Comparative digestive physiology of archosaurs with notes on bird origins

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It is widely accepted that birds evolved from theropod dinosaurs, and few paleontologists disagree preferring a more ancient split of the avian and dinosaur lineages. The difference in digestive physiology between members of the theropod and crocodile lineages, documented by fossil feces and gut contents, offers an opportunity to test these phylogenetic hypotheses. Birds share with crocodiles the functional gizzard that contains swallowed stones and where gastric pellets are formed before regurgitation, as well as a mechanism that prevents the passage of indigestible residues into the intestine. Both these adaptations are missing in unquestionable theropod groups (compsognathids, tyrannosaurids, allosaurids, coelophysids). The theropod ancestry of birds implies reappearance and strong development of a specific stomach functionality that either had been already lost in the theropod dinosaurs or was never present in their lineage. Coprolites of early archosaurs contain undigested bones, which suggests a short digestion time and higher metabolic rates than in extant crocodiles. Early archosaurs were similar to birds, but not to dinosaurs, in all these aspects of physiology.

Keywords: origin of birds, digestive physiology, bromalites
Introduction

Crocodiles and birds have a two-chambered stomach anatomy (Huntington 1903, Fisher 1981, Varricchio 2001, Wang et al. 2009, Fritz et al. 2011). The glandular stomach secretes the principal gastric acids and enzymes. It is followed by the muscular stomach (gizzard), which often contains geo-gastroliths (swallowed stones) and where indigestible remains are compressed into gastric pellets. These main stomach sections are followed by a small pylorus (Fig. 1). The function of gastroliths in crocodiles is a subject of discussion (Wings 2007) but it is remarkable that in crocodiles the pyloric sphincter prevents the passage of gastroliths and indigestible food items into the intestine (Fisher 1981, Xing et al. 2012). As crocodiles strongly decalcify bones, indigestible residues are basically keratin (hair, feathers) and chitin (insect exoskeletons) and are regurgitated as hairballs (Fisher 1981, Grigg and Gans 1993). Only less than one percent of ingested hair is occasionally found in crocodile feces (Fisher 1981) including elements of very small dimensions (Milàn 2012). On the other hand, birds regurgitate gastric pellets composed of bones with few chemical alterations (Dauphin et al. 2003) and other undigested items (hair, feathers, insect exoskeletons, seeds, plant fibers, etc.) (Halfpenny 2008, Wang et al. 2009).

Digestion in dinosaurs and early birds

Bone fragments are abundant in coprolites (fossil feces) attributable to theropod dinosaurs, and reach a half of the total volume of the fecal matter and centimetric dimensions, as seen in feces produced by coelophysids (Rinehart et al. 2005), allosaurids/ceratosaurids (Stone et al. 2000; Chin and Bishop 2007) and tyrannosaurids (Chin et al. 1998, 2003). These characteristics are
typical of excrements of modern felids and canids (Brönnimann et al. 2017). Thus, in theropods poorly digestible remains were abundantly excreted in feces rather than regurgitated. Moreover, coprolites of some ornithischian dinosaurs, most likely hadrosaurids, contain considerable proportions of wood fragments (13%–85%) (Chin 2007, Chin et al. 2017).

Theropods (and herbivorous dinosaurs) differed from birds and crocodiles also in that gastroliths are very rarely found in their gut contents (Wings 2004). Such rare occurrences of just small amounts of swallowed stones may represent accidental ingestion (Wings 2004, Bajdek et al. 2017). Whereas crocodiles are carnivores, in birds the use of gastroliths is often thought to characterize primarily herbivores and omnivores (Kobayashi et al. 1999) but deliberate ingestion of stones is well known in various birds of prey and in insectivorous species (Jenkinson and Mengel 1970, Wings 2007). The function of gastroliths includes trituration and mixing of foodstuff, mineral supplement, and stomach cleaning (Wings 2007). Among 'theropods' plausible gastroliths are known in some ornithomimosaurs (Kobayashi et al. 1999, Lee et al. 2014) and in the oviraptorosaur Caudipteryx zoui (Qiang et al. 1998). However, at least oviraptorosaurs may represent secondarily flightless birds (Maryańska et al. 2002) and it may be also the case of some other 'feathered theropods' (Feduccia 2012, Hutson and Hutson 2018). Gastroliths are known for the Late Jurassic Limusaurus inextricabilis (Xu et al. 2009, Wang et al. 2017), which is thought to represent a basal ceratosaur or an abelisauroid (e.g. Xu et al. 2009, Rauhut and Carrano 2016). However, if Limusaurus hand shows bilateral reduction of digits, as suggested by Xu et al. (2009), it may represent a secondarily flightless bird (see Feduccia 2002).

