Digestion in the porcupine *Hystrix africaeaustralis*

A.S. van Jaarsveld and Annette K. Knight-Eloff
Mammal Research Institute, University of Pretoria, Pretoria

The porcupine has a very efficient dental barrage, which enables digestion of cellular protein in the fully glandular unilocular stomach without coprophagy. Undigested fibre is passed to the enlarged caecum and proximal colon where it is subjected to microbial fermentation, with retention of the coarser, less digestible components in the caecum. The 'retention colon' probably plays an important role in the prevention of excessive water and electrolyte loss in faeces.

S. Afr. J. Zool. 1984, 19: 109 – 112

Die aangepaste gebit van die ystervark vergemaklik afbreking van veselagtige selwandbestanddele en sodoende word die sellulêre proteïene makliker aan verteringsappe in die maag blootgestel. Die hele maagwand van die ystervark se eenvoudige maag bestaan uit klieragtige weefsel. Die verteringsaanpassings maak koprofagie onnodig. Die onverteerde vesel word na die sekum en proksimale kolon gevoer waar retensie en mikrobiale fermentasie van groter en minder verteerbare dele plaasvind. Die herabsorpsie van water en mineralesoute in die 'retensiekolon' verhoed waarskynlik die verlies van groot hoeveelhede van dié komponente in die faeces.

S.-Afr. Tydskr. Dierk. 1984, 19: 109 – 112

A.S. van Jaarsveld* and Annette K. Knight-Eloff
Mammal Research Institute, University of Pretoria, Pretoria,
0002 Republic of South Africa
*To whom correspondence should be addressed

Received 22 August 1983; accepted 23 September 1983

Porcupines (Fam. Hystricidae) are Africa's largest rodents. The genus *Hystrix* is one of the two genera of porcupines in Africa that have existed since the Pleistocene. *Hystrix* consists of two species, the crested porcupine (*H. cristata*) found in northern Africa and *H. africaeaustralis* which is widely distributed in southern Africa. These species are sympatric in central and east Africa (de Graaff 1981).

The porcupine's natural diet includes bulbs, tubers, roots, rhizomes, corms and fruits (de Graaff 1981). They will also eat carrion (Roth 1964) and practise osteophagia in phosphorous-deficient areas (Skinner, Davies & Ilani 1980). They have a reputation for being destructive feeders, can cause extensive damage to crops (Smithers & Wilson 1979) and are notorious for their ring-barking of trees (de Graaff 1981), discarding the dry outer layer and concentrating mainly on scraping off the cambium.

Very few nutritional studies on the Hystricomorpha have been published, and none are available on *H. africaeaustralis*. Johnson & McBee (1967) studied the digestion of the yellow-haired porcupine (*Erethizon dorsatum epixanthum*) and found that considerable fermentation occurred in the expanded caecum. In *H. cristata* Mitchell (1905) found a distinct duodenal loop, a long and narrow caecum and an expanded proximal hindgut. For a more detailed description of the digestive tract of this species see Gorgas (1967).

The purpose of this study was to examine digestive morphology and hindgut fermentation in relation to feeding habits in *H. africaeaustralis*.

Material and Methods

Porcupines were obtained from the south-eastern Orange Fre State (Van Jaarsveld 1983). Within 60 min of capture the digestive tracts were removed and placed in a waterbath regulated to 39 °C. Gas samples were collected from the caecum and proximal colon of the intact tract with a hypodermic syringe and stored in 5 ml evacuated tubes (Bide 1978). The fermentation rates of the caecal and proximal colon contents were determined following the method of El-shazly & Hungate (1965).

pH of each segment was measured with a portable pH meter by inserting the copper electrode directly into the digesta. Samples of cardiac stomach contents were collected to determine food quality.

Samples of the stomach contents were dried to constant mass at 75 °C and finely ground. These samples were analysed for crude protein content using the Kjeldahl method of total N-determination (Horwitz 1970), and for neutral detergent fibre

Reproduced by Sabinet Gateway under licence granted by the Publisher (dated 2010).

(NDF) content following Goering & van Soest (1970), using a 'Fiber-tec 1020' hot extraction apparatus.

