

**The Comparative Gastrointestinal Morphology of *Jaculus jaculus* (Rodentia)
and *Paraechinus aethiopicus* (Erinaceomorpha)**

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Abstract

Jaculus jaculus (Lesser Egyptian jerboa) and *Paraechinus aethiopicus* (Desert hedgehog) are small mammals which thrive in desert conditions and are found, amongst others, in the Arabian Peninsula. *J. jaculus* is omnivorous while *P. aethiopicus* is described as being insectivorous. The study aims to describe the gastrointestinal tract (GIT) morphology of these animals which differ in diet and phylogeny. The GITs of *J.*

Jaculus (n=8) and *P. aethiopicus* (n=7) were weighed, photographed, and the length, basal surface areas and luminal surface areas of each of the anatomically distinct gastrointestinal segments were determined. The internal aspects of each area were examined and photographed while representative histological sections of each area were processed to wax and stained using haematoxylin and eosin. Both species had a simple unilocular stomach which was confirmed as wholly glandular on histology sections. *P. aethiopicus* had a relatively simple GIT which lacked a caecum. The caecum of *J. jaculus* was elongated, terminating in a narrow cecal appendix which contained lymphoid tissue on histological examination. The internal aspect of the proximal colon revealed distinct V-shaped folds. Stomach content analysis of *J. jaculus* revealed mostly plant and seed material and some insects, whereas *P. aethiopicus* samples showed plant material in addition to insects, indicating omnivorous feeding tendencies in areas where insects may be scarce.

Key words: Gastrointestinal tract; mammals; morphology; Saudi Arabia, *Jaculus jaculus*, *Paraechinus aethiopicus*

Introduction

Jaculus jaculus (Lesser Egyptian jerboa) and *Paraechinus aethiopicus* (Desert hedgehog) are two small mammals belonging to the orders Rodentia and Erinaceomorpha, respectively. *J. jaculus* belongs to the super family Dipodidea, in contrast *P. aethiopicus* is from the family Erinaceidae (Nowak & Paradiso, 1983; Wilson & Reeder, 2005). These animals are distributed in most areas of North Africa,

western Iran, and are commonly found within the desert regions of the Arabian peninsula (Harrison & Bates, 1991; Qumsiyeh, 1996). Unlike *Jaculus orientalis*, which is described as social, both *J. jaculus* and *P. aethiopicus* are solitary (Qumsiyeh, 1996). The gastrointestinal tract (GIT) of mammals is adapted to optimize food digestion specific to preferred forage. In insectivores, the GIT functions to handle easily digestible protein. Consequently, post gastric fermentation mechanisms are unnecessary and the intestinal tracts are often simple without much specialization (Stevens & Hume, 1995; Langer, 2002). In contrast, herbivores often have highly specialized fore- or hind guts to allow for fermentation mechanisms, as auto-enzymatic digestion alone is not an efficient means to break down high fiber forage (Clauss et al., 2010). Vorontsov (1967) demonstrated the variability of the GIT between rodent species and that gastrointestinal specialization occurs both in the foregut and hindgut. Langer (2002) concluded that specialization of the tract is found at the site of fermentation in the GITs of rodents that consume a high cellulose diet. Numerous studies have been conducted on the gastrointestinal morphology of mammals from various regions (Behmann, 1973; Perrin & Curtis, 1980; Langer, 1984; Langer, 2002; Lovegrove, 2010), but little is known about the GIT morphology of the species in the present study. In a comprehensive study on rodent intestinal morphology, Behmann (1973) briefly described the GIT anatomy of two *J. jaculus* specimens. Through observational studies Nowak and Paradiso (1983) reported *J. jaculus* as an omnivorous species consuming a variety of seed, plant and insect material whereas *P. aethiopicus* is recorded as being insectivorous (Harrison & Bates, 1991). Both species thrive in dry and arid desert regions where water and food are limited. As *P. aethiopicus* eats mainly insects, a simple GIT without a caecum is to be expected as observed in other small insectivores including *Crocidura cyanea*

(Reddish-grey Musk shrew) and *Amblysomus hottentotus* (Hottentot Golden mole) (Boonzaier et al., 2013). A more complex GIT is expected for *J. jaculus* which consumes both plant and animal material as observed in other small omnivorous rodents including *Acomys spinosissimus* (Southern African spiny mouse) (Boonzaier et al., 2013), *Meriones rex* (King jird), *Meriones libycus* (Libyan jird), *Acomys dimidiatus* (Eastern spiny mouse) and *Acomys cahirinus* (Egyptian spiny mouse) (Walters et al., 2014). It would be assumed that gut morphology of these species, specifically the hindgut, would be anatomically adapted to have longer colons for the conservation of water, as seen in *Parotomys branstii* (Brant's whisteling rat), *Parotomys littledalei* (Littledale's whisteling rat), and *Otomys unisulcatus* (Karoo bush rat) (Jackson & Spinks, 1998). The present study therefore aims to provide detailed descriptive and morphometric analyses of the GIT, including stomach content analyses of these two species. The study will provide details as to whether gastrointestinal morphology of these species is constrained by diet, ecological niche or phylogeny.

