). Most likely the seeds in the crops were produced by nonangiospermous seed plants, although presently there are no close matches among the Jehol seeds. Some of the nonangiospermous seed plants from the Jehol Biota with seeds of comparable size had fleshy seed coats (e.g., ginkgoaleans) or were enclosed in structures that were mostly fleshy (czekanowskialeans) and may have been attractive for the birds. Other seeds of comparable size from the Jehol Biota are known from conifers, borne in lax or dense cones.

Finally, it should also be noted that many raptorial birds like hawks and nectivorous birds like hummingbirds also have a crop. In these cases the crop does not seem to be linked with granivory. Unless we have more evidence about the distribution of the crop with diets in early birds, it is premature to argue that seed-eating was necessarily the driving force for the origin of the avian crop; however, the current known evidence seems to suggest that seed-eating was at least an important factor in early avian evolution.

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