RESEARCH ARTICLE

Aspects of Digestive Anatomy, Feed Intake and Digestion in the Chinese Pangolin (*Manis Pentadactyla*) at Taipei Zoo

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Pangolins are considered difficult to maintain in zoos, often attributed to problems in feeding management. Taipei Zoo's designation as a wildlife rescue center for Chinese pangolins (*Manis pentadactyla*) has resulted in long term feeding experience with development of diets that support recovery, maintenance, and reproduction, as well as experimental opportunities to further understand digestive physiology to optimize nutrition. Opportunistic dissection of 10 animals revealed details of the tongue, salivary glands, stomach and gastrointestinal tract (GIT), including confirmation of anatomical differences between Asian and African pangolin species. Length of the total GIT relative to body length (~9:1) was greater than found in domestic carnivores, more similar to omnivorous species. Intake and digestion trials conducted with 4 animals demonstrated that pangolins maintained body weights (BW; 6–9 kg) consuming diets containing 32–40% crude protein, 20–25% crude fat, and 13–28% crude fiber (DM basis). Daily DM intakes ranged from ~40 to 70 g per animal, with digestible energy intake 51.5–87.5 kcal /kg BW^{0.75}/day; pangolins consumed 9.4–15.2 g DM/kg BW^{0.75}/day. Dietary energy data support observations of low metabolism and maintenance requirements for this species, similar to values reported for other myrmecophageous species. Addition of 5% ground chitin to diets improved fecal consistency, and decreased digestibility of DM, protein, and energy; addition of chitosan (chitin treated with NaOH) resulted in diet rejection. This information may assist in enhancement of captive diets, as well as in controlling obesity in pangolins. Zoo Biol. 34:262–270, 2015.

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INTRODUCTION

Pangolin comes from the Malayan word 'Pengolin' and means that the animal can roll into a bullet. There are seven species of pangolins, all of the Order *Pholidota*, Family *Manidae* and Genus *Manis*; three are found in Asia whereas the latter four are African: Chinese pangolin (*M. pentadactyla*), Indian pangolin (*M. crassicaudata*), Malayan pangolin (*M. javanica*), Cape pangolin (*M. temminckii*), Giant pangolin (*M. gigantea*), Long-tailed tree pangolin (*M. tetradactyla*) and White-bellied tree pangolin (*M. tricuspis*). In the wild, pangolins are nocturnal, and move about in search of invertebrates. During the day they sleep in underground burrows that they excavate themselves. These secretive mammals are not often exhibited in zoos because of this nocturnal behavior and due to difficulties with dietary husbandry. Pangolins were quite common in zoos before the 1970s, but many died prematurely associated with inadequate diet. Today, pangolins are infrequently exhibited in

zoos, and considered rare and difficult to maintain [Yang et al., 1999; Yang et al., 2007].

Since Taipei Zoo moved to its current location in 1987, the zoo received many pangolins from the public, experimented with pangolin diets, and currently maintains more than 20 captive animals. Successful breeding at the Taipei Zoo is likely associated with improved feeding practices, including diets described herein. Previous studies on Formosan (Chinese) pangolins emphasized morphology

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[Pocock, 1924], home range and habitat [Aoki, 1913, 1930; Aoki and Tachishi, 1940], behavior [Sonami, 1923 1924], feeding habits [Sonami, 1912, 1941; Takahashi, 1934], and anatomy [Adachi, 1939]. With the exception of the dietary husbandry summaries of Tenaza and Young [1977] and Yang et al. [2007] few references were found on topics of captive feeding [Menzies, 1963; Heath and Vanderlip, 1988] or digestive physiology of pangolins.

The main natural food of pangolins, termites and ants, contains about 4% chitin (DM basis) in the exoskeleton [Redford, 1987], which may be considered dietary fiber thus we hypothesized that pangolins may be adapted to a “high fiber” diet. Next to cellulose, chitin is the most abundant biopolymer in nature. It is found in the exoskeleton of insects and crustaceans, the endoskeleton of mollusks, and the cell walls of fungi. Chitin can be obtained from the shells of shrimp and crab through treatment with acid and alkaline; chitosan is derived by further deacetylation of chitin with strong alkaline. Both chitin and chitosan are similar in structure to cellulose, and are considered functional dietary fibers [Yuan, 2000]. The objective of this study was to understand the digestive characteristics of Chinese pangolins (*M. pentadactyla*), including digestive tract anatomy, feed intake, passage and digestibility, and animal response(s) to various diet alterations (added fiber as chitin or chitosan), in an effort to further improve captive diets.