Materials and Methods

Intact gastrointestinal tract (GIT) specimens used in this study were obtained from animals which were captured in the wild from the central parts of Saudi Arabia for an unrelated study. Capturing and euthanasia of animals was carried out with permission from the Saudi Wildlife Authority and with ethical approval from the University of Pretoria (UP). Carcasses were fixed by perfusion and subsequent emersion using 4% paraformaldehyde. The total body mass of the animals was recorded prior to removal of the abdominal GIT (from the distal part of the esophagus to the distal colon). All

species were identified by genetic profiling and blasting against sequences on GenBank (www.ncbi.nlm.nih.gov/genbank/). Species information can be found in Table 1. The measurements were conducted as described by Walters et al., (2014).

Table 1: Species information, including the origin of the fixed GITs, mean GIT mass (intact) and body mass (\pm Std. Dev.)

Species	n	Mean BM (g)	Mean GIT mass (intact) (g)	Proportional GIT mass to total BM (%)
<i>Jaculus jaculus</i> (Linnaeus 1758)	8	56.50 \pm 7.75	5.88 \pm 1.01	10.50 \pm 1.64
<i>Paraechinus aethiopicus</i> (Ehrenberg 1832)	7	409.29 \pm 55.37	31.21 \pm 12.15	7.53 \pm 2.45

Intact filled GIT specimens were weighed, adhering mesenteries removed and photographed. Length measurements of each anatomically distinct gastrointestinal segment (stomach, small intestine, caecum and colon) were taken along the anti-mesenteric border using a pliable non-stretchable cord. Stomach length measurements were taken on the greater curvature of the stomach from the fundus to the pylorus. The mean lengths of the anatomically distinct parts were expressed as a percentage of the total GIT length.

The mean circumference of each anatomically distinct segment was determined by taking circumference measurements at three different points in each anatomically distinct region and multiplied with the length to determine the basal surface area (BSA) of each segment. All measuring methods remained constant for each sample.

Histological samples of *J. jaculus* (n=6) and *P. aethiopicus* (n=6), were harvested for each specimen at the fundus and corpus region of the stomach; proximal, middle and

distal portion of the small intestine, the proximal and distal end of the caecum and proximal and distal segments of the colon (Figure 1A). Due to the lack of a caecum in *P. aethiopicus*, samples were taken of the fundus and corpus region of the stomach and proximal, middle and distal portions of the combined small and large intestine (Figure 1B).

