1 **Comparative digestive physiology of archosaurs with notes on bird origins**

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8 It is widely accepted that birds evolved from theropod dinosaurs, and few paleontologists

9 disagree preferring a more ancient split of the avian and dinosaur lineages. The difference in

10 digestive physiology between members of the theropod and crocodile lineages, documented by

11 fossil feces and gut contents, offers an opportunity to test these phylogenetic hypotheses. Birds

12 share with crocodiles the functional gizzard that contains swallowed stones and where gastric

13 pellets are formed before regurgitation, as well as a mechanism that prevents the passage of

14 indigestible residues into the intestine. Both these adaptations are missing in unquestionable

15 theropod groups (compsognathids, tyrannosaurids, allosaurids, coelophysids). The theropod

16 ancestry of birds implies reappearance and strong development of a specific stomach

17 functionality that either had been already lost in the theropod dinosaurs or was never present in

18 their lineage. Coprolites of early archosaurs contain undigested bones, which suggests a short

19 digestion time and higher metabolic rates than in extant crocodiles. Early archosaurs were similar

20 to birds, but not to dinosaurs, in all these aspects of physiology.

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22 **Keywords:** origin of birds, digestive physiology, bromalites

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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

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47 typical of excrements of modern felids and canids (Brönnimann et al. 2017). Thus, in theropods

48 poorly digestible remains were abundantly excreted in feces rather than regurgitated. Moreover,

49 coprolites of some ornithischian dinosaurs, most likely hadrosaurids, contain considerable

50 proportions of wood fragments (13%–85%) (Chin 2007, Chin et al. 2017).

51 Theropods (and herbivorous dinosaurs) differed from birds and crocodiles also in that gastroliths

52 are very rarely found in their gut contents (Wings 2004). Such rare occurrences of just small

53 amounts of swallowed stones may represent accidental ingestion (Wings 2004, Bajdek et al.

54 2017). Whereas crocodiles are carnivores, in birds the use of gastroliths is often thought to

55 characterize primarily herbivores and omnivores (Kobayashi et al. 1999) but deliberate ingestion

56 of stones is well known in various birds of prey and in insectivorous species (Jenkinson and

57 Mengel 1970, Wings 2007). The function of gastroliths includes trituration and mixing of

58 foodstuff, mineral supplement, and stomach cleaning (Wings 2007). Among 'theropods' plausible

59 gastroliths are known in some ornithomimosaurs (Kobayashi et al. 1999, Lee et al. 2014) and in

60 the oviraptorosaur *Caudipteryx zoui* (Qiang et al. 1998). However, at least oviraptorosaurs may

61 represent secondarily flightless birds (Maryańska et al. 2002) and it may be also the case of some

62 other 'feathered theropods' (Feduccia 2012, Hutson and Hutson 2018). Gastroliths are known for

63 the Late Jurassic *Limusaurus inextricabilis* (Xu et al. 2009, Wang et al. 2017), which is thought to

64 represent a basal ceratosaur or an abelisauroid (e.g. Xu et al. 2009, Rauhut and Carrano 2016).

65 However, if *Limusaurus* hand shows bilateral reduction of digits, as suggested by Xu et al.

66 (2009), it may represent a secondarily flightless bird (see Feduccia 2002).

67 Gastroliths discovered in basal birds such as the granivorous *Sapeornis* and *Jeholornis*, and a

68 cohesive gastric pellet of a piscivorous enantiornithine bird from the Early Cretaceous point out

69 that the muscular gizzard was indeed present in early birds (Wang et al. 2016, O'Connor et al.

70   2017). Moreover, two bone aggregates found in the stomach of the early tetrapteryx bird

71   *Microraptor gui* (IVPP V17972A) might be tentatively interpreted as gastric pellets, situated in

72   the muscular and glandular chambers of stomach (see O'Connor et al. 2011). The intestine of

73   another *Microraptor gui* specimen (QM V1002) only contains items of micrometric dimensions

74   (Xing et al. 2013).

75   Abundant stomach stones have been found in the guts of the ceratopsians *Psittacosaurus*

76   *mongoliensis* and *Yinlong downsi* (Xu et al. 2006) and also of the ornithopod *Gasparinisaura*

77   *cincosaltensis* (Cerda 2008). However, the gastric mill is most typical of herbivorous birds which

78   are toothless, whereas *Psittacosaurus* and *Gasparinisaura* had sophisticated masticatory

79   apparatus, so the reason for evolving an unique double system of food processing would be

80   obscure (Fritz et al. 2011). Gastrolith finds are rare for other ornithischians and sauropods (Wings

81   2004). Animals consume considerable amounts of sediment while feeding (e.g. eastern painted

82   turtle 6%, bison 7%, nine-banded armadillo 17%) (Beyer et al. 1994, Bajdek et al. 2014) and

83   swallowed clastic grains may accumulate in the food chain passing into the guts of top predators

84   (Bajdek et al. 2017). Notably, there is no gastric mill in the pygmy hippopotamus despite gravel

85   may constitute 1/3 of its total wet stomach content (Wings et al. 2008).