Gastroliths discovered in basal birds such as the granivorous Sapeornis and Jeholornis, and a cohesive gastric pellet of a piscivorous enantiornithine bird from the Early Cretaceous point out that the muscular gizzard was indeed present in early birds (Wang et al. 2016, O’Connor et al. 2017).
Moreover, two bone aggregates found in the stomach of the early tetrapteryx bird *Microraptor gui* (IVPP V17972A) might be tentatively interpreted as gastric pellets, situated in the muscular and glandular chambers of stomach (see O’Connor et al. 2011). The intestine of another *Microraptor gui* specimen (QM V1002) only contains items of micrometric dimensions (Xing et al. 2013).

Abundant stomach stones have been found in the guts of the ceratopsians *Psittacosaurus mongoliensis* and *Yinlong downsi* (Xu et al. 2006) and also of the ornithopod *Gasparinisaura cincosaltensis* (Cerda 2008). However, the gastric mill is most typical of herbivorous birds which are toothless, whereas *Psittacosaurus* and *Gasparinisaura* had sophisticated masticatory apparatus, so the reason for evolving an unique double system of food processing would be obscure (Fritz et al. 2011). Gastrolith finds are rare for other ornithischians and sauropods (Wings 2004). Animals consume considerable amounts of sediment while feeding (e.g. eastern painted turtle 6%, bison 7%, nine-banded armadillo 17%) (Beyer et al. 1994, Bajdek et al. 2014) and swallowed clastic grains may accumulate in the food chain passing into the guts of top predators (Bajdek et al. 2017). Notably, there is no gastric mill in the pygmy hippopotamus despite gravel may constitute 1/3 of its total wet stomach content (Wings et al. 2008).

Conclusive data on the theropod digestive physiology are provided by the stomach and intestine contents of two specimens of the compsognathid *Sinocalliopteryx gigas* (Xing et al. 2012). One of them reveals no presence of gastroliths, meanwhile in the other specimen gastroliths are present in intestines rather than retained in stomach (Xing et al. 2012). In ostriches, gastroliths are not excreted until the swallowed grit is reduced in size to sand (Wings 2004). Moreover, the gut contents of one of the specimens comprise remains of birds and ornithischian dinosaurs in different stages of digestion, what indicates a hiatus between the meals (Xing et al. 2012). In
contrast, as gastric pellets travels up from the muscular stomach to the glandular stomach, where they stay awhile for further digestion and in consequence block the alimentary canal, owls cannot consume more foodstuff until they regurgitate the residues from the previous meal (Wang et al. 2009). This is because owls lack the esophageal crop, which was probably absent also in the basal bird Jeholornis (O’Connor et al. 2017). Dissection of crocodiles revealed the presence of gastric pellets in the upper region of stomach where digestive acids are acting (Fisher 1981). Crocodiles regurgitate indigestible remains for keeping available space for large prey items (Chabreck 1996). The presence of bones in intestines of Sinocalliopteryx gigas points out that they were not regurgitated (Xing et al. 2012). Intestine of the compsognathid Scipionyx samniticus also contains bone fragments, that led Dal Sasso and Maganuco (2011) to the conclusion that the digestive physiology of Scipionyx was more like that of extant lepidosaurs than that of extant archosaurs. No process of gastric pellet formation is visible in stomach contents of the compsognathids Scipionyx samniticus (Dal Sasso and Maganuco 2011), Sinocalliopteryx gigas (Xing et al. 2012), Compsognathus longipes (Conrad 2017) and Sinosauropteryx prima (Smithwick et al. 2017), and neither in the coelophysid Coelophysis bauri (Nesbitt et al. 2006).