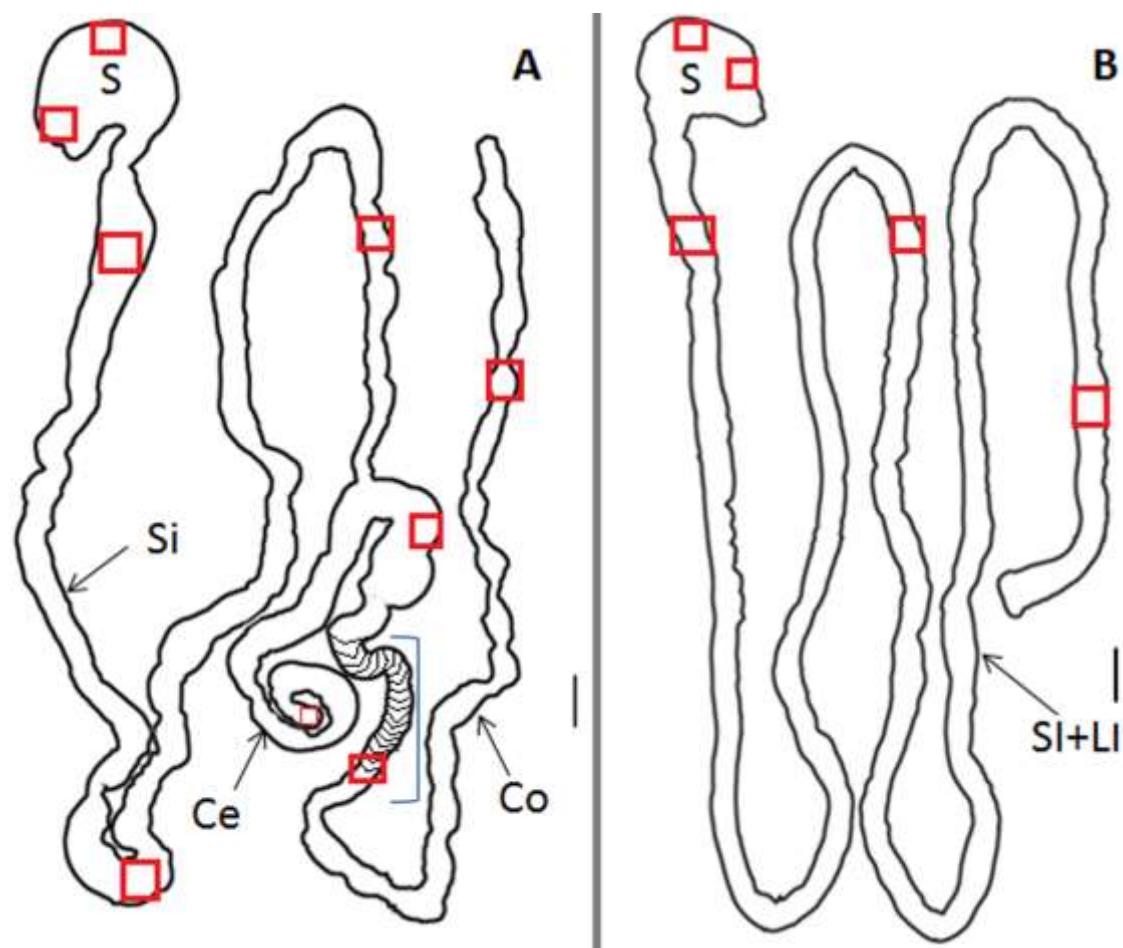


Figure 1: The GIT of *J. jaculus* (A) and *P. aethiopicus* (B) the site of tissue harvesting is indicated by squares. For *J. jaculus* tissue was taken from the fundus and corpus of the stomach (S), proximal middle and distal portions of the small intestine (Si), proximal and distal end of the caecum (Ce) and the proximal and distal end of the colon (Co). The blue parentheses indicates the V- shaped mucosal folds in the proximal colon. For *P. aethiopicus* tissue was acquired from the fundus and corpus of the stomach (S)

and from the proximal middle and distal portions of the combined small and large intestine (SI+LI). Bar= 1 cm

Samples were routinely processed, embedded in paraffin wax, sectioned at 5 μ m and stained using Haematoxylin and Eosin (H&E). Each serial section was photographed using the Zeiss Axioskope 2 light microscope. Microscopic measurements of the outer surface and epithelial surface length were conducted for each distinct gastrointestinal segment using the NIS Elements Basic Research (version 3.10) imaging software. By dividing the epithelial surface length with the outer surface length, a surface enlargement factor (SEF) was found for each individual gastrointestinal segment. By multiplying the BSA with the SEF, the luminal surface (LSA) was determined in order to account for the effect that the villi and folds have on the surface area of the GIT.

When available, stomach contents were removed, processed to wax, sectioned at 9 μ m in thickness and stained using H&E. The stomach content was photographed and analyzed using a Zeiss Axioskope 2 light microscope. The area of recognizable tissue was measured in μm^2 . Material was sorted into recognizable seed, plant and animal material as seen in Walters et al., (2014). Unrecognizable tissue was excluded from calculations. The sum of the surface area of a specific type of tissue on each slide was calculated and given a percentage of the total sum of the surface area of recognizable tissue.

When macroscopically visible and undigested contents was found, it was sifted using gauze and distilled water and was sorted in related groups (seeds, grasses, insects etc.), and photographed using the Leica GLS 100 dissecting microscope in both species.

The length, BSA and LSA of each species was calculated for each GIT segment. For statistical analysis Statistica version 12 (Copyright © Statsoft, 2014) was used. Normal probability plots were prepared to determine the distribution of data. The raw data was plotted and compared against a theoretical normal. Descriptive statistics were performed while mean values, standard deviation and standard errors were obtained. An analysis of variance (ANOVA) was performed to determine the statistical significance of the data. For verification purposes Lavene's test for homogeneity of samples was performed to calculate p-values. A p-value <0.05 was taken to be significant. The length, BSA and LSA were correlated against the total body weight of each specimen using Pearson and Spearman correlations.

Results

Descriptive morphology

Macroscopically, the intestinal tract morphology of the two species differed greatly. *P. aethiopicus* had a relatively simple GIT compared to *J. jaculus* due to the lack of a caecum. Consequently, for *P. aethiopicus* the GIT was divided into two parts for descriptive purposes, namely the stomach and the combined small and large intestine (SI+LI) (Figure 1B).

Both species displayed simple, single chambered, wholly glandular stomachs with a macroscopically visible transition of stratified squamous epithelium to glandular stomach epithelium at the cardio-esophageal junction. Elongation of the pylorus was visible in *P. aethiopicus*. There was no transition in the type of epithelium between the fundus at the corpus regions in both species (Figure 2).