86   Conclusive data on the theropod digestive physiology are provided by the stomach and intestine

87   contents of two specimens of the compsognathid *Sinocalliopteryx gigas* (Xing et al. 2012). One

88   of them reveals no presence of gastroliths, meanwhile in the other specimen gastroliths are

89   present in intestines rather than retained in stomach (Xing et al. 2012). In ostriches, gastroliths

90   are not excreted until the swallowed grit is reduced in size to sand (Wings 2004). Moreover, the

91   gut contents of one of the specimens comprise remains of birds and ornithischian dinosaurs in

92   different stages of digestion, what indicates a hiatus between the meals (Xing et al. 2012). In

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93   contrast, as gastric pellets travels up from the muscular stomach to the glandular stomach, where

94   they stay awhile for further digestion and in consequence block the alimentary canal, owls cannot

95   consume more foodstuff until they regurgitate the residues from the previous meal (Wang et al.

96   2009). This is because owls lack the esophageal crop, which was probably absent also in the basal

97   bird *Jeholornis* (O'Connor et al. 2017). Dissection of crocodiles revealed the presence of gastric

98   pellets in the upper region of stomach where digestive acids are acting (Fisher 1981). Crocodiles

99   regurgitate indigestible remains for keeping available space for large prey items (Chabreck 1996).

100   The presence of bones in intestines of *Sinocalliopteryx gigas* points out that they were not

101   regurgitated (Xing et al. 2012). Intestine of the compsognathid *Scipionyx samniticus* also contains

102   bone fragments, that led Dal Sasso and Maganuco (2011) to the conclusion that the digestive

103   physiology of *Scipionyx* was more like that of extant lepidosaurs than that of extant archosaurs.

104   No process of gastric pellet formation is visible in stomach contents of the compsognathids

105   *Scipionyx samniticus* (Dal Sasso and Maganuco 2011), *Sinocalliopteryx gigas* (Xing et al. 2012),

106   *Compsognathus longipes* (Conrad 2017) and *Sinosauropteryx prima* (Smithwick et al. 2017), and

107   neither in the coelophysid *Coelophysis bauri* (Nesbitt et al. 2006).

108   Summig up, evidence of the bird-like muscular gizzard (such as cohesive gastric pellets and

109   abundant gastroliths) is missing for theropod dinosaurs. In theropods poorly digestible remains

110   were abundantly excreted in feces as shown by cololites and coprolites of coelophysids,

111   allosaurids, tyrannosaurids, and compsognathids. Notwithstanding, it cannot be ruled out that

112   theropods occasionally regurgitated large bones in form of a mostly loose material. Such behavior

113   is encountered in some tetrapods, including basal amniotes (Silva et al. 2017).

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115   **Digestion in early archosaurs**

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117   Some clues about the physiology of early archosaurs are provided by the comparative physiology

118   of birds and crocodiles (Table 1). In birds, regurgitation allows to remove from the

119   gastrointestinal tract tough food items of limited nutritional value, which cannot be decomposed

120   via digestion. It allows maximization of food intake which satisfies high energetic requirements

121   of birds. Regurgitation in modern crocodiles would be conceivable as a vestige of their ancestors

122   of a comparable physiology.

123   Endotherms are characterized by higher energetic requirements than ectotherms and consequently

124   by larger food intake and much shorter digestion than ectotherms of a comparable body mass

125   (Fritz et al. 2010, Bajdek et al. 2016). Mammals defecate bones with few chemical alterations

126   (Brönnimann et al. 2017, Stannard et al. 2017). Interestingly, coprolites attributable likely to the

127   oldest proterosuchid *Archosaurus rossicus* from the latest Permian–earliest Triassic of Russia

128   contain mostly well-resistant to digestion bone fragments, such as the compact cortical bone

129   tissue, archosaur teeth crowns and ganoine fish scales, meanwhile less resistant elements have

130   been digested (Bajdek et al. 2017). It is remarkable that modern crocodiles and other extant

131   reptiles (snakes) completely digest bones (Fisher 1981, Secor 2008, Milàn 2012). Ganoine fish

132   scales and archosaur teeth fragments found in the studied coprolites reveal no signs of digestion

133   (Bajdek et al. 2017), whereas crocodiles decalcify ganoine and also their own teeth when

134   accidentally broken and swallowed (Fisher 1981). Probable archosauromorph coprolites from the

