Stomach histology of *Crocodylus siamensis* and *Gavialis gangeticus* reveals analogy of archosaur "gizzards", with implication on crocodylian gastroliths function

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Abstract. Two groups of extant Archosauria, Crocodylia and Neornithes, have two-chambered stomachs and store gastroliths inside their "gizzards". Morphological similarities of the "gizzards" lead some previous studies to assume that the presence of this structure, organ "gizzard" is synapomorphic to Archosauria. However, the homology of archosaur "gizzards" had never been tested. This study provides general histological descriptions of stomachs of two crocodylian taxa, *Crocodylus siamensis* and *Gavialis gangeticus*, to determine the homology of crocodylian and neornithine "gizzards". Our study demonstrates that both *Crocodylus siamensis* and *Gavialis gangeticus* have longer, more complex glands in the fundic stomach (crocodylian "gizzard") than in the pyloric stomach. Additionally, we found that compound glands are present in the fundic stomach of *Crocodylus siamensis*. Therefore, crocodylian stomach histomorphological structures are concordant with those of other non-avian reptiles, despite the unique gross morphology. The pyloric regions of non-avian reptile stomachs are known to be homologous with the pyloric regions of mammalian stomachs as well as neornithine ventriculus (neornithine gizzard). Therefore, crocodylian and neornithine "gizzards" are morphologically analogous but not homologous. The presence of PAS-positive layer in the pyloric stomach of *Gavialis gangeticus*, which resembles the koilin layer of neornithine ventriculus, further supports this interpretation. At the same time, however, the similarity in gastroliths mass/body mass ratio and the correlations between gastroliths occurrence and diet types suggest that crocodylian gastroliths might have contributed to the digestion of ingesta, even though crocodylian and neornithine "gizzards" are not homologous.

Keywords. Histology, gizzard, gastroliths, Crocodylia, stomach.

INTRODUCTION

Crocodylians present the most complex stomach known in existing members of non-avian reptiles (hereafter referred to as reptiles) (Owen, 1866; Richardson et al., 2002). Crocodylian stomachs are composed of two distinct units: fundic and pyloric chambers. Neornithes (a least inclusive clade of living birds), the closest living relatives of crocodylians, also have two-chambered stomachs: a glandular stomach (proventriculus) and a muscu-

lar stomach (ventriculus or gizzard) (Ziswiler and Farner, 1972; Denbow, 2015). While the proventriculus excretes the mucus, pepsin, and hydrochloric acid necessary for chemical digestion, the ventriculus performs mechanical digestion of ingesta. Some neornithines, mostly herbivores, consume stones and store them inside gizzards as gastroliths (geo-gastroliths, Wings, 2007) to aid gastric mechanical digestion (Fritz, 1937; Hetland et al., 2003; Jin et al., 2014). Several crocodylians are also known to contain gastroliths inside their fundic stomachs (e.g., Corbet,

1960; Cott, 1961). Since both crocodylians and neornithines have two-chambered stomachs and store gastroliths inside them, some studies refer crocodylian fundic stomach as a "gizzard" (Reese, 1915; Grigg and Gans, 1993).

Based on the phylogenetic bracket of the two-chambered stomachs, together with the generality of gastroliths among archosaurs including non-avian dinosaurs, (e.g., Kobayashi et al., 1999; Cerda, 2008; Lee et al., 2014), neornithine style muscular "gizzard" had previously been considered as a plesiomorphic feature of Archosauria (Varricchio, 2001; Fritz et al., 2011). However, the homology of avian and crocodylian "gizzards" is considered ambiguous (Schwenk and Rubega, 2005). While some studies considered that crocodylian "gizzards" are homologous with neornithine gizzards (Varricchio, 2001; Fritz et al., 2011), some studies refute the homology (Jones, 1861; Huang et al., 2016). Additionally, the functions of crocodylian gastroliths are still under debates (e.g., food processing, hydrostatic function, accidental intake; Cott, 1961; Davenport et al., 1990; Taylor, 1993; Wings, 2007; Uriona et al., 2019).