ANIMALS AND METHODS

Gut Anatomy Measures

All pangolins used in these experiments were brought into the facility (Taipei Zoo) as wildlife rescue cases; however, due to severe physical injuries (i.e., head trauma, broken spine, crushed limbs) or sickness, they died and opportunistic necropsies were performed. Three females (♀) and seven males (♂) were dissected to investigate anatomy of the digestive tract; three animals (2 ♂, 1 ♀) were <0.5 yr of age, whereas the remainder were considered subadults or

adults. The digestive tract tissues were washed with water and total empty weights and lengths measured to the nearest 0.5 g and 0.1 cm, respectively. Body length (from the tip of the muzzle to the vent), tongue length, and intestinal canal length were measured to the nearest 0.1 cm. The mass of the body, sub-maxillary salivary glands, and empty stomach were also weighed to the nearest 0.5 g. Ratios of tongue length:body length, intestinal canal length:body length, salivary gland weight:body mass and stomach mass:body mass were calculated.

Intake and Digestion Studies

General husbandry

All pangolins used in these experiments were brought into the facility as wildlife rescue cases. After a 30-day quarantine, clinically healthy animals were selected and kept in stainless steel cages ($72 \times 60 \times 60 \text{ cm}^3$) with a $2 \times 3 \text{ cm}^2$ mesh; a stainless steel plate was placed 15 cm below the cage to collect fecal samples. Enclosure temperatures and food remains were recorded daily, body weight was measured weekly at the same time to the nearest 1 g on an LCS-12 Nagata scale.

Diets were prepared fresh (1400–1500 hr), and offered between 1630 and 1700 hr daily. Customized feeding and watering trays (diameter 25 cm; segments 10 cm high, 8 cm deep) were made of stainless steel and weighed 3 kg, with a steel frame on top to prevent young animals from falling in and drowning (see Fig. 1).

Diet ingredients

Diet 1 consisted of 200 g mixed dry powder (ground dried silkworm larvae: yeast: coconut powder in a 10:2:1 ratio), 1000 g bee larvae, 650 g apple, 450 g mealworm larvae, 200 g raw egg yolks, and 600 g water. Ingredients were mixed in a food processor, steamed, and cooled before adding 5 ml vitamin supplement (per ml: Vitamin A 1500 IU, Vitamin C 35 mg, Vitamin D 400 IU, Vitamin E 5 IU,

Fig. 1. The feeding bowl used for Chinese pangolins (*Manis pentadactyla*) at the Taipei Zoo. This bowl is also used to provide clean water.

Vitamin B₁ 0.5 mg, Vitamin B₂ 0.6 mg, Niacin 8 mg, Vitamin B₆ 0.4 mg, and Vitamin B₁₂ 2 µg). This quantity was fed to 10 animals daily, with water supplied *ad libitum*.

Diet 2 comprised 1000 g bee larvae, 650 g apples, 450 g mealworm larvae, 27 g yeast powder, 14 g coconut powder, 100 g egg yolks, 9 g calcium carbonate, 600 g water, 15 g added powdered supplement (per g: Vitamin E 120 mg, Biotin 60 µg, folic acid 2 mg, Fe 5 mg, Zn 2.6 mg, Mn 0.9 mg, and Se 0.2 mg), and 5 ml vitamin supplements (as above) for 10 animals. To determine the effect of dietary fiber on diet digestibility and fecal consistency, 5% chitin (Diet 3) or chitosan (Diet 4) were added to the Diet 2 formulation (Kiotek food grade chitin and chitosan (crab- and shrimp-shell based), Kiotek Bio-Chemical Co., LTD, Taiwan). Feces were scored qualitatively by observation as either liquid, semi-formed, or formed.

Feeding Trials

Intake

Two ♂ (8.7 kg and 7.2 kg BW) and two ♀ (6.6 kg and 5.8 kg BW) pangolins were kept in individual cages for at least seven days prior to data collection. Month 1 (Aug): each individual was fed 40 g (wet wt) Diet 1/ kg BW daily, with 4% additional water added. Month 2 (Sep), the added water was removed from the diets, and each individual was fed 40 g Diet 1/ kg BW. Months 3 (Oct) and 4 (Nov), the total amount of diet was reduced to 30 g Diet 1/ kg BW. Feed intake was recorded daily for individual animals, and body weight measured weekly (Mondays at 1500 hr).