135   Early Triassic of Australia also contain incompletely digested bones (Niedźwiedzki et al. 2016).

136   This might suggest that gastric fluids of the early archosaurs were not highly acidic. However, the

137   acidity of gastric fluids depends on the trophic group of the animal rather than is correlated

138   phylogenetically (Beasley et al. 2015). For example, scavengers are often characterized by high

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139   stomach acidity for protection from foreign microbes (Beasley et al. 2015) and digestion may be

140   particularly strong in bone-eating specialists (Gargalida 2008). Also, it may be pointed out that

141   early archosaurs were characterized by shorter digestion and likely some higher metabolic rates

142   than crocodiles (and other extant reptiles). Digestion is comparatively shorter in reptiles of small

143   body mass (Lillywhite et al. 2002) but coprolites discussed herein have been mostly produced by

144   big carnivores. The extent of acid degradation of bones in excrements of early archosaurs

145   (Niedźwiedzki et al. 2016, Bajdek et al. 2017) seems comparable to that in theropod coprolites

146   (Chin and Bishop 2007, Chin et al. 1998) indicating such moderate strength of digestion in both

147   groups. However, bone inclusions in feces of early archosaurs (Owocki et al. 2012, Niedźwiedzki

148   et al. 2016, Bajdek et al. 2017) were far less abundant than in certain bone-rich theropod fecal

149   masses (Chin and Bishop 2007, Chin et al. 1998, 2003) and rarely exceeded sand-sized

150   dimensions (Bajdek et al. 2017). Either bones were not ingested in large amounts (e.g., prey was

151   not swallowed whole) or some early archosaurs regurgitated most of the bones like birds do

152   (Bajdek et al. 2017).

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154   **Implications for bird origins**

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156   The usage of gastroliths vary between distinct crocodile and bird groups but the anatomical

157   predisposition of the gastrointestinal tract is likely inherited from the common ancestor of

158   crocodiles and birds (Varricchio 2001, Fritz et al. 2011). Deliberate ingestion of stones was not

159   necessarily typical of each theropod group. However, the lack of a mechanism that prevents the

160   passage of indigestible residues (stones and tough food items) into the intestine (via the action of

161   pyloric sphincter, muscular stomach, and subsequent regurgitation) in theropods is even more

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162   intriguing. Fundamental physiology that birds share with their closest living relatives, crocodiles,

163   would have been highly expected to characterize the direct ancestors of birds as well. The

164   theropod ancestry of birds is a problematic scenario, as it would imply independent development

165   of a specific complex stomach anatomy in birds and crocodiles.

166   The hypothesis that birds evolved from theropods is supported by numerous cladistic analyses

167   (Smith et al. 2015), but most of these reflect overall similarity and are incapable of dealing with

168   superficial convergence. The methodology of cladistic studies (e.g. Nesbitt et al. 2017, Cau 2018)

169   may be easily misleading when applied to closely related groups (Feduccia 2002, 2013).

170   Phylogenetic systematics relies on a large number of studies which are nowadays virtually all

171   based on a single method, that does not conform to the requisite of triangulation of lines of

172   evidence in science (see Munafò and Smith 2018). A more convincing phylogenetic hypothesis

173   would include a variety of biological data (embryology, ecology, etc.) and discuss the functional

174   value of adaptations (Dodson 2000, Feduccia 2002). Opponents of the hypothesis that birds

175   evolved from derived theropods suggest that birds had their origin in more basal archosaurs that

176   lived in the Triassic (Feduccia 2002; Czerkas and Feduccia 2014). Three non-theropod

177   hypotheses are taken into consideration: the early archosaur hypothesis and the dinosauromorph

178   hypothesis (which differ in the timing of branching of birds), and also the crocodylomorph

179   hypothesis (which is not popular today) (Feduccia 2012). Whereas the theropod hypothesis

180   appears problematic, each of these three non-theropod hypotheses is consistent with the data on

181   digestive physiology of archosaurs presented herein (Table 1).

182   Dinosaurs and early birds are variously interpreted as ectothermic (e.g. Ruben et al. 2003) or

183   endothermic (e.g. Bakker 1975). The scenario presented here suggest that an incipient

184   endothermy appeared early in the archosaurian evolution, likely by the Early Triassic (Fig. 2).

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185 Theropods inherited such moderate metabolic rates. Undigested muscle tissue preserved in a

186 tyrannosaurid coprolite is clearly indicative of a short digestion period unlike that in extant

187 reptiles (Chin et al. 2003). On the other hand, digestion of bones in certain theropods seems

188 stronger than in birds and mammals, as noticed by Xing et al. (2012). Energetic requirements

189 decreased in the lineage of crocodiles, perhaps due to their semi-aquatic lifestyle (Seymour et al.