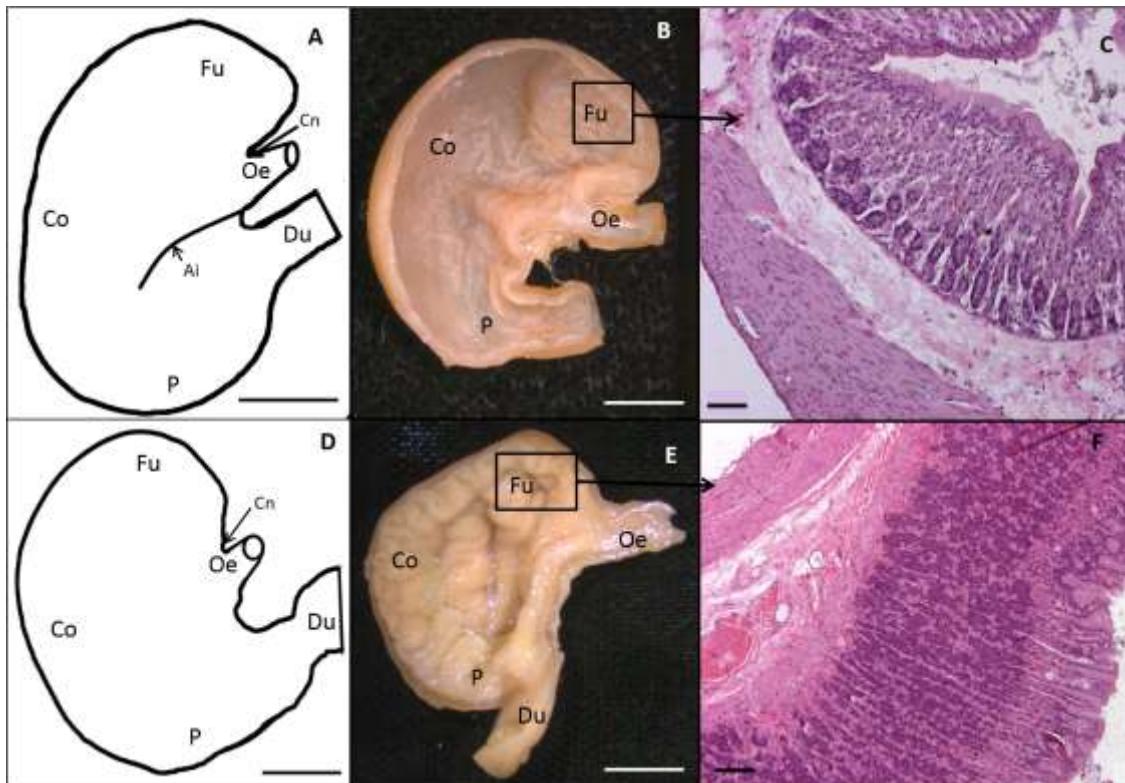


Figure 2: The macroscopic and microscopic stomach morphology of *J. jaculus* (A, B and C) and *P. aethiopicus* (D, E and F). Oe= Esophagus, Fu= Fundus, Co=Corpus, P= Pylorus, Du= Duodenum, Cn= cardiac notch and Ai= angular incisure. Bar on A, B, D and E = 1 cm. Bar on C and F = 100 μ m.

In *J. jaculus* a distinct widening of the duodenum just distal to the pyloric region was a constant feature in all samples (Figure 3A). Histologically, the small intestine demonstrated finger-like villi throughout the gastrointestinal segment, while in *P. aethiopicus* the villi were leaf-shaped. Both the proximal and middle segment of the GIT of *P. aethiopicus* demonstrated characteristic leaf-like villi however this was absent in the distal segment. In four of the six samples the ileo-caecal opening was directly adjacent to the caeco-colic opening (Figure 3B) while in two samples these openings were comparatively far apart (Figure 3C).