The composition of the fermentation gas was determined by gas-solid chromatography using a 'Pye Unicam GVF' gas chromatograph with a thermal conductivity detector. A 5Å molecular sieve 90/100 mesh column packing was used with argon as the carrier gas at a flow rate of 50 ml/min. The column length was 1,5 m.

The stomachs were examined macroscopically as described by Perrin & Curtis (1980). Histological sections were prepared from gastric tissue fixed in Bouin's fluid, stained with haematoxylin and counterstained with eosin; or fixed in AFA (water:ethanol:formalin:acetic acid — 5:3:1:1) and stained with Masson's trichrome stain. For comparative purposes eight measurements, taken at random, of each stomach wall layer from typical antrum and corpus regions were taken.

Results and Discussion

The porcupine's dentition is highly adapted to the breaking down of cell walls (Figure 1). The teeth are hypsodont with intricate enamel patterns on the occlusal surfaces and an enlarged molariform PM^4 is present (de Graaff 1981).

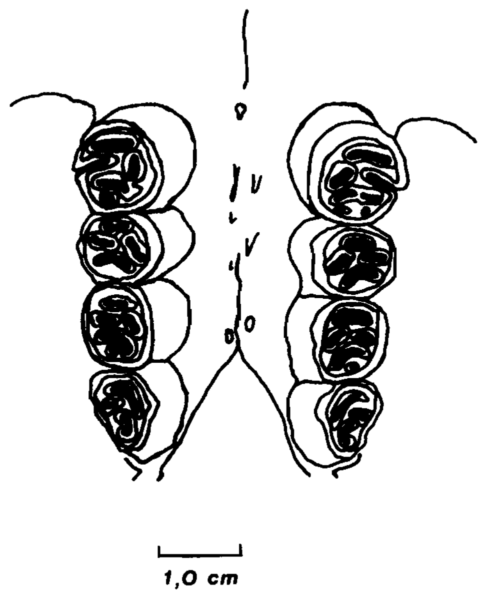

Figure 1 Cheek teeth of *H. africaeaustralis* (maxilla).

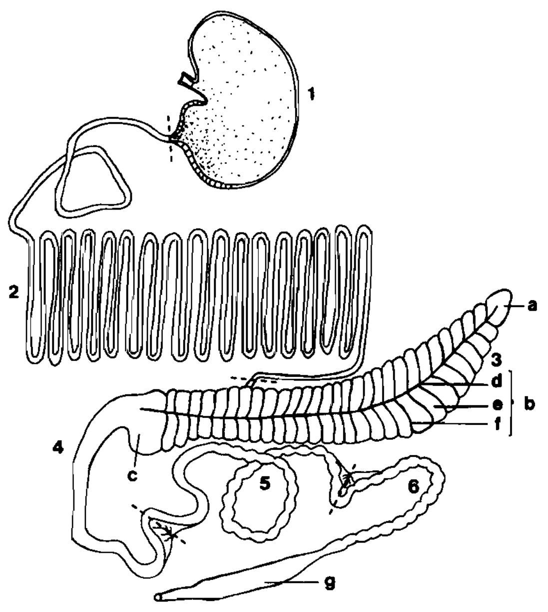

Figure 2 The digestive tract of an adult *H. africaeaustralis*. (1) Fully glandular unilocular stomach; (2) Small intestine; (3) Caecum; (4) Proximal colon; (5) Transverse colon; (6) Descending colon; (a) Ampulla ceci; (b) Corpus ceci; (c) Apex ceci; (d) Taeniae; (e) Haustra; (f) Semi-lunar fold; (g) Retention colon.

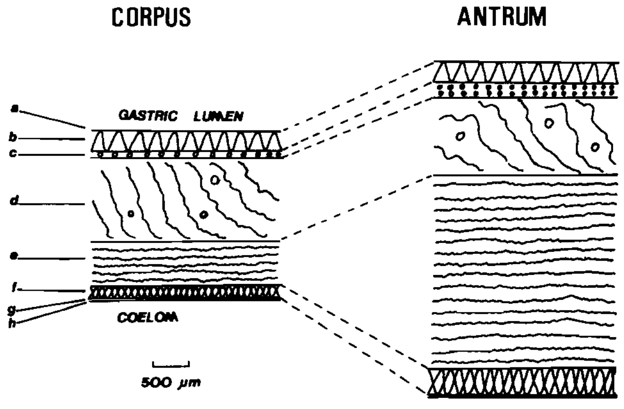

Figure 3 Stomach-wall histology of *H. africaeaustralis*. (a) Lamina epithelialis mucosa; (b) Lamina propia; (c) Muscularis mucosa; (d) Tunica submucosa; (e) Circular layer of tunica muscularis; (f) Longitudinal layer of tunica muscularis; (g) Tela subserosa; (h) Tunica serosa.

