STRUCTURE AND FUNCTION OF THE DIGESTIVE TRACT OF THE HOATZIN (*OPISTHOCOMUS HOAZIN*): A FOLIVOROUS BIRD WITH FOREGUT FERMENTATION

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ABSTRACT.—The Hoatzin (*Opisthocomus hoazin*) is a unique obligate folivorous bird with a well-developed foregut fermentation system. Its relative gut capacity is equivalent to 9% of the adult body mass (ca. 680 g). The large crop and lower esophagus represent 77% of the total gut capacity. The crop is folded into two interconnected chambers, and the lower esophagus is a multichambered organ. Both are unusually muscular with constrictions between chambers. The interior lining of the crop and esophagus has longitudinal ridges covered by cornified epithelium. The crop and esophagus are the main fermentation organs, with pH and volatile-fatty-acids levels equivalent to those found in mammals with foregut fermentation. The proventriculum and gizzard are much reduced in capacity. A combination of abrasion and microbial action effectively reduces particle size along the gut. A trial with markers made out of thin (0.6-mm) plastic film demonstrated that large particles (10 mm²) are retained longer than medium (4-mm²) or small (1-mm²) particles at the anterior fermentation sites. The extreme gut adaptations in the Hoatzin are more similar to those of small mammals with foregut fermentation than to any known bird. This suggests that a similar set of evolutionary constraints may affect the evolution of foregut fermentation in vertebrates. *Received 8 June 1992, accepted 25 November 1992.*

THE HOATZIN (*Opisthocomus hoazin*) is a Neotropical folivorous bird that inhabits oxbow lakes, flooded forests, and lowland swamps of the Guianas, Orinoco, and Amazon basins. Up to 87% of its diet consists of leaves (Grajal et al. 1989). Obligate folivory is unusual in birds because leaves are bulky, have low nutritional value, and may contain noxious chemicals. These properties are in direct conflict with the flying ability and energy demands typical of most birds. Much of the organic matter of plant tissues is structural carbohydrate in cell walls, of which cellulose is one of the main components and also is the most common organic compound in nature. Because no vertebrate produces the enzymes necessary to digest cellulose, many herbivores have enlarged chambers in their gut, where anaerobic microbes secrete enzymes that digest cellulose.

The Hoatzin is the only bird known to possess a fully-functional foregut fermentation system (Grajal et al. 1989). The voluminous crop and posterior esophagus have become functional fermentation chambers, analogous to

those of mammalian foregut fermenters. The crop and esophagus are situated in front of a greatly reduced sternal carina, and leave little area for flight muscles to attach (Fig. 1). As a result, hoatzins are not powerful fliers, preferring to hop from branch to branch (Strahl 1988). The peculiarities of Hoatzin anatomy were the subject of many early descriptive studies attempting to establish the evolutionary affinities between Hoatzins and other birds (L'Hermenier 1837, Perrin 1877, Goeldi 1886, Parker 1891, Pycraft 1895, Huxley 1868, Verheyden 1956). The presence of functional wing claws in Hoatzin chicks, the reduced sternal carina, and the poor flying abilities of the Hoatzin were regarded as the primitive characteristics of a "missing link" between the first fossil birds such as *Archaeopteryx* and modern birds (Parker 1891). Present systematic studies place the Hoatzin within the Cuculiformes (Sibley and Ahlquist 1973, 1990, de Queiroz and Good 1988, Sibley et al. 1988). Some early authors attempted to relate the large gut capacity to a folivorous diet in the Hoatzin (L'Hermenier 1837, Gadow 1891, Böker 1929). In fact, Goeldi (1886) and Young (1888) described the smell of the gut contents as resembling that of fresh cow manure. However, none of these authors suggested that fore-

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Fig. 1. Schematic representation of anterior gut of adult Hoatzin seen from left, showing (A) crop, (B) posterior esophagus, (C) proventriculus, and (D) gizzard. Anterior sternum is much reduced to make room for large fermentation chambers, resulting in drastic reduction in area available for flight-muscle attachment to (E) sternal carina; (F) "resting" pad at end of sternum used while perching with full crop.

gut fermentation was the primary function of the large gut capacity of Hoatzins.