Digesta passage

Two male (9.2 kg and 7.3 kg BW) and two female (6.9 kg and 6.0 kg BW) pangolins were kept in individual cages and fed 30 g Diet 1/ kg BW. Following a seven-day adaptation period, one gram of Cr₂O₃ per 100 g diet was administered and total feces were collected for the next four days to determine digesta passage through visual observation (green color produced by Cr₂O₃). Animal defecation was checked hourly between 0800 and 1700 h and data summarized on a 12 hr interval basis. Transit (first appearance of marker) and retention (hours from first to last appearance of marker following the pulse dose) were recorded; mean retention time (MRT) for individuals was calculated by dividing retention by two.

Digestibility

A digestion trial was carried out for 30 days with two male (9.2 and 7.3 kg BW) and two female (6.9 and 6.0 kg BW) pangolins, during which total intake and fecal output were recorded daily to calculate apparent digestibility of dry matter (DM), crude fat (CF), crude protein (CP), ash and gross energy in the diet. Animals were fed 30 g Diet 1/ kg BW daily. Sub-samples (100 g) of diet and all feces were collected, dried and ground for proximate analysis [AOAC,

2000] and gross energy measured by oxygen bomb calorimeter (Parr 1262 Calorimetry, Parr Instrument Co., Moline, IL). Digestibility coefficients were determined using the general equation:

Apparent digestibility (%) = [(Nutrient intake – Nutrient in feces)/Nutrient intake] × 100.

Fiber digestion was not addressed in this study due to limited amounts of feces for analysis.

Effect of fiber source

Six adult pangolins (two males (7–9 kg BW) and four females (6–7 kg BW)) were used in a Latin square design to test the effects of the 2 different dietary chitin sources. Diet 2, fed at 30 g / kg BW, served as control. Diets 3 and 4 comprised Diet 2, with ground chitin or ground chitosan added at 5 g/100g diet, respectively. Each experiment lasted 21 days, including a seven-day adaptation period, seven days of sample/data collection, and a seven-day washout period. The effect of the added fiber source on apparent digestibility of the diet was measured using total intake and fecal collection data as described above.

Data were analyzed by ANOVA using SAS statistical software (SAS, 6.03 ed., SAS Institute, Cary, NC), with significance set at $P < 0.05$.

RESULTS AND DISCUSSION

Anatomy of Digestive Tracts

Tongue and salivary glands

A pair of lacteous-colored submaxillary glands occurred lateral to the anterior esophagus (Fig. 2a). In adult animals, body length ranged from 38.1 to 67.5 cm and body weight ranged from 6150 to 9585 g. The submaxillary glands taken were 4.0 to 6.0 cm in length, 3.0–5.0 cm wide, and weighed 9–14 g. Adult ($n = 4$) submaxillary glands comprised a smaller percentage of the body mass compared to those of younger individuals (age <0.5 yr, $n = 3$; $P < 0.05$ see Table 1). No teeth were found inside the mouth. The styloid-shaped tongue is connected to the inner wall of the xiphisternum (Fig. 2b). The tongue of adult animals varied between 37.8 and 40.8 cm in length and 0.9–1.1 cm in width; total body length ranged from 38.0 to 67.5 cm. Adult tongues were relatively longer compared to those of younger animals ($P < 0.05$; Table 1).

Stomach

The axis diameter of adult pangolin stomachs was 7.0–9.0 cm, with the widest part 4.6–6.0 cm, and an empty mass of 51–69 g. Three distinct parts of the stomach were identified in the pangolins: the gastric sac (S), fundic gland tissue (G), and pyloric musculature (P) (see Figs. 3 and 4). The interior surface of the fundic gland region contained both smooth tissues similar to that found in stomachs of other monogastric animals, as well as a highly ridged section with

Fig. 2. Ventral view of the tongue and salivary gland of the Chinese pangolin (*Manis pentadactyla*): (a) submaxillary gland, (b) individual aperture in oral cavity and spatulate xiphoid process.

apparently expanded surface area (Fig. 4a). Occasional ulcerations were seen in the fundic gland region (Fig. 4b). Together, the fundic gland tissue was approximately 2.5–3.5 cm in diameter. The pyloric musculature comprised circular muscle tissue with a wall thickness between 1.1 and 1.6 cm. The interior surface of the stomach was covered with a yellow keratinized epithelium (Fig. 4b), similar to the structure of poultry gizzards. The pyloric sphincter was 1.0–2.0 cm in length and 0.5–1.0 cm in width (Fig. 4c).