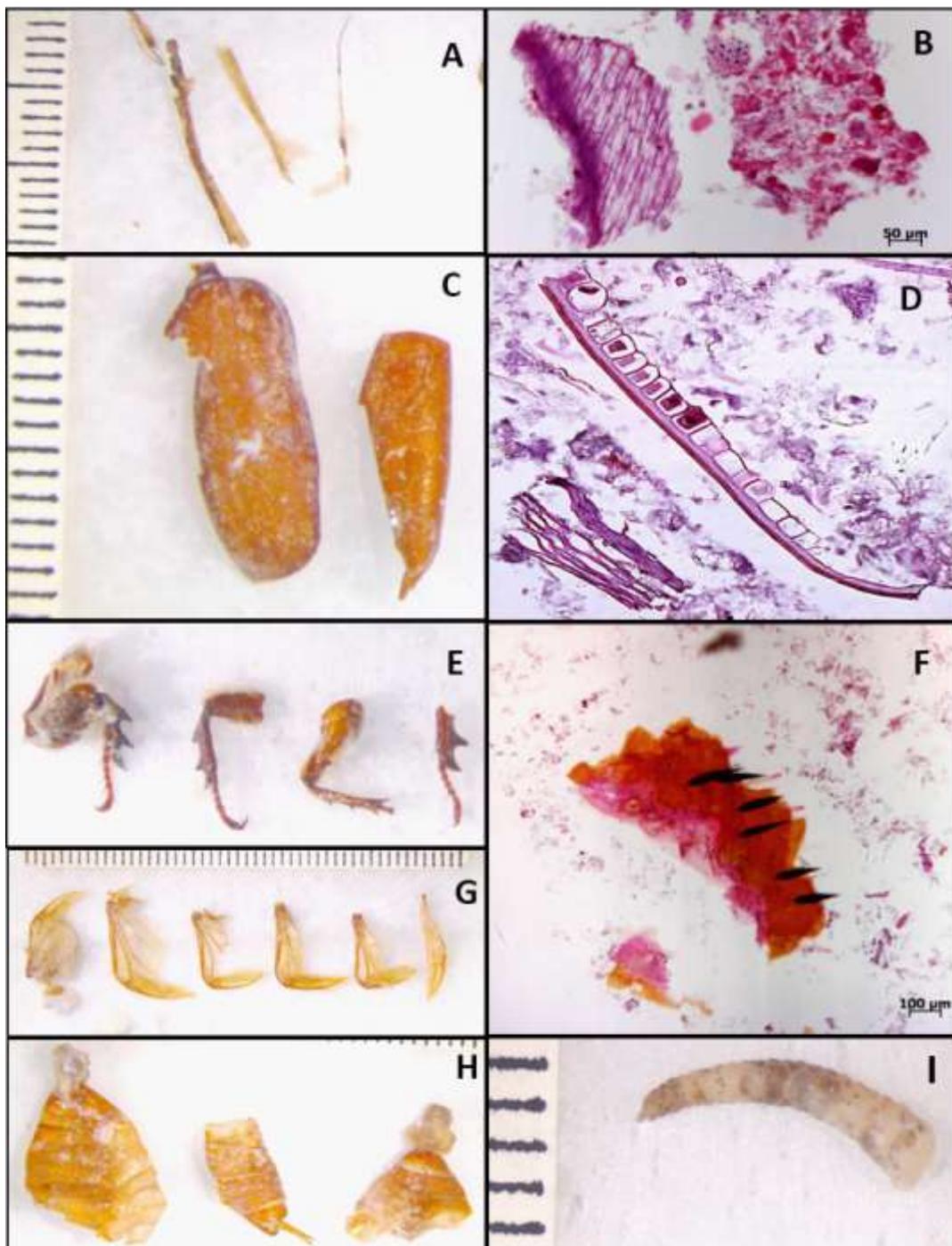


Figure 3: Macroscopic features of the GIT of *J. jaculus* and *P. aethiopicus*: (A) The stomach and widened duodenum of *J. jaculus*. (B) The ileo-caecal and caeco-colic openings in *J. jaculus* situated close together (red arrow). (C) The ileo-caecal and caeco-colic openings situated far apart. (D) Macroscopically visible lymphoid aggregations in the cecal appendix of *J. jaculus* (red arrows). (E) Histology section of the cecal appendix showing a lymphoid aggregation (red arrow). (F) The macroscopically visible V-shaped fold in the cecal appendix of *P. aethiopicus*. (G) Macroscopic view of the cecal appendix of *P. aethiopicus*. (H) Macroscopic view of the cecal appendix of *P. aethiopicus*. (I) Histology section of the cecal appendix of *P. aethiopicus*.

shaped colonic mucosal folds of *J. jaculus*. (G) Mucosal folds shown on a histological section. (H) Two colonic loops indicated by the red arrowheads in the *Jaculus*. (I) Longitudinal colonic folds of *P. aethiopicus* (red arrow). S=Stomach, Du=Duodenum, Si=Small Intestine, Ce=Caecum, Ap= Cecal appendix, Co= Colon, Prox= Proximal, Dist= Distal. Bar= 5mm Histology bar=100 μ m

The caecum of *J. jaculus* was long and spiraled whilst the narrowed tip resembled a cecal appendix (Figures 3 B, C). The latter showed distinct lymphoid aggregations which were visible macroscopically and confirmed on histology (Figure 3 D, E).