I describe the gross anatomy and function of the gastrointestinal tract of the Hoatzin, and then compare the Hoatzin's gastrointestinal tract to other herbivorous birds and foregut-fermenting mammals. I measured the gut capacity of Hoatzins and explored relevant functions, such as particle dynamics, and nutritional and physical characteristics of gut contents. If foregut fermentation is nutritionally important for Hoatzins, one would expect gut capacity to be similar or exceed that of mammalian foregut fermenters. Also, the Hoatzin's digestive tract might be expected to reduce particle size and show selective particle retention to optimize the nutritional use of plant cell wall. Understanding the anatomy and function of the Hoatzin digestive tract can provide insights into the evolutionary limits of foregut fermentation in vertebrates and birds in particular.

MATERIALS AND METHODS

Hoatzins were shot at the following sites in the Llanos of Venezuela: Masaguaral (67°35'W, 8°34'N), Guárico River (67°28'W, 8°33'N), Suapure River (66°20'W, 6°8'N), and Piñero (68°4'W, 8°82'N). The total body mass of each bird was recorded immediately using a portable spring scale (± 1 g), after which the gastrointestinal tract was removed and weighed. The gut was divided with string knots and then cut into anterior esophagus, crop, posterior esophagus, proventriculus, gizzard, small intestine, caeca, and large intestine. The wet mass of the contents of each section was determined by subtraction of the mass of each section with and without its contents. The pH of the contents from each segment was measured *in situ* with a portable pH-meter, usually within 20 min of the bird's death. Samples from each segment were fixed with concentrated sulfuric acid and frozen in dry ice for later measurement of the concentration of volatile fatty acids. Other fresh samples were weighed and dried at 100°C until their mass remained constant for determination of percentage dry matter. Samples of the contents from some segments were fixed in buffered formalin for particle-size analysis, and the remaining contents were frozen and later dried at 60°C until their mass remained constant for nutritional analysis. Tissue samples from the gut were fixed in 10% buffered formalin for histological analysis.

Gut contents were analyzed for dry matter, cell wall, nitrogen, ash, volatile fatty acids, and particle size. Cell wall and ash content were determined following the neutral-detergent fiber (NDF) method of Goering and Van Soest (1970). Nitrogen content was

determined by the Kjeldahl method (Van Soest 1982). The concentration of volatile fatty acids was determined using gas chromatography (Wilkie et al. 1986). Mean particle size in some gut sections was measured using a computerized particle-analysis video system and a video camera mounted on a microscope. This system allowed a statistical analysis of particle size frequency. Small sample sizes at the intestine or caeca did not allow an accurate measurement of particle size, so the contents of all hindgut sites were pooled.

Particle retention at various portions of the gut was measured in a single captive adult Hoatzin. The bird was acclimated to a maintenance diet for more than 60 days (Grajal et al. 1989). The maintenance diet consisted of romaine lettuce, soybean protein powder, ground alfalfa pellets and fresh young shoots of *Enterolobium cyclocarpum*, *Pithecellobium saman*, *Guazuma ulmifolia* and *Phthirusa* cf. *orinocensis*. The Hoatzin was force-fed a gel capsule containing plastic markers made out of brightly-colored commercial flagging tape (0.6mm thickness). The inert plastic markers were cut in three sizes (10, 4, and 1 mm²) and administered in a single pulse dose (Warner 1981). The specific gravity of this material is almost one (1.01), so it resembles the specific gravity of wet food particles in the fermentation chambers (Warner 1981). The captive Hoatzin was housed in an individual custom-made metabolic cage with removable floor trays and given food *ad libitum*. All feces were collected after the pulse dose, and all markers present in the feces were counted. After 24 h of administration of the single pulse dose, the bird was killed and the plastic particles in each gut portion were counted. Acclimating Hoatzins to captivity is an expensive and time-consuming effort, so this experiment was not repeated.

Statistical comparisons of bird masses, gut contents, and mean particle size were done using two-tailed tests at the 0.05 probability level. Individual birds were considered experimental units for the tests.

All killed birds were used for other complementary experiments on *in vitro* fermentation rates, microbial population studies, and general histology (Grajal et al. 1989, Grajal in prep.) In addition, complete skeletons of these birds were prepared for museum collections and deposited at the Profauna Museum at Maracay, Aragua state, Venezuela, and the Florida Museum of Natural History at Gainesville, Florida, USA.

RESULTS

Mean body mass of adult Hoatzins was 730.7 ± SD of 38.9 g for males, and 705.9 ± 39.4 g for females, with a group mean of 716.1 ± 39.9 g. The difference between sexes was not statistically significant (Mann-Whitney *U*-test). Similarly, no significant differences in body mass

were found among capture sites or times of capture (Mann-Whitney *U*-test).