Intestine

No cecum was present between the small and large intestine, and no substantial difference was identified between small and large intestinal tissues on gross examination (Fig. 5a). In 4 of 10 animals, however, a curve was observed at approximately 90% the length of the

intestine (Fig. 5b). At that juncture, the intestine widened from 0.8 to 1.1 cm to 1.8–2.2 cm in diameter. This may be the point of intersection between small and large intestinal tissue in pangolins; histology would be needed for confirmation. Anatomy thus varies distinctly from domestic dogs and cats, which display a cecum, and more closely resembles aspects of more insectivorous or omnivorous carnivores (aardwolves and bears, respectively; Stevens and Hume [1996]). The length of adult pangolin intestinal tracts ranged from 370.0 cm to 520.0 cm, about 8–10 times of body length; the younger animals had intestines about 7–10 times the body length, with no significant difference detected in proportion due to age (Table 1).

While some anatomical adaptations for myrmecophagy in pangolins (i.e., forelimbs for digging, a pointed snout with reduced teeth, large salivary glands) reflect those reported in other ant-eating species, the pangolin's tongue differs from that of other ant-eating specialists, with the terminal musculature attached to the inner membrane of the sternum on the ensiform process, in contrast to only the

TABLE 1. Length and weight ratios of organ to body of pangolins (*Manis pentadactyla*) at different ages.

	Age <0.5 Year	Age >0.5 Year
Body length, cm		
Mean $\pm$ SD	34.3 $\pm$ 2.5	49.4 $\pm$ 10.5
Range (N)	32.2–37.8(3)	38.0–67.5(6)
Organ length/body length $\times$ 100 (%)		
Tongue, length		
Mean $\pm$ SD	62.1 $\pm$ 4.7 ^b	89.5 $\pm$ 6.7 ^a
Range (N)	59.3–67.6(3)	82.0–97.3(4)
Intestine, length		
Mean $\pm$ SD	816.0 $\pm$ 155.0	913.2 $\pm$ 64.8
Range (N)	675.1–983.8(3)	809.2–1019.5(6)
Body weight, g		
Mean $\pm$ SD	2646 $\pm$ 801	7494 $\pm$ 1580
Range (N)	1996–3542 (3)	6150–9585(4)
Organ weight/body weight $\times$ 100 (%)		
Salivary gland, weight		
Mean $\pm$ SD	0.3 $\pm$ 0.0 ^a	0.2 $\pm$ 0.0 ^b
Range (N)	0.3 – 0.4(3)	0.2 – 0.2(4)
Stomach, weight		
Mean $\pm$ SD	1.6 $\pm$ 0.1 ^a	0.9 $\pm$ 0.0 ^b
Range (N)	1.5 – 1.6(3)	0.8 – 0.9(4)

N = sample size; ^{ab} Means in same row with different superscripts differ significantly ($P < 0.05$).

Fig. 3. External view of the stomach from Chinese pangolins (*Manis pentadactyla*), identifying the gastric sac (S), fundic gland tissue (G) and pyloric musculature (P).

Fig. 4. Internal (or luminal) view of the Chinese pangolin (*Manis pentadactyla*) (a) stomach (gastric sac (S), fundic gland tissue (G) and pyloric musculature (P)), (b) fundic gland tissue (G), and (c) pyloric musculature (P) and sphincter (PS).

sternum in anteaters [Owen, 1854]. It appears there are even anatomical differences between Chinese and African pangolin tongue structures, with the Chinese pangolin's xiphisternum spoon-shaped [Cheng, 1986] compared with a strip in African species [Doran and Allbrook, 1973].

Stomach structure was as previously reported by Imai et al. [1973]; the very muscular stomach sometimes contains gravel and grit which may assist with digestion [Cheng et al., 1986], in much the same function as a gizzard. Quantitative data on the actual occurrence of soil in the gastrointestinal tracts of ant- and termite specialists, however, or its impact on digestive physiology, are limited and details remain to be investigated (see Gull et al., [2014] for a more detailed discussion of this topic). As opposed to observations in *M. pendactyla*, no keratinous spines have been reported in the stomachs of *M. gigantea*, *M. tetradactyla*, or *M. tricuspis* [Krause and Leeson, 1974]; this appears to be a true difference between Asian pangolins and African pangolins. There is also a conspicuous sphincter at the pylorus (Fig. 4c), which may

control the rate of food leaving the stomach to ensure food is ground adequately and mixed with gastric juices. The pyloric musculature in terms of coloration and keratinization was similar to that previously reported by Cheng et al. [1986].