Previous studies on crocodylian stomach microstructures were based only on *Alligator mississippiensis* (Eisler, 1889; Reese, 1915; Staley, 1925). This lack of knowledge of crocodylian stomach structures cannot allow determining the plesiomorphic status of archosaur "gizzard". Our study provides the first histomorphological information of the stomachs of *Crocodylus siamensis* and *Gavialis gangeticus* to test the homology of crocodylian and neornithine "gizzards". Besides, this study conducts analyses that provide new implications of the digestive function of crocodylian gastroliths. Neornithine gastrolith mass is known to be correlated with a body mass (Wings and Sander, 2007), and the relationship is utilized as a proxy for the digestive use of dinosaur gastroliths (Wings and Sander, 2007; Cerda, 2008; Lee et al., 2014). Furthermore, avian dietary habits are strongly related to the occurrence frequencies of gastroliths (Best and Gionfriddo, 1991; Gionfriddo and Best, 1996; Gionfriddo and Best, 1999). Our study tests if crocodylian gastroliths have the same relationship as observed in neornithines to assess the digestive function of crocodylian gastroliths. The clarifications of archosaur "gizzard" homology and the crocodylian gastroliths functions are expected to contribute to better understandings of crocodylian physiology and the evolutionary history of the archosaur digestive system.

MATERIAL AND METHOD

Corpora of four juvenile individuals of captive *Crocodylus siamensis* which were dead during winter are provided from a local farmer Koike Wani Sohonpo Co. Ltd. in Shizuoka Pre-
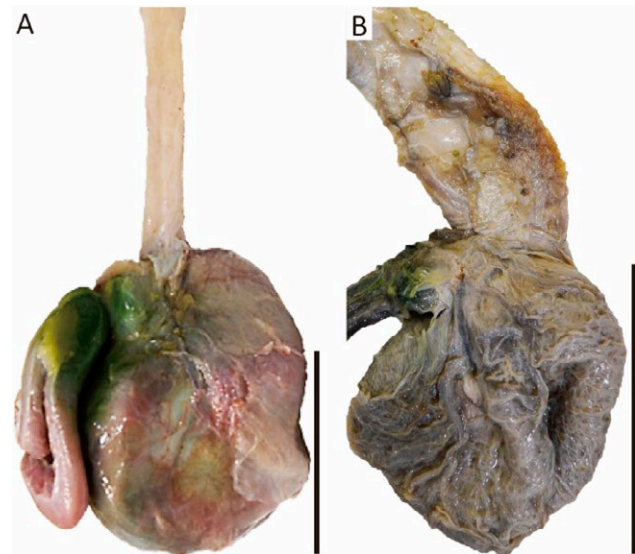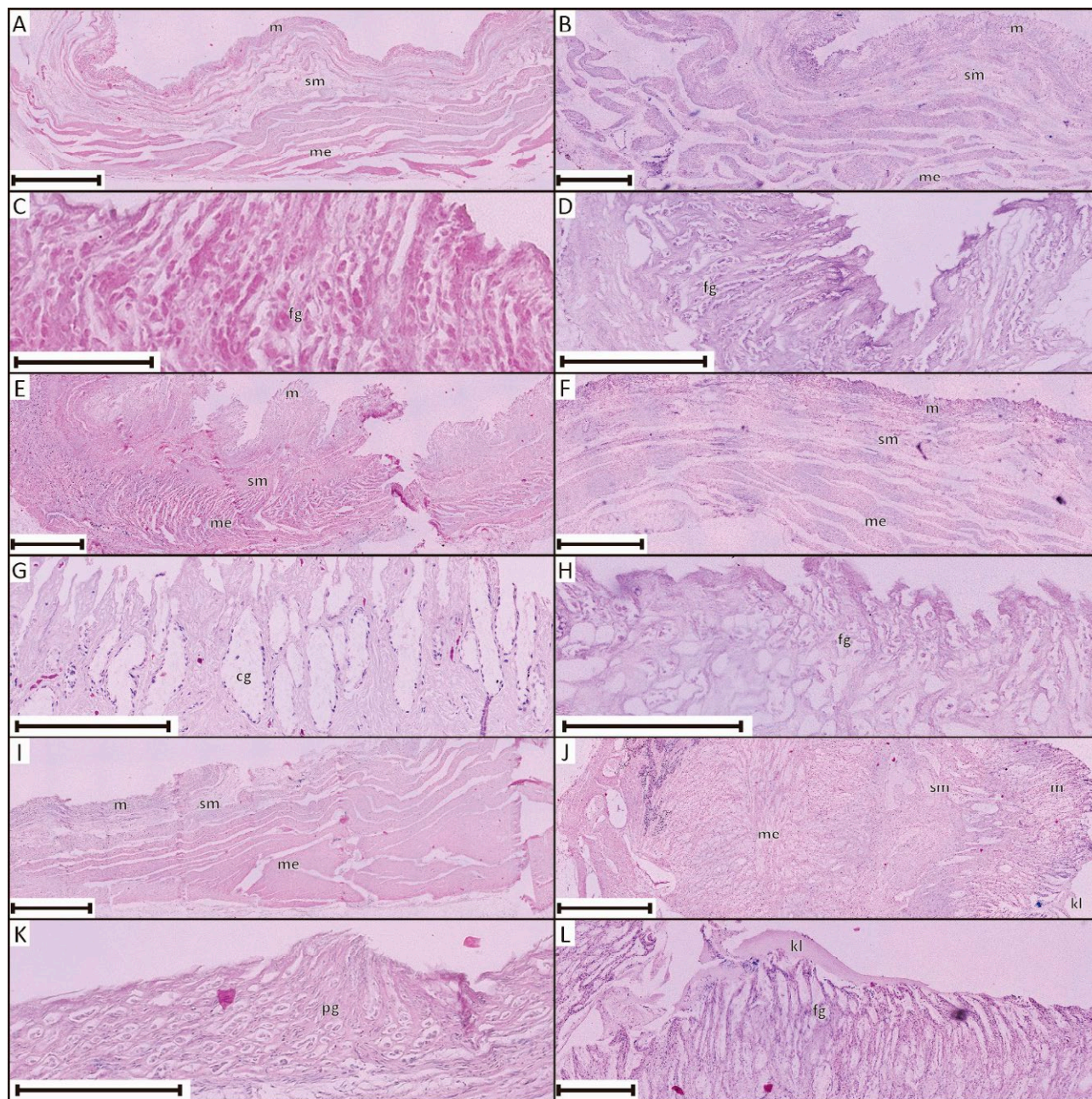