Digestive-tract morphology.—The mouth region and other regions of the gut have been partially described by early authors (Mitchell 1896, 1901, Banzhaf 1929, Böker 1929). The general structure of the bill looks more galliform than cuckoolike, which may explain the classification of the Hoatzin as a member of the Galliformes for many years (Huxley 1868, Banzhaf 1929). The bill has sharp edges that probably help in cutting leaves. The lanceolate tongue has sharp posteriorly directed papillae at its base that resemble backward-pointing spines, and probably assist in swallowing large pieces of leaves. A pair of large sublingual mandibular salivary glands (*glandula mandibularis externa* sensu McLelland 1979) are evident. Although I did not measure the composition of the saliva from these glands, it was quite thick and sticky. Other salivary glands in the corner of the mouth (*glandula anguli oris*) and in the cheeks are relatively smaller (F. Michelangeli pers. comm.). Although the salivary glands are not large, the saliva is thick and probably contains mucoproteins and buffering salts. It is not clear how Hoatzins regulate pH levels in the foregut fermentation sites, but the ridges of the interior lining of the crop increase the absorption area, diminishing the acidifying effect of volatile fatty acids accumulating in the fermentation organs. The upper esophagus is smooth, soft, and elastic, with almost no muscle. Near the entrance of the crop, the upper esophagus starts to show some inner longitudinal ridges and thick muscle tissue, resembling the upper crop.

The crop is a large muscular organ folded into two chambers and wrapped by mesenteries. The two-crop chambers are connected through a constricted zone with circular muscles that resemble the pillars found in ruminant stomachs. The crop extends ventrally and is harbored in a concave depression of the sternum keel (Fig. 1). The muscle wall of the crop is thick, with several circular muscle layers. The interior lining is covered by cornified epithelium and shows parallel longitudinal ridges and folds. The ridges are generally higher (up to 4 mm) on the ventral side of the crop, and shorter and stouter on the dorsal side of the crop. The terminal portion of the second crop chamber has the shortest ridges. The crop ends in a narrow pillar zone connecting to the posterior esoph-

TABLE 1. Volatile fatty acids (in mmol/L of contents) and pH ($\bar{x} \pm$ SD, $n = 5$). Mean pH value in proventriculus was 2.1 ± 0.3.

	Crop	Posterior esophagus	Caeca
Total volatile fatty acids (mmol/L)	114.5 ± 62.3	170.3 ± 121.0	94.7 ± 42.1
Acetic acid (%)	68.1 ± 5.8	69.8 ± 3.6	77.4 ± 0.6
Propionic acid (%)	13.2 ± 4.8	13.9 ± 1.3	13.3 ± 0.6
Butyric acid (%)	8.3 ± 2.3	7.7 ± 3.1	—
Isobutyric acid (%)	10.4 ± 1.6	8.6 ± 1.8	13.6 ± 9.5
pH	6.4 ± 0.4	6.6 ± 0.3	7.5 ± 0.1

agus. The crop contents were a heterogeneous green mixture of fully recognizable leaves, partially broken leaves and unrecognizable plant material.

The posterior esophagus also is heavily muscular and quite rigid. Its inner lining shows longitudinal ridges, but these ridges are shorter and less uniform. The posterior esophagus consists of a series of small sacculated chambers. Most of these chambers are separated by pillars and constriction zones, sometimes completely circular or otherwise resembling semilunar folds. Most of these muscular folds and constrictions are longitudinally connected, resembling short haustrations. The contents of the posterior esophagus seemed to be drier than those in the crop and were less diverse in size. Few recognizable complete leaves were present in the posterior esophagus, except small leaves, such as *Acacia* spp. (ca. 4 × 2 × 0.5 mm).

The glandular stomach or proventriculus is small, barely wider, and less muscular than the connecting posterior esophagus. An abrupt change in pH (Table 1) suggests that the proventriculus is the secretory region of gastric acids. The gizzard is also small but muscular, with a hardened keratinous inner lining. Two transverse muscle types are found in the gizzard, but none is thicker than the muscles of the crop. No grit was present in any Hoatzin gizzard, as expected, considering that the birds rarely go to the forest floor. The contents of the gizzard were thoroughly ground, and only a few leaf veins and petioles could be identified.