The length of intestines—about nine times that of the body length, is intermediate to that reported for carnivores (cats, 4×; dogs 6×) and ruminants (cattle 20×; goat and sheep 27×), and similar in comparison with omnivores such as the black bear [10×; Stevens and Hume, 1996], pig (14X) or single-stomached herbivores such as the horse (12×) [Pond et al., 1995]. Due to the chitin fiber fraction in natural diets, pangolins may require more time to digest their food compared with digesting solely protein and fat, thus the longer length of the intestines compared with carnivores may be adaptive. While the presence of chitinase enzyme has been determined in other myrmecophagous species [Jeuniaux, 1962], it has not, to our knowledge, been investigated in pangolins, so their intrinsic ability to break down chitin is still unknown.

Fig. 5. Observation of the (a) intestinal tract of the Chinese pangolin (*Manis pentadactyla*) and the curve (boxed area; close up in Fig. 5b) in the tract that may be the demarcation between small and large intestine.

Intake and Digestion

Nutrient composition of diets is seen in Table 2. Diet 1 was much lower in calcium (with an inverse Ca:P ratio) and crude fiber than the typical wild diet of pangolins, ants (Table 2), and should not be considered adequate for long term nutritional balance. Initial modifications sought to

correct this deficiency; thus changes to Diet 2 included added CaCO_3 , removal of the silkworm powder, and lower egg yolk content. Diet 3, modified from Diet 2—with further added crude fiber in the form of chitin—was more similar to the chemical composition of native ants. Diet 4 (5% added chitosan) was abandoned and not analyzed, as animals refused to eat this formulation; even reducing chitosan addition to 3% of the diet resulted in total feed refusal.

Dry matter intake (DMI) during feeding trials with Diet 1 is found in Table 3, and changes in body mass relative to digestible energy intake (DEI) are displayed in Figure 6. Females weighed 6 to 7 kg, whereas males ranged from 7 to 9 kg. All animals gained weight when Diet 1 contained a higher DM content (Aug vs. Sep), and body gains continued even when less food was offered daily (Sep vs Oct); stable weights were obtained after about a month. The daily DMI ranged from 39 to 71 g per animal, and daily DEI was calculated between 51.5 and 87.5 kcal/kg $\text{BW}^{0.75}$ /day. Thus pangolins consumed between 9.4 and 15.2 g/kg $\text{BW}^{0.75}$ /day. Overall maintenance energy requirement for adult animals averaged 67.6 ± 8.3 kcal/kg $\text{BW}^{0.75}$ /day ($\sim 282.6 \pm 34.9$ kJ/kg $\text{BW}^{0.75}$ /day), which is 80% of the estimated requirement recently determined for another myrmecophagous species, the giant anteater [Stahl et al., 2012], and 48–60% of energy requirements of the domestic dog. Earlier studies [Heath 1987] documented low metabolic rates for the Chinese pangolin (25–30% lower than placental mammal models); these dietary data support those observations. Insert Table 3 and Figure 6 about here

Diets fed to growing pangolins (average 5.5 kg after doubling BW in 15 mo) described in a published report [Heath 1987] were calculated to provide ~ 180 kcal/kg $\text{BW}^{0.75}$ /day, or about 2.5-fold the value estimated here for maintenance—estimates that would be suitably associated with mammalian growth requirements (2 to $3 \times$ basal metabolism). Thus the lower metabolism of pangolins must be recognized in feeding programs, and overfeeding should be avoided to minimize too rapid growth of young pangolins, or obesity of adults.

The inclusion of 1% Cr_2O_3 as a marker for the passage studies did not affect intakes, but turned the feces color from brown to green. Transit times ranged from 12 (1 animal) to 48 hr (2 animals) post-dosing. Passage time (first appearance

TABLE 2. Nutritional composition of mixed diets for captive Chinese pangolins (*Manis pentadactyla*) at the Taipei Zoo.