Fig. 1. Stomachs of *Crocodylus siamensis* (A) and *Gavialis gangeticus* (B). Scales: 5cm for A, 10cm for B.

fecture of Japan, and four stomachs of captive post-mortem *Gavialis gangeticus* are provided from Atagawa Tropical & Alligator Garden in Shizuoka Prefecture of Japan (Fig. 1). All the specimens were stored frozen before sampling. Small segments were sampled from the greater curvature wall, ventral wall, and pyloric wall of the stomach. The segments are fixed in 10% formalin neutral buffer solution, then dehydrated in ascending grades of ethyl alcohol, cleared with xylene, and embedded in paraffin. Sections were cut at 3μm in thickness and stained with Haematoxylin-Eosin (HE), Periodic Acid Schiff (PAS), and Alcian-Blue (AB) pH 2.5 for general histological observations. To avoid confusion due to different terminologies used in previous studies, this study uses the term "gizzard" for a stomach chamber that may possess gastroliths. Terms fundic stomach and pyloric stomach are used for first and second chambers of the crocodylian stomach, respectively. Terms proventriculus and ventriculus are used for first and second chambers of the avian stomach, respectively.

Crocodylian body and gastroliths weights are compiled from previous studies (Corbet, 1960; Cott, 1961; Kennedy and Brockman, 1965; Brazaitis, 1969; Pauwels et al., 2007). Stomach contents of crocodylians are gathered from previous studies (Corbet, 1960; Cott, 1961; Tucker et al., 1996; Platt et al., 2006; Wallace and Leslie, 2008; Platt et al., 2013). Body mass and gastroliths mass are log10 transformed and occurrence frequencies of gastroliths and different food types are arcsine transformed before statistical analyses. Statistical analyses are conducted using the software JMP version 14.3.

RESULTS

The stomach walls of all of the observed specimens are composed of 4 layers: mucosa, submucosa, muscula-

Fig. 2. Histological structures of *Crocodylus siamensis* (A, C, E, G, I, K) and *Gavialis gangeticus* (B, D, F, H, J, L). A-D, greater curvature wall; E-H, ventral wall; I-L, pyloric wall. Abbreviations: cg, compound gland; fg, fundic gland; kl, possible koilin layer; m, mucosa; me, muscularis externa; sm, submucosa; pg, pyloric gland. Scales: 1000μm for A, B, E, F, I, and J; 250μm for C, D, G, H, K, and L.