The small intestine is uniform in diameter. The soft and elastic intestinal walls are covered only with thin muscle layers. The small intestine is never completely full, and the contents are generally distributed in lumps. The contents in this region are dark green. Almost no recognizable plant particles can be found. The plant matter of the small intestine is mixed with

a thick, sticky mucous substance. The paired caeca are relatively small for a herbivorous bird (Inman 1973, Gasaway et al. 1975, McLelland 1979, Ziswiler and Farner 1979) and lined with thin muscle. The caeca were partially full with an homogeneous dark green-brown material with the consistency of thick pudding. The large intestine is short and not clearly differentiated from the small intestine. No obvious morphological differentiation between the large intestine and the cloaca is evident (Fig. 2). In two individuals, white mucous streaks were found
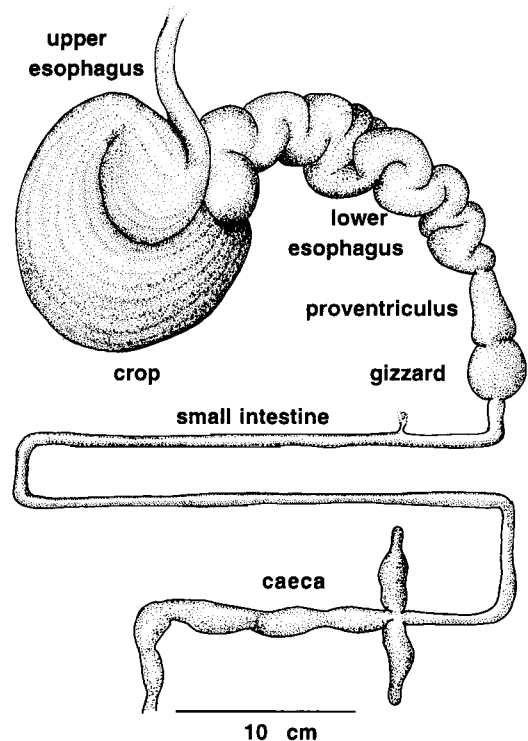

Fig. 2. Unique form and function of Hoatzin digestive tract is more like that of mammals with foregut fermentation than any known bird.

TABLE 2. Linear dimensions, relative capacity (as percent of body mass), and percent dry matter of gut contents of Hoatzins ($\bar{x} \pm$ SD, $n = 8$). Mean body mass for this sample was 712 ± 56.6 g ($n = 8$).

	Length (cm)	Relative capacity	Percent dry matter of gut contents
Crop	25	7.5 ± 1.2	22.9 ± 3.0
Posterior esophagus	15	1.4 ± 0.3	28.3 ± 2.6
Proventriculus	3	0.1 ± 0.0	27.7 ± 9.9
Gizzard	3	0.2 ± 0.0	30.8 ± 6.0
Small intestine	63	1.5 ± 0.3	20.3 ± 3.6
Caeca	3	0.3 ± 0.1	19.3 ± 1.4
Large intestine	15	0.6 ± 0.2	19.9 ± 2.2

at the end of the large intestine. Whether these streaks were thick mucous aggregations or refluxed uric acid was not determined.

Gut contents.—The fresh contents of the large crop and posterior esophagus averaged about 9% of total body mass, roughly equivalent to 77% of the mass of the total digestive-tract contents (see Table 2). The crop contents had a significantly lower percent dry matter than the young, tender leaves that constitute the typical Hoatzin diet (Mann-Whitney $U = 0$, $P = 0.006$, $n = 5$; Grajal et al. 1989). The contents of the posterior esophagus had a significantly higher percentage of dry matter than those of the crop (Mann-Whitney $U = 1$, $P = 0.016$, $n = 5$), but similar to those of the proventriculus and the gizzard. The hindgut contents had the lowest percent dry matter (Table 2).

Nutritional characteristics of gut contents were significantly different at different sections of the gut (Table 3). Cell-wall levels were significantly different among all three measured gut sections (Kruskal-Wallis one-way ANOVA, $H = 12.5$, $P = 0.002$, $n = 5$). The nitrogen content and organic matter also were significantly different among gut sections (both analyses; Kruskal-Wallis one-way ANOVA, $H = 12.5$, $P = 0.002$, $n = 5$).