Sample	GE (Kcal/100g as fed)	DM		Nutrient (% of DM)				
		%	CP	EE	C F	Ash	Ca	P
Diet 1	141.3	22.4	44.8	29.4	3.7	3.8	0.3	0.8
Diet 2	108.5	20.5	40.0	24.6	13.0	5.5	2.5	0.5
Diet 3	106.3	24.3	32.2	19.8	27.8	4.4	2.0	0.4
Ants*		32.6	52.9	22.1	37.2	4.9	1.6	0.7

E: gross energy; DM: dry matter; CP: crude protein; EE: ether extracts; C F: crude fiber. NA = not analyzed Diet 3: Diet 2 + chitin (5% wt/ wt).

*Ants (*Crematogaster rogenhoferi*) were collected from in northern Taiwan, then dried, ground and analyzed.

TABLE 3. Individual animal variation in feed intake of Chinese pangolins (*Manis pentadactyla*) at the Taipei Zoo over a 4 mo period.

Animal ID	13 ♂	27 ♀	34 ♀	36 ♂
Body weight, g				
Begin	8740	6645	5780	7240
End	9280	6988	5980	7345
Diet treatments*	Dry matter intake, g/day			
A	61.5 ± 9.5 ^b	38.7 ± 9.3 ^c	41.2 ± 7.6 ^b	56.6 ± 10.6 ^b
B	71.3 ± 16.2 ^a	49.5 ± 9.1 ^a	47.7 ± 6.8 ^a	66.9 ± 17.0 ^a
C	61.7 ± 2.5 ^b	45.9 ± 3.6 ^b	45.9 ± 3.7 ^a	51.2 ± 1.9 ^c
D	58.5 ± 2.7 ^b	47.4 ± 3.0 ^{ab}	45.6 ± 2.8 ^a	47.9 ± 5.3 ^c

^{abc}Values in the same column with different superscripts differ significantly ($P < 0.05$).

*Individuals were fed Diet 1 (wet wt) daily in different months. A (August): 40 g / kg BW, with 4% additional water added; B (September): 40 g Diet 1/ kg BW; C (October) and D (November): 30 g Diet 1/ kg BW.

Fig. 6. Weight change (○: male, ●: female) in relation to digestible energy intake (DEI) of 4 adult Chinese pangolins (*Manis pentadactyla*) during feeding trials at the Taipei Zoo.

of color) was 12 hr, whereas retention time (first appearance to last appearance following the pulse dose) ranged from 12 to 60 hr ($n = 4$ animals) for Diet 1. Calculated MRT was 43.5 ± 14.2 hr (range 24–54; $n = 4$). This value is in accordance with those reported for particulate retention in giant anteaters (39.5 ± 10.1 hr) as well as MRT in domestic dogs and cats (~ 24 – 37 hr) weighing < 40 kg [Gull et al., 2014], suggesting similar digestive physiologic processes.

Digestibility coefficients are displayed in Table 4. There was no difference detected in digestibility of crude fat between Diets 1 and 3, but other nutrients showed significantly

decreased digestibility with added chitin. After removing the dry silkworm powder from the diet (Diet 2), the animals' feces became darker (Fig. 7b), but were still not solidly formed until chitin was added (Fig. 7c). Addition of psyllium seed powder to pangolin diets, reported by Heath [1987], also resulted in improved stool quality thus it seems apparent that addition of some type of physical fiber may be important to maintain gastrointestinal function in this species. Inclusion of peat or ground chitin to diets has also been reported to improve fecal consistency in tamanduas and anteaters [Dierenfeld et al., 1995 Wyss et al., 2013; Gull et al., 2014].

Apparent digestibility coefficients for specific nutrients in Diet 1 fed to the pangolins were high, especially crude fat and energy (both $> 90\%$). The ability to digest fat was similar to that expected for dogs ($> 90\%$) [Huber et al., 1986]. The results suggest that pangolins can utilize dietary fat effectively, which may lead to obesity if the fat content of the diet is too high. Unfortunately, fiber digestion was not addressed in this study due to limited amounts of feces for analysis, and the fact that we were originally seeking only to decrease energy and fat digestibility with the added dietary fiber in an effort to limit obesity.

Various studies document the efficacy of added dietary chitosan in reducing fat digestibility, thus energy intake [i.e., Deuchi et al., 1994; Razdan and Pettersson, 1994]. However, the addition of chitosan to pangolin diets at either 3 or 5% (by weight) to Diet 2 resulted in diet rejection by all individuals. The chitosan may alter diet palatability associated with its distinct odor or possibly a chemical reaction between the compounds in the chitosan powder and diet ingredients (the

TABLE 4. Digestion coefficients (mean ± SD) for Chinese pangolins (*Manis pentadactyla*) ($n = 4$ or 6) fed standardized diets at the Taipei Zoo.