ris externa, and serosa layers from inner to outer layers (Fig. 2). The greater curvature wall is the thickest among the observed regions (Fig. 1B, 2A, 2B). Submucosa comprises nearly half of the stomach wall in thickness in *Crocodylus siamensis* (~800μm), while the muscularis externa occupies more than half of the wall in thickness in *Gavialis gangeticus* (~2000μm). The gastric folds, supported by thick submucosa, are shorter than wide in both *Crocodylus siamensis* and *Gavialis gangeticus*. The mucosa (~200μm in *Crocodylus siamensis* and ~300μm in *Gavialis gangeticus*) is thinner than submucosa and has long fundic glands in both taxa. The fundic glands are tubular and branched (Fig. 2C, 2D) although postmortem damage obscures the details. The fundic glands are
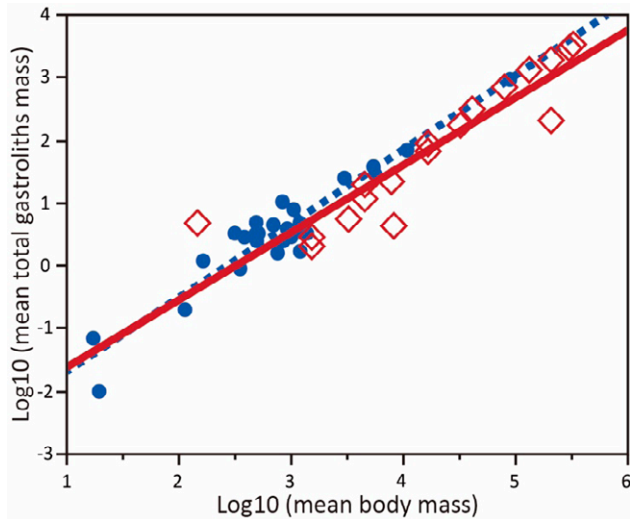
Fig. 3. Relationships of body mass to gastroliths mass in crocodylians (red diamond) and crown birds (blue circle). The red solid line represents the regression line for crocodylians and the blue dashed line represents the regression line for crown birds.

mainly composed of dark oxynticopeptic cells, as previously reported in the stomachs of *Alligator mississippiensis* (Eisler, 1889; Staley, 1925). There are no morphologically distinct mucous neck cells reported in most snakes (Jacobson, 2007).

The ventral wall is slightly thinner than the greater curvature wall (Fig. 2E, 2F). The submucosa of the ventral wall is thin, and the muscularis externa comprises the largest proportion of the ventral wall. The gastric folds are well-developed in *Crocodylus siamensis*, but it is absent in *Gavialis gangeticus*. The mucosa is proportionally thinner than it is in the greater curvature wall, resulting in shorter fundic glands than in the greater curvature wall in both taxa. The fundic gland structures are generally the same as those in the greater curvature wall. However, gastric glands in the ventral wall are markedly larger than in the other stomach walls and form a lobule-like compound gland in *Crocodylus siamensis* (Fig. 2G). These gastric glands are separated from each other with thick connective tissue. The lobule-like compound glands could not be observed in *Gavialis gangeticus*, partly because available stomachs are not well-preserved compared to *Crocodylus siamensis*.

The pyloric walls of the two crocodylian taxa are largely different from the greater curvature and the ventral walls in their extremely thick muscularis externa, which represents up to 80% of the stomach wall thickness (Fig. 2I, 2J). On the other hand, the submucosa is reduced, unlike what was observed in the fundic stomach. Muscularis mucosa is also much thicker than in

the other two regions. Pyloric glands are simple tubular glands and are significantly short compared to the fundic glands (Fig. 2K). Unfortunately, details of the pyloric glands are not available due to the impact of postmortem damage, especially in the stomachs of *Gavialis gangeticus*. The internal surface of the pyloric wall is locally covered by a PAS-positive layer in *Gavialis gangeticus* (Fig. 2L).