The histological investigation revealed that the porcupine has a fully glandular, unilocular stomach (Figure 2), in which all of the gastric layers (Ham 1957) are easily distinguishable (Figure 3). This is in contrast with the partially glandular stomach described for the crested porcupine by Gorgas (1967).

If, as Vorontsov (1962) proposed, rough abrasive material causes cornification of the stomach wall, one would expect porcupines, beavers and lagomorphs to have partially cornified stomachs, as these animals regularly consume quantities of rough abrasive material. All these animals do, however, possess fully glandular stomachs (Todd 1927; Dalke 1942; Nasset 1953; de Graaff 1981).

The porcupine's stomach wall shows a significant (Table 1) thickening of the muscle layers towards the antrum (Figure 3), which probably enhances the mixing of digesta and ensures a more effective comminution of coarse foodstuffs (Carleton 1973).

The fully glandular stomach of the porcupine has a relatively low pH of 2 ± 0,5 (Figure 4), consistent with extensive HCl secretion by the glandular tissue. This HCl secretion probably enables the animal to extract the maximum amount of protein from its food as it has been demonstrated that porcupines are very efficient at extracting protein from a herbaceous diet. When subjected to digestibility trials (Van Jaarsveld 1983) they digested 83,79% of the total crude protein content of a diet with a composition very similar to that of their natural diet (Table 2).

Although their natural diet does not include excessive quantities of fibre (Table 2), porcupines require a well-developed dental barrage (Figure 1), to break down cell walls, thus enabling protein digestion to occur in the stomach before microbial fermentation occurs. This is in contrast to the lagomorphs which digest protein by coprophagy after microbial fermentation.

The porcupine does, however, consume some fibre (Table 2), which is a potential energy source if subjected to microbial

Reproduced by Sabinet Gateway under licence granted by the Publisher (dated 2010).

Table 1 Quantitative data of stomach-wall histology are means and standard deviations from eight random measurements (* = different at $P < 0{,}05$; NS = non significant)

	Corpus (μm)	Antrum (μm)	Difference[a]
Lamina epithelialis mucosa	7,62 ± 1,05	7,78 ± 0,50	NS
Lamina propia	234,49 ± 33,53	258,05 ± 37,60	NS
Muscularis mucosa	82,06 ± 9,84	193,21 ± 28,43	*
Tunica submucosa	1082,09 ± 102,29	1012,86 ± 212,95	NS
Circular layer of tunica muscularis	571,35 ± 54,50	2524,11 ± 359,83	*
Longitudinal layer of tunica muscularis	168,68 ± 39,69	366,76 ± 70,95	*
Tela subserosa	6,71 ± 1,26	8,18 ± 2,13	NS
Tunica serosa	6,04 ± 0,55	6,14 ± 0,89	NS