Internally, distinct V-shaped mucosal folds were observed in the proximal colon of *J. jaculus* with the tip of the V directed distally (away from the cecum). These folds were observed on average up to 112 mm from the caeco-colic opening (Figures 1, 3F, G), continued for around 305 mm after which it stopped abruptly. Fecal balls were observed in the distal colon. Externally distinct taenia and haustra were absent in the colon of *J. jaculus*. The colon was arranged in a double loop (Figure 3H) connected by a short mesenterial fold in five samples and a single loop in three samples.

Macroscopically visible villi were absent in the most distal segment of the intestinal tract where distinct longitudinal mucosal folds were seen in all *P. aethiopicus* samples (Figure 3I).

Statistical analysis

Statistical significance was observed between anatomically distinct gastrointestinal segments of both species (Table 2). Correlations showed the length of the caecum to be significantly ($p= 0.035$) longer in *J. jaculus* when correlated with the absolute body mass of the species. The BSA of the colon was significantly larger ($p= 0.024$) when

correlated in the *Jaculus* samples. For the *Paraechinus* species significant differences were seen in all areas of the tract unlike *J. jaculus* (Table 2).

Table 2: The average length, Basal Surface Area (BSA), Surface Enlargement Factor (SEF), proportional Luminal Surface Area (LSA) (%) and standard deviations (\pm) of the different gastrointestinal segments of *J. jaculus* and *P. aethiopicus*.

Proportional mean Lengths (%)	<i>Jaculus jaculus</i>	<i>Paraechinus aethiopicus</i>
Stomach	6.80 ± 0.83^d	7.88 ± 2.24^a
Small intestine	47.30 ± 1.72^a	—
Caecum	16.62 ± 1.43^c	—
Colon	29.30 ± 1.70^b	—
SI + LI	93.20 ± 0.83	92.12 ± 2.24^b
Mean total GIT length (mm)	584.63 ± 82.06	954.14 ± 345.19
Proportional mean BSA's (%)		
Stomach	6.70 ± 6.43^c	17.58 ± 4.00^a
Small intestine	20.22 ± 14.35^a	—
Caecum	11.24 ± 9.74^{bc}	—
Colon	13.37 ± 11.30^b	—
SI + LI	44.83 ± 34.43	82.42 ± 4.00^b
Mean total GIT BSA (mm²)	29823.82 ± 20651.08	23006 ± 11252.85
Average SEF		
Stomach	1.79 ± 0.50^b	1.69 ± 0.54^a
Small intestine	1.79 ± 0.50^a	—
Caecum	2.25 ± 0.59^b	—
Colon	1.90 ± 0.48^b	—
SI+ LI	93.20 ± 0.83	92.12 ± 2.24^b
Proportional LSA (%)		
Stomach	5.60 ± 1.387^c	12.55 ± 2.24^a
Small intestine	67.42 ± 8.72^a	—
Caecum	12.79 ± 3.47^b	—
Colon	14.20 ± 5.50^b	—
SI+ LI	94.40 ± 1.30	87.45 ± 6.03^b
Average total GIT LSA (mm²)	31784.79 ± 9338.99	62749.92 ± 34210.37

Stomach content analysis

A variety of plant, seed and insect material was observed in both species suggesting an omnivorous diet. Histological assessment of both species suggested a predominantly herbivorous diet of plant and seed material, while some animal material (insect or otherwise) was visible microscopically (Figure 4). Descriptive analysis of the stomach contents is found in Table 3. One sample of *P. aethiopicus* contained large amounts of



Figure 4: Macroscopic and microscopic images of the stomach content of *P. aethiopicus* including plant material (A and B), seed (C, D) and insect material (E, F, and G, H). Image (I) shows a small vertebrate tail (presumed to be the tail of a small lizard).

Table 3: The proportional amounts (%) and standard deviations (\pm) of plant, seed and animal material found in stomach contents of the different species.

Species	n	Plant %	Seed %	Animal %
<i>Jaculus jaculus</i>	5	49.75 \pm 8.80	46.57 \pm 8.80	3.67 \pm 8.80
<i>Paraechinus aethiopicus</i>	3	40.96 \pm 9.80	30.41 \pm 9.80	28. 62 \pm 9.80

undigested plant, seed, insect and vertebrate material (Figure 4). The stomach content of the *J. jaculus* specimens examined here contained less animal matter than that of *P. aethiopicus*.