Body mass and gastroliths mass of Crocodylia (Table 1) demonstrates that the average proportion of gastroliths mass relative to body mass is 0.66%. The value is slightly higher than that in neornithines (0.55%), but the difference is not statistically significant (Student's t-test, P = 0.50). Regression analysis demonstrates the correlation of crocodylian body mass and gastroliths mass (Fig. 3; r^2 = 0.84, P < 0.001) as in neornithines (Wings and Sander, 2007). Neither the slope nor the intercept of the regression line differs from those of neornithines (P = 0.43 and 0.73, respectively), indicating that the relationship between gastroliths mass and body mass of crocodylians are statistically indistinctive from that of neornithines. Regression analyses on occurrence frequencies of gastroliths and different food types (Table 2) demonstrate that occurrence frequency of gastroliths are positively correlated with those of vertebrates and negatively correlated with those of most invertebrates (Table 3). The correlations are statistically significant (P < 0.05) in Insecta, Pisces, Amphibia, and Mammalia.

DISCUSSION

Histological evaluations of *Crocodylus siamensis* and *Gavialis gangeticus* stomachs demonstrate that general stomach morphology is similar to each other. Both taxa have long, tubular branched fundic glands and short, simple pyloric glands (Fig. 2). The result is concordant with the stomach microstructure of *Alligator mississippiensis* as reported in Staley (1925), indicating that members of Crocodylia share generally the same fundic and pyloric gland structures. The long, complex fundic glands and short, simple pyloric glands are also in agreement with general features of reptilian stomachs (Luppa, 1977; Jacobson, 2007). Furthermore, the lobule-like compound fundic glands that are present in the ventral wall of *Crocodylus siamensis* (Fig. 2G) are also reported in fundic stomachs of other reptiles including *Caretta caretta* (Oppel, 1896), *Chamaeleon afticanus* (Hamdi et al., 2014), *Laudakia stellio* (Koca and Gurcu, 2011), *Ophisops elegans* (Çakici and Akat, 2013), and *Varanus niloticus* (Ahmed et al., 2009). Therefore, the present observations demonstrate that general histomorphological structures of crocodylian stomach glands are concordant with those

Table 1. Mean total gastroliths mass and body mass of crocodylians compiled.

Species	Mean total gastrolith mass[g]	Mean body mass[g]	Sample size	Relative weight of gastroliths [%]	Reference (gastroliths)	Reference (body mass)
Crocodile acutus	174.00	32206	2	0.54%	Brazaitis (1969)	Brazaitis (1969)
Alligator mississippiensis	22.00	7800	1	0.28%	Kennedy and Brockman (1965)	Kennedy and Brockman (1965)
Osteolaemus t. tetraspis (Rabi oil fields)	5.54	3241	14	0.17%	Pauwels et al. (2007)	Pauwels et al. (2007)
Osteolaemus t. tetraspis (Loango National Park)	4.33	8193	8	0.05%	Pauwels et al. (2007)	Pauwels et al. (2007)
Crocodilus niloticus 0.5-1.0m	2.04	1524	101	0.13%	Cott (1961)	Cott (1961)
Crocodilus niloticus 1.0-1.5m	11.70	4518	102	0.26%	Cott (1961)	Cott (1961)
Crocodilus niloticus 1.5-2.0m	88.87	16540	76	0.54%	Cott (1961)	Cott (1961)
Crocodilus niloticus 2.0-2.5m	312.50	40900	73	0.76%	Cott (1961)	Cott (1961)
Crocodilus niloticus 2.5-3.0m	700.30	79390	69	0.88%	Cott (1961)	Cott (1961)
Crocodilus niloticus 3.0-3.5m	1321.20	131900	52	1.00%	Cott (1961)	Cott (1961)
Crocodilus niloticus 3.5-4.0m	1906.20	206500	16	0.92%	Cott (1961)	Cott (1961)
Crocodilus niloticus 4.0-4.5m	2940.40	298700	5	0.98%	Cott (1961)	Cott (1961)
Crocodilus niloticus 4.5-5.0m	3356.00	325500	3	1.03%	Cott (1961)	Cott (1961)
Crocodilus niloticus 0.3-0.5m	4.80	146	2	3.29%	Corbet (1960)	Corbet (1960)
Crocodilus niloticus 0.5-1.0m	2.87	1524	23	0.19%	Corbet (1960)	Corbet (1960)
Crocodilus niloticus 1.0-1.5m	19.79	4518	18	0.44%	Corbet (1960)	Corbet (1960)
Crocodilus niloticus 1.5-2.0m	66.80	16540	2	0.40%	Corbet (1960)	Corbet (1960)
Crocodilus niloticus 3.5-4.0m	206.50	206500	1	0.10%	Corbet (1960)	Corbet (1960)

of other reptiles, despite the unique gross morphology of crocodylian stomach among Reptilia.