190 2004), meanwhile in birds they increased hypothetically with the development of the active flight

191 ability.

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432   Table 1. Features of digestive physiology in archosaurian groups.

|	indigestible food items	swallowed stones	metabolic rates
early archosaurs	likely regurgitated in the common ancestor of birds and crocodiles, and possibly in early proterosuchids	likely retained in stomach in the common ancestor of birds and crocodiles	moderate
extant crocodiles	regurgitated	common and retained in stomach	low
extant birds	regurgitated	common and retained in stomach	high
theropods	excreted in feces	rare and excreted in feces	moderate

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445 Fig. 1. Stomach anatomy of the American alligator (*Alligator mississippiensis*) **(A)** and the red-

446 throated loon (*Gavia stellata*) **(B)**; modified from Huntington (1903). Both alligators and loons

447 are carnivores. Some workers think that the two-part stomach with an enzyme-producing

448 glandular stomach followed by a thick-walled muscular gizzard is an archosaur synapomorphy

449 (e.g. Varrichio 2001), whereas others do not recognize homology of crocodilian and avian

450 gizzards (e.g. Wang et al. 2016).

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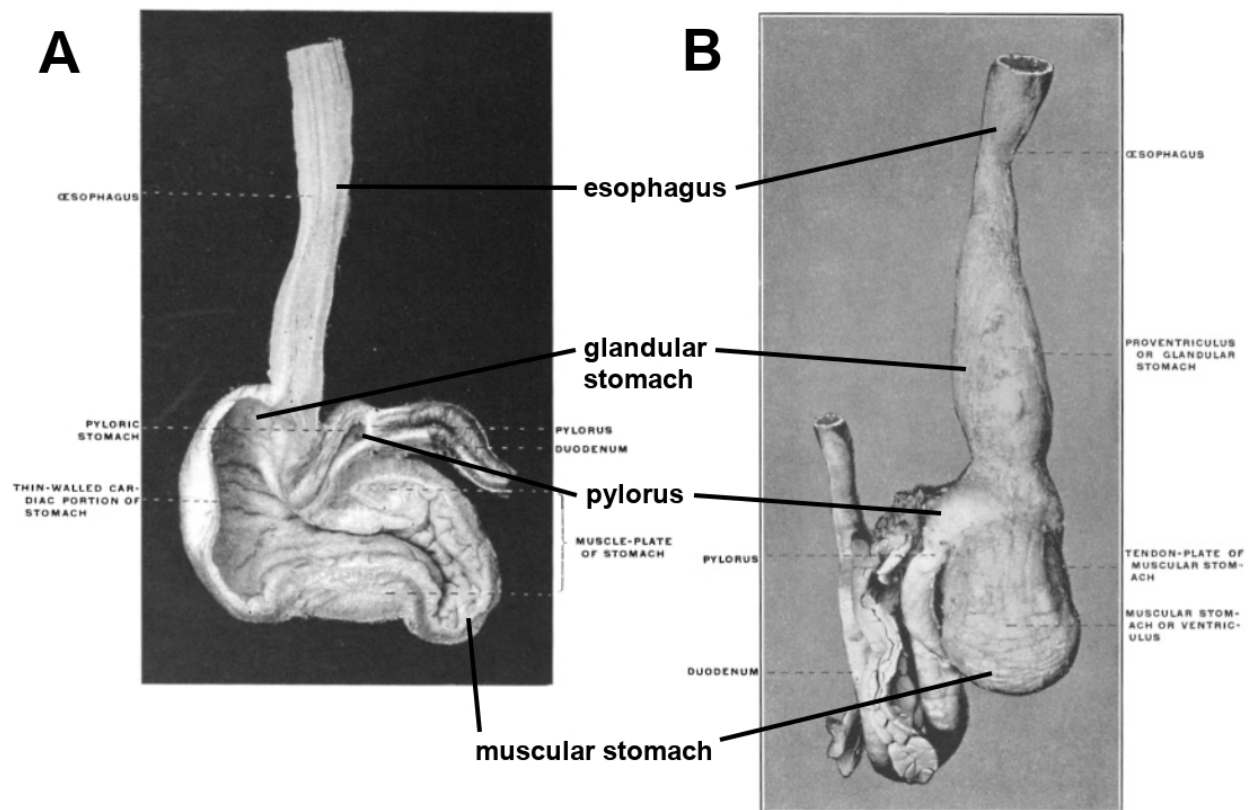
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457   Fig. 2. Digestive physiology of archosaurs placed on a simplified phylogenetic tree, based on the

458   present study. This is an unorthodox interpretation as birds are not necessarily nested within

459   theropods. Note that the stomach of theropods did not act as a gastric mill.

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