Discussion

Multiple factors influence gastrointestinal morphology including body mass, diet, phylogeny and the frequency of food intake (Kararli, 1995; Stevens & Hume, 1995; Langer, 2002; Clauss et al., 2007). The two species presented here differ in taxonomy, diet and GIT morphology; the complexity of the *Jaculus* GIT to that of *P. aethiopicus* demonstrate that gastrointestinal morphology does not influence the success of these species in arid environments. In fact diet, behavior, life history and body size are factors that are also considered for the success of species in any environment (Stevens & Hume, 1995; Langer, 2002). Observational studies reported that the rodent *J. jaculus* consumes a combination of seed, plant and insect material whereas *P. aethiopicus* belongs to the order Erinaceomorpha and consumes predominantly insects (Nowak & Paradiso, 1983; Harrison & Bates, 1991; Wilson & Reeder, 2005). Stomach content

analysis provides an indication of the diet consumed by these species at the time of death and would be influenced by the digestibility of contents, the availability of food, and the area of capture (Walters et al., 2014). In the present study, *P. aethiopicus* showed varying amounts of seed, plant, and animal material in the stomach content. The discovery of a lizard tail, presumably the Common Fan-footed gecko (*Tyodactylus hasselquistii*) which is commonly found in the area, implies that the hedgehog is not only insectivorous as described in Harrison and Bates (1991). This signifies that *P. aethiopicus* could have opportunistic tendencies to include animal prey much like *Acomys dimidiatus*, *Acomys cahirinus* and *Meriones libycus* (Harrison & Bates, 1991; Wilson & Reeder, 2005; Walters et al., 2014).

P. aethiopicus showed gastrointestinal simplicity compared to *Jaculus* as it lacks a caecum, in line with the high protein content in its diet. The absence of a caecum is observed in other insectivore mammals including the Tailless tenrec (*Centetes ecaudatus*) (Mitchell 1905), *Crocidura cyanea* and *Amblysomus hottentotus* (Boonzaier et al., 2013). The morphology of *J. jaculus* is consistent with the omnivorous diet as observed in similar rodent species including *Merionus rex*, *Merionus libycus*, *Acomys dimidiatus* and *Acomys cahirinus* (Walters et al., 2014). Both species have simple unilocular glandular stomachs as described in a variety of rodent and insectivorous species (Carleton, 1973; Myrcha, 1976; Perrin & Curtis, 1980). The wholly glandular morphology of the stomach of *P. aethiopicus* corresponds to the observation of Myrcha (1976) on the external morphology of two *P. aethiopicus* samples, stating that the most distinct character of the stomach of *P. aethiopicus* was elongation of the pylorus compared to *Talpidae* (moles) and *Soricidae* (shrews) as observed in the present study. A wholly glandular stomach was observed in other insectivorous mammals including

Soricidae (shrews) and *Talpidae* (moles) families (Myrcha, 1976). The wholly glandular morphology is also evident in mostly herbivorous small rodents species including African mole-rats, *Georychus capensis* and *Cryptomys hottentotus* (*Bathyergidae*) (Kotzé et al., 2010), and the southern African Myomorph rodent, *Grahiurus murinus* (Perrin & Curtis, 1980).

Length measurements alone are an inadequate representation of the diets of species (Perrin & Curtis, 1980). To compensate for misinterpretation through length measurements, the basal surface area (BSA) and luminal surface area (LSA) were calculated, providing a more accurate representation of intestinal parts. This has been proven to be successful in previous studies including those of mole-rats (Kotzé et al., 2010) and rodents (Boonzaier et al., 2013; Walters et al., 2014). The length, BSAs and LSAs of the stomach of both species were small in relation to other gastrointestinal segments. The specialized hindgut morphology of *Jaculus* and the simplicity of the tract in *P. aethiopicus* may correspond to the reduction in size and capacity of the stomachs, which has been observed in animals including *A. hottentotus* and *C. cyanea* (Boonzaier et al., 2013).

The caecum of *J. jaculus* was long and spiraled in macroscopic shape but not voluminous as shown through the BSAs and LSAs of these parts. In fact, the caecum was the second longest gastrointestinal segment of the GIT. This contradicts the finding of Jackson & Spinks (1998) where the length of the caecum was reduced in size compared to the large intestine, although, the volume was greater of the arid living rodents *Parotomys brabdstii*, *Paraotomys littledalei* and *Otomys unisulcatus*. The length of the caecum in *J. jaculus* corresponds to statements made by Stevens and Hume (1995), that the caecum of rodents is large, in relation to other GIT portions, but that the

relative capacity of the caecum in the Jerboa (as seen in this study) is less than in common rodent species. As seen in Behmann (1973) the ileocacal and caeco-colic openings enter at the same point in this species however, interspecies variations do occur as observed in two samples whereby these openings were relatively far apart.