Particle dynamics.—The mean particle size was significantly different at all three gut sites (Kruskal-Wallis one-way ANOVA, $H = 11.2$, $P = 0.004$, $n = 5$). Mean particle size was lower (and less variable) at the hindgut than at either foregut site. The experiment on particle retention showed that the larger the particle, the longer it remains in the anterior fermentation organs (Fig. 3). After 24 h, 92.5% of the large 10-mm^2 plastic markers remained in the crop and esophagus, none was found in the hindgut, and only a few (3.7%) were excreted (Fig. 3). The observation that almost all excreted 10-mm^2 plastic markers were folded supports the idea that there is a minimum size threshold for escape to the lower gut. The 4-mm^2 plastic markers moved similarly along the gut, but were not folded. None of the markers entered the caeca, suggesting that caecal filling can be highly selective (Björnhag 1989). Even the 1-mm^2 plastic markers may have been too large to enter the caeca, which were filled with an homogeneous thin paste.

DISCUSSION

Digestive morphology.—In the Hoatzin, obligate folivory has produced remarkable anatomical specializations (Fig. 2). Given their anatomy and function, the crop and esophagus are probably the primary organs for digestion and fer-

TABLE 3. Mean particle size (in μm) and mean values of organic matter, nitrogen, and cell wall of gut contents of Hoatzins, presented as percent of dry matter ($\bar{x} \pm$ SD, $n = 5$). Hindgut values represent pooled contents of caeca, large intestine, and lower small intestine.

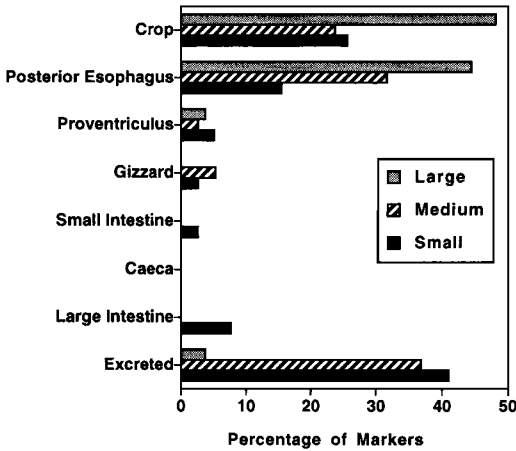|	Crop	Posterior esophagus	Hindgut
Particle size (μm)	467.2 ± 158.4	279.6 ± 122.7	138.6 ± 5.1
Organic matter (%)	92.4 ± 0.2	93.4 ± 0.2	91.0 ± 0.8
Nitrogen (%)	4.4 ± 0.1	4.7 ± 0.1	4.1 ± 0.1
Cell wall (neutral detergent fiber; %)	51.0 ± 2.3	59.3 ± 2.4	37.1 ± 3.0

Fig. 3. Percentage of plastic markers found at gut sites after 24 h from single pulse dose of 27 large (10-mm²), 38 medium (4-mm²), and 39 small (1-mm²) markers.
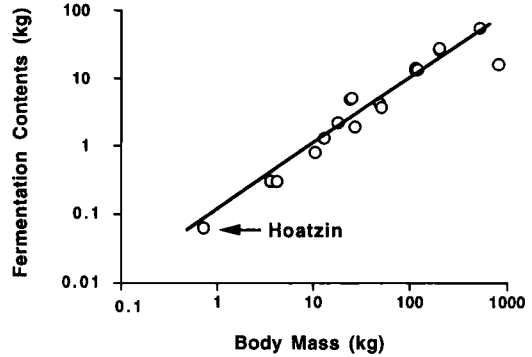

Fig. 4. Relationship between body mass (kg) and fermentation contents (kg) of wild ruminants (from Demment and Van Soest 1983). Line represents regression $\log y = -1.02 + 0.998 \log x$ ($R^2 = 0.95$). Fermentative capacity of crop and esophagus of Hoatzin falls within the 95% confidence limits of regression line.

mentation. As a consequence, the morphology of the gut is more similar to that of small mammals with foregut fermentation (Hofmann 1989) than to any known herbivorous bird. Indeed, the crop and the esophagus are the functional equivalent of multichambered fermentation organs in mammals. The relative capacities at these sites are among the largest fermentation capacities that have been reported for birds (Herd and Dawson 1984, Dawson et al. 1989), and quite similar to the relative fermentation capacity reported for mammals with foregut fermentation (e.g. Parra 1978, Demment and Van Soest 1983, 1985; Fig. 4). Similarly, the pH and level of volatile fatty acids are within the range of mammals with foregut fermentation (Table 1; Grajal et al. 1989). Since volatile fatty acids can be absorbed actively at the fermentation sites, the inner folds of the crop and esophagus increase area for absorption of volatile fatty acids and probably help in the selective passage of particles. The rich blood supply to the mesenteries that surround the crop probably enhance oxygen supply and absorption of volatile fatty acids (Dominguez-Bello et al. 1993).