[a] = Student's *t* test

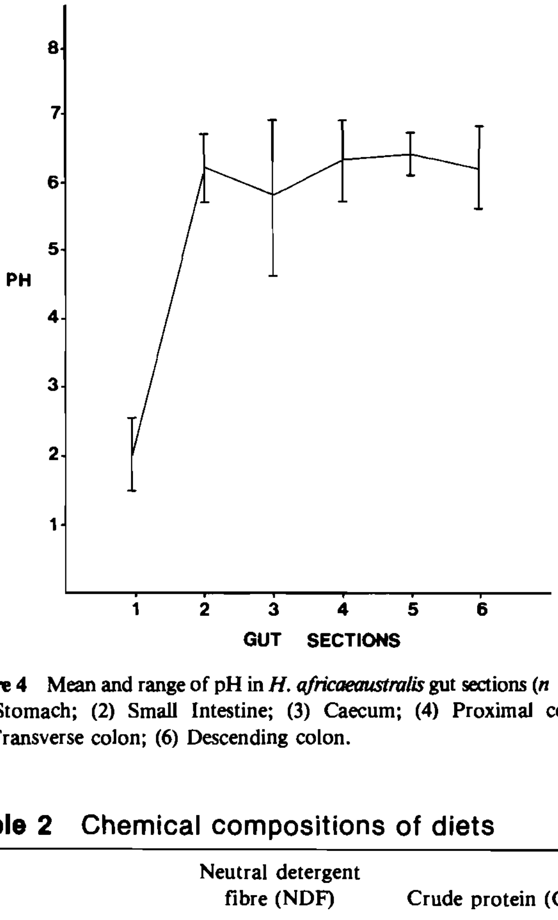

Figure 4 Mean and range of pH in *H. africaeaustralis* gut sections (n = 7). (1) Stomach; (2) Small Intestine; (3) Caecum; (4) Proximal colon; (5) Transverse colon; (6) Descending colon.

Table 2 Chemical compositions of diets

Diet	Neutral detergent fibre (NDF)	Crude protein (CP)
Field diet	29,43%	12,21%
Laboratory diet[a]	20,00%	15,13%

[a]From van Jaarsveld (1983).

fermentation. The porcupine ferments this fibre in an expanded caecum and proximal colon (Van Jaarsveld 1983). The caecum is characterized by the following features:

(i) Haustra (± 31): formed by dilations of the circular muscles and are not fixed sacculations.

(ii) Semilunar folds (± 30): formed by the slight contractions of the circular muscles.

(iii) Taeniae (3): which are longitudinal muscles, occurring in all herbivorous mammals or in omnivores with a predominantly herbivorous diet (Langer 1982).

These haustra, semilunar folds and taeniae are responsible for the movement of digesta as well as the selective retention of relatively indigestible carbohydrates (Langer 1983). The selective retention of larger particles has been demonstrated in another large hystricomorph rodent, the capybara (*Hydrochoerus hydrochaeris*) (Baldizan, Dixon & Parra 1983). This retention in the caecum was probably the cause of the increased transit time of digesta when porcupines were fed a high fibre diet (Van Jaarsveld 1983), resulting in a more efficient fibre digestion.

The hindgut seems to be a very effective digesting apparatus since porcupines can digest 65,80% of the NDF content of the laboratory diet (Table 2) (Van Jaarsveld 1983). The fermentation rates in the caecum and proximal colon are low, with a low rate of methane production (Table 3). However, according to Bergen & Yokoyama (1977) low methane production could be an indicator of a more efficient fermentation process. The production of volatile fatty acids (± 2,06 mmol/100ml/h) has been detected in the caecum and proximal colon of the porcupine (unpubl. data) which is similar to the volatile acid production of the hyrax *Provacia capensis*, a very efficient hindgut fermenter (Eloff 1981). The relative contribution of hindgut fermentation to the basal metabolic requirements of porcupines can be expected to vary in accordance

Table 3 Fermentation rates, methane production and gas compositions in caeca and proximal colons of *H. africaeaustralis* on a natural diet (n = 7) (* = different at $P < 0{,}05$; NS = non significant; DM = dry matter)

	Caecum (C)	Proximal colon (PC)	Difference between C and PC
Fermentation rate[a] (μmol/gDM/h)	91,07 ± 27,23	75,18 ± 12,95	NS
Total gas production[a] ℓ/day	0,11 ± 0,00	0,11 ± 0,06	NS
Methane production[a] ℓ/day	0,11 ± 0,001	0,01 ± 0,00	NS
[b]Gas composition (%)			
CH_4	12,20	9,98	NS
CO_2	54,22	46,98	NS
H_2	0,14	0,07	NS
N_2	26,07	33,59	NS
O_2	7,37	11,37	NS

[a] = Student's *t* test.

[b] = Mann Whitney U test.

Reproduced by Sabinet Gateway under licence granted by the Publisher (dated 2010).

with the seasonal availability of less fibrous foods.

Increased intake of plant materials would result in an increase of indigestible material which could be expected to stimulate secretions, such as saliva and mucus throughout the length of the gut. There would follow a need to reabsorb water, electrolytes and metabolites from these secretions lower down in the gut to avoid excessive loss. Thus there would be a selective advantage in slowing down the rate of passage of digesta to allow time for reabsorption to proceed (Hume & Warner 1980).