The general histomorphological features of reptilian fundic and pyloric glands resemble neornithine gastric glands of proventriculus and ventriculus, respectively. Neornithine proventriculus contains highly branched compound glands that compose lobules, and the ventriculus contains simple tubular glands covered by the PAS-positive koilin layer (Ziswiler and Farner, 1972). Through stomach muscle structure comparisons, Pernkopf (1929) suggested that the reptilian pyloric stomach is homologous to the pyloric region of the mammalian stomach, which is homologous to neornithine ventriculus (Smith et al., 2000). The present results suggest that the croco-

dylian pyloric stomach is homologous with neornithine ventriculus (neornithine gizzard), whereas the crocodylian fundic stomach (crocodylian "gizzard") is homologous with neornithine proventriculus. Since crocodylian and neornithine "gizzards" are not homologous, the previous assumption that "gizzard" is synapomorphic to Archosauria (Varricchio, 2001; Fritz et al., 2011) is dismissed.

Although crocodylian and neornithine "gizzards" are not homologous, the absence of statistical difference in the body mass-gastroliths mass relationship between the two groups suggests the digestive function of crocodylian gastroliths based on previous interpretations (Wings and Sander, 2007). The relationships between gastroliths

Table 2. Stomach contents of crocodylians compiled.

Species	Body Length (cm)	SVL (cm)	Sample #	Occurrence Frequencies (%)										Reference
				Gastroliths	Insecta	Araneida	Crustacea	Mollusca	Pisces	Amphibia	Reptilia	Aves	Mammalia	
Crocodylus niloticus	<100	-	30	76.67	96.55	13.79	10.34	13.79	17.24	24.14	0.00	0.00	6.90	Corbet (1960)
Crocodylus niloticus	100-199	-	25	92.00	77.27	4.55	18.18	9.09	45.45	9.09	0.00	18.18	0.00	Corbet (1960)
Crocodylus niloticus	30-50	-	12	0.00	91.67	16.67	0.00	0.00	0.00	25.00	0.00	0.00	0.00	Cott (1961)
Crocodylus niloticus	50-100	-	142	50.00	82.39	13.38	23.94	7.04	9.86	11.97	2.82	3.52	4.93	Cott (1961)
Crocodylus niloticus	100-150	-	141	67.24	58.16	2.13	28.37	17.73	16.31	12.77	2.84	2.13	10.64	Cott (1961)
Crocodylus niloticus	150-200	-	111	82.29	26.13	0.90	10.81	22.52	37.84	0.90	7.21	9.91	10.81	Cott (1961)
Crocodylus niloticus	200-250	-	117	89.69	10.26	0.00	7.69	26.50	45.30	0.85	5.98	5.98	9.40	Cott (1961)
Crocodylus niloticus	250-300	-	129	100.00	2.33	0.00	3.10	17.83	43.41	0.00	9.30	10.85	12.40	Cott (1961)
Crocodylus niloticus	300-350	-	113	100.00	0.88	0.00	5.31	20.35	42.48	0.00	14.16	9.73	21.24	Cott (1961)
Crocodylus niloticus	350-400	-	49	100.00	0.00	0.00	2.04	12.24	44.90	0.00	20.41	12.24	26.53	Cott (1961)
Crocodylus niloticus	400-450	-	23	100.00	0.00	0.00	4.35	8.70	13.04	0.00	34.78	13.04	47.83	Cott (1961)
Crocodylus niloticus	450-500	-	12	100.00	0.00	0.00	0.00	0.00	33.33	0.00	41.67	0.00	58.33	Cott (1961)
Crocodylus niloticus	-	17.0-38.9	151	3.60	57.10	57.10	0.00	0.00	10.70	7.10	0.00	0.00	3.60	Wallace and Leslie (2008)
Crocodylus niloticus	-	39-66.3	82	20.80	45.80	41.70	8.30	0.00	12.50	4.20	4.20	0.00	4.20	Wallace and Leslie (2008)
Crocodylus niloticus	-	66.4-115.8	53	50.00	20.00	10.00	0.00	0.00	80.00	0.00	0.00	0.00	10.00	Wallace and Leslie (2008)
Crocodylus moreletii	<30	-	71	11.27	84.51	29.58	0.00	2.82	16.90	0.00	0.00	0.00	0.00	Platt et al. (2006)
Crocodylus moreletii	30.1-50	-	117	5.98	91.45	26.50	7.69	5.13	5.98	0.85	0.85	0.00	0.00	Platt et al. (2006)
Crocodylus moreletii	50.1-100	-	121	18.18	68.60	6.61	18.18	20.66	25.62	5.79	6.61	1.65	9.92	Platt et al. (2006)
Crocodylus moreletii	100.1-150	-	63	17.46	34.92	1.59	14.29	41.27	31.75	3.17	3.17	4.76	3.17	Platt et al. (2006)
Crocodylus moreletii	>150	-	48	14.58	12.50	0.00	20.83	70.83	31.25	0.00	2.08	10.42	2.08	Platt et al. (2006)
Crocodylus acutus	-	<15	19	0.00	63.16	0.00	31.58	0.00	5.26	0.00	0.00	0.00	0.00	Platt et al. (2013)
Crocodylus acutus	-	15.1-40	16	0.00	75.00	0.00	68.75	6.25	12.50	0.00	6.25	0.00	0.00	Platt et al. (2013)
Crocodylus acutus	-	40.1-65	28	28.57	14.29	0.00	89.29	3.57	25.00	3.57	0.00	3.57	3.57	Platt et al. (2013)
Crocodylus acutus	-	65/1-90	16	31.25	18.75	0.00	87.50	0.00	0.00	0.00	12.50	12.50	0.00	Platt et al. (2013)
Crocodylus acutus	-	>90	18	16.67	0.00	0.00	94.44	5.56	11.11	0.00	0.00	11.11	0.00	Platt et al. (2013)
Crocodylus johnsoni	-	10-19.9	29	59.00	66.00	48.00	0.00	0.00	10.00	3.00	0.00	0.00	0.00	Tucker et al. (1996)
Crocodylus johnsoni	-	20-29.9	62	89.00	66.00	45.00	5.00	0.00	31.00	7.00	0.00	0.00	2.00	Tucker et al. (1996)
Crocodylus johnsoni	-	30-39.9	49	82.00	59.00	31.00	10.00	0.00	34.00	16.00	0.00	0.00	2.00	Tucker et al. (1996)
Crocodylus johnsoni	-	40-49.9	43	91.00	42.00	40.00	14.00	0.00	21.00	19.00	0.00	0.00	0.00	Tucker et al. (1996)
Crocodylus johnsoni	-	50-59.9	39	87.00	33.00	41.00	5.00	0.00	13.00	15.00	3.00	0.00	3.00	Tucker et al. (1996)
Crocodylus johnsoni	-	60-69.9	24	96.00	29.00	8.00	8.00	0.00	8.00	75.00	4.00	0.00	0.00	Tucker et al. (1996)
Crocodylus johnsoni	-	70-79.9	36	94.00	11.00	11.00	6.00	0.00	3.00	56.00	8.00	0.00	6.00	Tucker et al. (1996)
Crocodylus johnsoni	-	>80	42	91.00	12.00	12.00	10.00	0.00	0.00	52.00	2.00	2.00	10.00	Tucker et al. (1996)