The crop and posterior esophagus probably are important sites for selective retention of different gut-content fractions. Thick muscle tissues of the crop and esophagus probably squeeze the digesta, resulting in the observed gradual increase in the percent dry matter from the crop to the esophagus. The low percentage dry matter of the crop contents, relative to the average

Hoatzin diet, indicates that saliva secretions into the first portion of the fermentation chambers are significant. An abrupt change in percentage dry-matter contents between the gizzard and the small intestine seems to indicate an increased absorption of water and digestible soluble nutrients. The selective retention of solid food particles in the foregut sites is another important gut function that enhances the nutritional use of plant matter by foregut fermenters, although it has not been reported for other birds (Warner 1981). Indeed, most other birds eating a bulky diet are able to either regurgitate or pass refractory solids faster than the more digestible liquids (Duke and Rhoades 1977, Warner 1981, Levey 1986, Björnhag 1989, Levey and Grajal 1991).

Gut contents.—The large volume, pH, and concentrations of volatile fatty acids in the crop and posterior esophagus demonstrate that these are the main fermentation sites where most cell walls are broken down and microbially digested. In addition, gastric digestion of hemicellulose can be important in the overall disappearance of the cell-wall fraction (Keys et al. 1969, Parra 1978, Dawson et al. 1989). Usually, as the cell walls are broken by physical abrasion and microbial fermentation, digestible cell contents disappear rapidly. I could not discern which proportion of the cell contents is used by foregut microbes and which proportion is moved on to the lower gut to be absorbed by the host.

Levels of pH and volatile fatty acids in the paired caeca demonstrate additional fermentation in the hindgut. Caecal fermentation is probably important in water and nitrogen recycling, as well as microbial production of essential vitamins (Mead 1989, Remington 1989). Higher microbial density can explain the significantly higher levels of nitrogen and organic matter in the esophagus.

Particle dynamics.—The constrictions and sacculations of the crop and posterior esophagus are presumably important adaptations for selective particle retention (Grajal and Parra 1995). A large proportion of the large and medium plastic markers remained in the crop and esophagus after 24 h. The relatively long retention time of large plastic markers in the foregut was probably artificially high, since the markers could not be broken into smaller particles or attacked by microbes. Normally, large food particles are broken by a combination of physical abrasion and microbial fracture of the cell walls. Although these plastic markers were inert to these digestive processes, they were appropriate for measuring selective passage for two reasons. First, the specific gravity of these plastic tape markers closely resembled that of food particles. Second, the standardized sizes allowed quantification of markers by category at the various gut sites.

Particle-size reduction is an important factor in overall plant-material digestion, because smaller plant particles can be more easily attacked by fermenting bacteria. Thus, particle-size reduction in toothless vertebrates is a crucial component of cell-wall and cell-contents digestion (Bjorndal et al. 1990). Significant reductions and homogenization of particle size in the crop and esophagus probably are achieved by the combined action of muscular pressure, abrasion by the cornified lining of the crop, and microbial digestion of the cell walls. The result is a functional equivalent to the remastication that gives ruminants their name, but with the advantage that fermentation and trituration occur at the same site. Further particle reduction probably takes place in the midgut, where the combined effects of gastric digestion in the proventriculus and physical grinding in the gizzard result in significantly smaller particles at the hindgut. Even though small sample sizes did not allow measurement of particle size in the caeca, the texture of their contents and the

fact that no plastic markers were present indicate that the caeca are sites for selective entrance of fluid and small particles.

Foregut fermentation in a 680-g flying endotherm is theoretically unexpected. In most vertebrate herbivores, gut capacity scales directly with body mass, while metabolism scales with body mass at a power of 0.75 (Parra 1978, Demment and Van Soest 1983). Accordingly, an endotherm below 3 to 5 kg should not be able to support its normal metabolic requirements using foregut fermentation alone (Parra 1978, Demment and Van Soest 1983). Moreover, large fermentation chambers place an additional constraint on flying ability, because power requirements scale directly with body mass (Pennycuick 1969). The presence of a well-developed foregut fermentation system in the Hoatzin provides new insights into the morphological and functional constraints of foregut fermentation in vertebrates. Gut capacity, particle reduction, and selective retention are important characteristics for an efficient use of plant leaves as a food source. Dietary characteristics like the higher digestibility of fresh young shoots (Short et al. 1974) and the presence of secondary compounds in the Hoatzin's diet help explain the presence of foregut fermentation in the Hoatzin.

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