Treatment	DM	EE	CP	Ash	GE
Diet 1	88.8 ± 1.0 ^a	95.9 ± 0.9 ^a	86.4 ± 1.6 ^a	68.0 ± 5.6 ^a	91.0 ± 1.1 ^a
Diet 2 Diet 3	85.0 ± 2.1 ^a	90.9 ± 2.1 ^b	85.7 ± 1.9 ^a	49.9 ± 5.5 ^b	88.4 ± 1.3 ^b
	67.3 ± 3.4 ^b	94.4 ± 2.1 ^a	68.2 ± 3.8 ^b	34.2 ± 12.1 ^c	73.5 ± 2.0 ^c

M: dry matter; EE: ether extracts; CP: crude protein; GE: gross energy. Diet 3: Diet 2 + chitin (5% wt/wt).

^{abc}Values in the same column with different superscripts differ significantly ($P < 0.05$).

Fig. 7. Fecals of Chinese pangolins (*Manis pentadactyla*) fed Diet 1 (a) with silkworm powder and (b) after silkworm powder was removed from the diet. Note the darker color without ilkworm powder. (c) The fecal of a Chinese pangolin (*Manis pentadactyla*) after adding 5% chitin powder into the diet.

color of diet became black). In either case, chitosan was shown to be unsuitable as a fiber additive for pangolins. Although stereochemistry of chitosan is similar to chitin [Yuan 2000], chitosan (as a derivative of chitin) is a smaller molecule and produces suspensions of lower viscosity [Rao and Stevens, 2005], depending particularly on the degree of deacetylation. Chitin, as a dietary fiber source, is insoluble, whereas chitosan is variably soluble in aqueous acidic solutions [Dutta et al., 2004], thus both physical characteristics [Maezaki et al., 1993] and organoleptic properties could vary substantially between these two compounds.

The addition of powdered chitin decreased apparent digestibility of DM, CP, ash, and gross energy, but had no apparent effect on fat digestion of a 20% fat diet (DM basis) in pangolins. These findings contrast with results reported when chitin (comprising 15% or 25% dietary ADF) was added to the diet for another insectivore, the African white-bellied hedgehog (*Atelerix albiventris*). In that study, DM and CP digestibility were not affected by fiber inclusion, and the digestibility of fat increased in the high fiber treatment diet (containing 30% fat) compared to the control diet (with 40% fat) [Graffam et al., 1998]. Possible interactions of passage rates with dietary differences may underlie these disparate results, but were not quantified, thus remain speculative. Nonetheless, addition of chitin may be a practical method to control the weight of captive pangolins fed a highly digestible diet, if only through nutrient dilution. Further, addition of 5% ground chitin resulted in improved fecal consistency, assessed visually.

Although diets fed in this study were typical of those historically used for feeding captive insectivorous species (i.e., complex wet mixtures), there is no apparent reason to provide a liquid diet to pangolins. They freely drink [Menzies, 1963] and will also consume semi-moist as well as dry diet ingredients [Heath, 1987]; the need for dietary bulking agents may possibly be reduced with higher dry matter diets. Because diarrhea and gastrointestinal imbalances are reported regularly for various insectivores [see, for example, Gull et al., 2014], further studies of impacts of both physical and chemical characteristics of diets are warranted.

CONCLUSIONS

Unique characteristics of digestive anatomy that may be adaptive for consumption of an insect-based diet were confirmed through dissection of ten Chinese pangolins, including specialized attachment of the tongue musculature, keratinized spines in the stomach epithelium, and a longer, yet simple intestinal tract compared with domestic carnivores.

- 1 Gut retention times of 12–60 hr for particulate material suggest a physiology that is similar to that measured in other carnivores with analogous gut anatomy, including dogs and cats, as well as the giant anteater.
- 2 Daily DM intakes ranged from 39 to 71 g per animal, and daily maintenance energy intakes (DEI) were low, associated with reported low metabolism in this species. Feeding programs should take into account the low metabolic rates of pangolins in determining amounts of diet to feed on a daily basis.
- 3 Addition of 5% ground chitin to diets improved fecal consistency, and decreased digestibility of dry matter, protein, and energy and thus may be helpful to control obesity in this species.

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