Table 3. Results of regression analyses between the occurrences of different food types and gastroliths.

Group	Coefficient	p-value	R^2	Correlation
Insecta	-0.659	0.002	0.280	Negative
Araneida	-0.222	0.496	0.015	Negative
Crustacea	-0.478	0.065	0.106	Negative
Mollusca	0.000	0.999	0.000	-
Pisces	0.762	0.041	0.106	Positive
Amphibia	0.407	0.228	0.047	Positive
Reptilia	1.342	0.004	0.237	Positive
Aves	0.937	0.110	0.080	Positive
Mammalia	1.398	0.000	0.352	Positive

occurrence frequency with dietary types (Table 3) further support their digestive function. The positive correlations with vertebrate diets, although supported statistically only in mammals, may suggest that gastroliths are possibly beneficial for digesting bones. Although the gastroliths might have not served as "teeth" to strongly grind ingesta as they do in herbivorous birds (Moore, 1998; Moore, 1999), they might have benefited digestion through ingesta mixing and facilitating stomach juice excretion (Wings, 2007). These functions do not contradict with other possible gastroliths functions such as buoyancy control (Taylor, 1993). Therefore, the results of this study suggest a possibility that although crocodylian "gizzard" is not homologous with that of neornithines, their "gizzard" efficiently utilized gastroliths for digestion.

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