The cecal appendix is identified in a wide range of species including birds and Lagomorphs (rabbits) (Stevens & Hume, 1995; Smith et al., 2009; Smith et al., 2013) and the Cape-dune mole rat (Kotze et al., 2006). In *J. jaculus*, the cecal appendix was a narrow extension of the distal caecum similar to that observed in various mammalian species (Kotzé et al., 2006; Smith et al., 2013). Behmann (1973) mentions the presence of a cecal appendix in the two *J. jaculus* specimens he examined with the occurrence of lymph aggregates against the anti-mesenterial wall which corresponds with observations in the present study. The cecal appendix is characterized by the presence of lymphoid tissue. Recently, the cecal appendix has been documented to act as a “safe house” for sustaining gut microflora and is supported by an immune function in humans (Bollinger et al., 2007); it was concluded that the position of the cecal appendix at the distal end of the blind ending caecum is an ideal place to prevent the contamination of the microflora by possible pathogens in the gut. The position, shape and the amount of lymphoid tissue observed in the present study confirms the presence of a cecal appendix in *J. jaculus*. Two colonic loops were observed in the colon of *J. jaculus* and is consistent with the findings made by Behmann (1973) who described W-shaped loops which were observed in all but two samples in the present study where only a single loop was observed. The V-shaped mucosal folds seen at the proximal segment of the colon in *J. jaculus* was consistent with that seen in almost all myomorph rodents (Behmann, 1973) and in various other small rodents including *Meriones* and *Acomys* species (Behmann,

1973; Boonzaier et al., 2013; Walters et al., 2014), in *Clethrionomys glareolus* (Behmann, 1973). In the Scandinavian Lemming (*Lemmus lemmus*) these folds were described as being in a “fish-bone pattern” (Björnhag & Snipes, 1999). In the two *Jaculus* specimens examined by Behmann (1973) the folds were reported as irregular parallel folds and were not illustrated. The presence of the folds may indicate a mechanism to slow down the passage of digesta in the proximal colon and may be indicative of a colonic separation mechanism (CSM). The CSM allows for the selective retention of easily digested contents while ridding the tract of larger food particles (Sperber et al., 1983; Holtenius & Björnhag, 1985; Björnhag & Snipes, 1999; Hume, 2002). This mechanism is specifically beneficial for small mammals consuming large quantities of low quality forage, whereby micro-organisms are specifically separated and retained in the colon for extended periods while small particles are returned to the caecum via retrograde movements forming caecotrophs (Sperber et al., 1983; Holtenius & Björnhag, 1985; Björnhag & Snipes, 1999) as seen in Myomorph rodents (Hume, 2002), and the Lagomorphs (Björnhag and Snipes, 1999). Although auto-coprophagy has not been observed, this mechanism would be a beneficial adaptation to *J. jaculus* specifically during food scarcities, often associated with arid regions. The mean LSA of the colon was only slightly greater than that of the caecum despite the presence of colonic folds. The larger and more complex hindgut favors the herbivorous specialization of the GIT as observed *Myocastor coypus* and *Aethomys namaquensis* (Woodall & Mackie, 1987).

Longitudinal colonic folds observed in *P. aethiopicus* were similar to those seen in *C. cyanea* and *A. hottentotus* (Boonzaier et al., 2013). The function of these folds is unclear, however Boonzaier et al. (2013) postulated that these folds may not be

permanent structures and would disappear when digesta fills this part of the tract. Unlike *C. cyanea* (Boonzaier et al., 2013) and the Musk shrew (Kurohamaru et al., 1980), villi was not observed throughout the tract. The leaf-like pattern of the villi observed from the proximal to the distal segments of the GIT as seen in the Musk shrew, was only observed in proximal and middle segments of the tract in *P. aethiopicus*. Boonzaier et al. (2013) stated that the appearance of villi from proximal to the distal intestine is an adaptation for animals that cannot have large gastrointestinal lengths due to flight or climbing restrictions. *P. aethiopicus* is not constrained to these conditions, which may correspond to the lack of villi in the distal portion of the GIT.

Stomach content analysis of the present study indicates that *P. aethiopicus* would consume seeds and plant material and even small vertebrates, presumably when there is a scarcity of insects in the immediate environment. This is despite the fact that it has a typical insectivore GIT morphology similar to that described by Boonzaier et al. (2013) and Walters et al. (2014). The findings of the present study therefore suggest that the environment occupied by these species seems to play a subordinate role in relation to GIT morphology as observed in *P. aethiopicus*, whereas diet and taxonomy contributes a more significant role to GIT morphology. The wholly glandular, simple stomach and lack of a caecum are usually associated with a purely insectivorous diet which is rich in readily available protein (Stevens & Hume, 1995; Boonzaier et al., 2013). In addition, the complex, large caecum and extensive colonic folds seen in *J. jacchus* are hindgut morphologic features normally associated with herbivores, while the stomach contents analyzed in the present study were more suggestive of an omnivorous diet. The presence of a cecal appendix is an additional unique feature relating to the phylogeny of this species (Smith et al., 2013). These discrepancies may be associated with the fact that

both species studied here are forced to be adaptable by consuming alternative forage in an arid and harsh environment where preferred foods are not always readily available.

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