Summing up, evidence of the bird-like muscular gizzard (such as cohesive gastric pellets and abundant gastroliths) is missing for theropod dinosaurs. In theropods poorly digestible remains were abundantly excreted in feces as shown by cololites and coprolites of coelophysids, allosaurids, tyrannosaurids, and compsognathids. Notwithstanding, it cannot be ruled out that theropods occasionally regurgitated large bones in form of a mostly loose material. Such behavior is encountered in some tetrapods, including basal amniotes (Silva et al. 2017).

**Digestion in early archosaurs**
Some clues about the physiology of early archosaurs are provided by the comparative physiology of birds and crocodiles (Table 1). In birds, regurgitation allows to remove from the gastrointestinal tract tough food items of limited nutritional value, which cannot be decomposed via digestion. It allows maximization of food intake which satisfies high energetic requirements of birds. Regurgitation in modern crocodiles would be conceivable as a vestige of their ancestors of a comparable physiology.

Endotherms are characterized by higher energetic requirements than ectotherms and consequently by larger food intake and much shorter digestion than ectotherms of a comparable body mass (Fritz et al. 2010, Bajdek et al. 2016). Mammals defecate bones with few chemical alterations (Brönnimann et al. 2017, Stannard et al. 2017). Interestingly, coprolites attributable likely to the oldest proterosuchid *Archosaurus rossicus* from the latest Permian–earliest Triassic of Russia contain mostly well-resistant to digestion bone fragments, such as the compact cortical bone tissue, archosaur teeth crowns and ganoine fish scales, meanwhile less resistant elements have been digested (Bajdek et al. 2017). It is remarkable that modern crocodiles and other extant reptiles (snakes) completely digest bones (Fisher 1981, Secor 2008, Milàn 2012). Ganoine fish scales and archosaur teeth fragments found in the studied coprolites reveal no signs of digestion (Bajdek et al. 2017), whereas crocodiles decalcify ganoine and also their own teeth when accidentally broken and swallowed (Fisher 1981). Probable archosauromorph coprolites from the Early Triassic of Australia also contain incompletely digested bones (Niedźwiedzki et al. 2016). This might suggest that gastric fluids of the early archosaurs were not highly acidic. However, the acidity of gastric fluids depends on the trophic group of the animal rather than is correlated phylogenetically (Beasley et al. 2015). For example, scavengers are often characterized by high
stomach acidity for protection from foreign microbes (Beasley et al. 2015) and digestion may be particularly strong in bone-eating specialists (Gargalida 2008). Also, it may be pointed out that early archosaurs were characterized by shorter digestion and likely some higher metabolic rates than crocodiles (and other extant reptiles). Digestion is comparatively shorter in reptiles of small body mass (Lillywhite et al. 2002) but coprolites discussed herein have been mostly produced by big carnivores. The extent of acid degradation of bones in excrements of early archosaurs (Niedźwiedzki et al. 2016, Bajdek et al. 2017) seems comparable to that in theropod coprolites (Chin and Bishop 2007, Chin et al. 1998) indicating such moderate strength of digestion in both groups. However, bone inclusions in feces of early archosaurs (Owocki et al. 2012, Niedźwiedzki et al. 2016, Bajdek et al. 2017) were far less abundant than in certain bone-rich theropod fecal masses (Chin and Bishop 2007, Chin et al. 1998, 2003) and rarely exceeded sand-sized dimensions (Bajdek et al. 2017). Either bones were not ingested in large amounts (e.g., prey was not swallowed whole) or some early archosaurs regurgitated most of the bones like birds do (Bajdek et al. 2017).

Implications for bird origins

The usage of gastroliths vary between distinct crocodile and bird groups but the anatomical predisposition of the gastrointestinal tract is likely inherited from the common ancestor of crocodiles and birds (Varricchio 2001, Fritz et al. 2011). Deliberate ingestion of stones was not necessarily typical of each theropod group. However, the lack of a mechanism that prevents the passage of indigestible residues (stones and tough food items) into the intestine (via the action of pyloric sphincter, muscular stomach, and subsequent regurgitation) in theropods is even more
intriguing. Fundamental physiology that birds share with their closest living relatives, crocodiles, would have been highly expected to characterize the direct ancestors of birds as well. The theropod ancestry of birds is a problematic scenario, as it would imply independent development of a specific complex stomach anatomy in birds and crocodiles.

The hypothesis that birds evolved from theropods is supported by numerous cladistic analyses (Smith et al. 2015), but most of these reflect overall similarity and are incapable of dealing with superficial convergence. The methodology of cladistic studies (e.g. Nesbitt et al. 2017, Cau 2018) may be easily misleading when applied to closely related groups (Feduccia 2002, 2013). Phylogenetic systematics relies on a large number of studies which are nowadays virtually all based on a single method, that does not conform to the requisite of triangulation of lines of evidence in science (see Munafò and Smith 2018). A more convincing phylogenetic hypothesis would include a variety of biological data (embryology, ecology, etc.) and discuss the functional value of adaptations (Dodson 2000, Feduccia 2002). Opponents of the hypothesis that birds evolved from derived theropods suggest that birds had their origin in more basal archosaurs that lived in the Triassic (Feduccia 2002; Czerkas and Feduccia 2014). Three non-theropod hypotheses are taken into consideration: the early archosaur hypothesis and the dinosauromorph hypothesis (which differ in the timing of branching of birds), and also the crocodylomorph hypothesis (which is not popular today) (Feduccia 2012). Whereas the theropod hypothesis appears problematic, each of these three non-theropod hypotheses is consistent with the data on digestive physiology of archosaurs presented herein (Table 1).

Dinosaurs and early birds are variously interpreted as ectothermic (e.g. Ruben et al. 2003) or endothermic (e.g. Bakker 1975). The scenario presented here suggest that an incipient endothermy appeared early in the archosaurian evolution, likely by the Early Triassic (Fig. 2).
Theropods inherited such moderate metabolic rates. Undigested muscle tissue preserved in a tyrannosaurid coprolite is clearly indicative of a short digestion period unlike that in extant reptiles (Chin et al. 2003). On the other hand, digestion of bones in certain theropods seems stronger than in birds and mammals, as noticed by Xing et al. (2012). Energetic requirements decreased in the lineage of crocodiles, perhaps due to their semi-aquatic lifestyle (Seymour et al. 2004), meanwhile in birds they increased hypothetically with the development of the active flight ability.

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Table 1. Features of digestive physiology in archosaurian groups.

<table>
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<tr>
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<th>indigestible food items</th>
<th>swallowed stones</th>
<th>metabolic rates</th>
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<tr>
<td>early archosaurs</td>
<td>likely regurgitated in the common ancestor of birds and crocodiles, and possibly in early proterosuchids</td>
<td>likely retained in stomach in the common ancestor of birds and crocodiles</td>
<td>moderate</td>
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<tr>
<td>extant crocodiles</td>
<td>regurgitated</td>
<td>common and retained in stomach</td>
<td>low</td>
</tr>
<tr>
<td>extant birds</td>
<td>regurgitated</td>
<td>common and retained in stomach</td>
<td>high</td>
</tr>
<tr>
<td>theropods</td>
<td>excreted in feces</td>
<td>rare and excreted in feces</td>
<td>moderate</td>
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Fig. 1. Stomach anatomy of the American alligator (*Alligator mississippiensis*) (A) and the red-throated loon (*Gavia stellata*) (B); modified from Huntington (1903). Both alligators and loons are carnivores. Some workers think that the two-part stomach with an enzyme-producing glandular stomach followed by a thick-walled muscular gizzard is an archosaur synapomorphy (e.g. Varrichio 2001), whereas others do not recognize homology of crocodilian and avian gizzards (e.g. Wang et al. 2016).
Fig. 2. Digestive physiology of archosaurs placed on a simplified phylogenetic tree, based on the present study. This is an unorthodox interpretation as birds are not necessarily nested within theropods. Note that the stomach of theropods did not act as a gastric mill.