The last 40% of the descending colon of the porcupine has an increased diameter which accounts for the formation of the characteristic droppings, consisting of a number of stacked pellets. This retention colon will probably result in a reduced flow rate, enhancing water and electrolyte reabsorption.

Acknowledgements

We would like to thank the following people for their advice and assistance: Mr P.J. Apps, Mrs E. Boomker, Dr N. Fairall, Mr M.H. Knight, Dr P. Langer and Mr R.J. van Aarde. Financial support was provided by the Mammal Research Institute, University of Pretoria and the Council for Scientific and Industrial Research.

References

BALDIZAN, A., DIXON, R.M. & PARRA, R. 1983. Digestion in the capybara (*Hydrochoerus hydrochaeris*). *S. Afr. J. Anim. Sci.* 13: 27 – 28.

BERGEN, W.E. & YOKOYAMA, M.T. 1977. Productive limits to rumen fermentation. *J. Anim. Sci.* 46: 573 – 584.

BIDE, R.W. 1978. Evacuated blood collecting tubes as containers for taking and storing gas samples. *J. Chromat.* 161: 315 – 318.

CARLETON, M.P. 1973. A survey of gross stomach morphology in New World Cricetinae (Rodentia, Muroidea), with comments on functional interpretations. *Mus. Zool. Univ. Michigan* 146: 1 – 42.

DALKE, P.D. 1942. The cottontail in Connecticut. *Bull. Conn. St. Geol. Nat. Hist. Surv.* 65: 1 – 97.

DE GRAAFF, G. 1981. The Rodents of Southern Africa. Butterworths, Pretoria.

ELOFF, A.K. 1981. The digestion in the hyrax, *Procavia capensis* (Pallas, 1766). M.Sc. thesis, University of Pretoria.

EL-SHAZLY, K. & HUNGATE, R.E. 1965. Fermentation capacity as a measure of net growth of rumen micro-organisms. *Appl. Microbiol.* 13: 62 – 69.

GOERING, H.K. & VAN SOEST, P.J. 1970. Forage fibre analysis. Agricultural Handbook No. 379, Agricultural Research Services, Washington, D.C.

GORGAS, M. 1967. Vergleichend-anatomische Untersuchungen am Magen-Darm-Kanal der Sciuromorpha, Hystricomorpha und Caviomorpha (Rodentia). *Z. Wiss. Zool.* 175: 237 – 404.

HAM, A.W. 1957. Histology. J.B. Lippincott Comp. Montreal.

HORWITZ, W. 1970. Official methods of analysis of the Association of Clinical Agricultural Chemists. 9th ed., Benjam Franklin Sta., Washington, D.C.

HUME, I.D. & WARNER, A.C.I. 1980. Evolution of microbial digestion in mammals. In: Digestive physiology and metabolism in ruminants, (eds) Ruckebusch & Thivend, P. M.T.P. Press, Lancaster.

JOHNSON, L.J. & McBEE, R.H. 1967. The porcupine caecal fermentation. *J. Nutr.* 91: 540 – 546.

LANGER, P. 1982. Wandel der Querschnittsgeometrie des Darmstraktes als Anpassung an die Herbivorie bei Säugern. *Verh. Dtsch. Zool. Ges.*, Gustav Fischer Verlag, pp.280.

LANGER, P. 1983. Anatomical and nutrition adaptations in wild herbivores. Symposium on herbivore nutrition in the subtropics and tropics: Proceedings — Summaries of invited papers: pp 31. CSIR, Pretoria.

MITCHELL, P.C. 1905. On the intestinal tract. *Transact. Zool. Soc. Lond.* 17: 437 – 536.

NASSET, E.S. 1953. Gastric secretion in the beaver (*Castor canadensis*). *J. Mammal.* 34: 204 – 209.

PERRIN, M.R. & CURTIS, B.A. 1980. Comparative morphology of the digestive system of 19 species of Southern African myomorph rodents in relation to diet and evolution. *S. Afr. J. Zool.* 15: 22 – 24.

ROTH, H.H. 1964. Note on the early growth development of *Hystrix africaeaustralis*. *Z. Saugetierk.* 29: 313 – 316.

SKINNER, J.D., DAVIES, S. & ILANI, G. 1980. Bone collecting by striped hyaenas, *Hyaena hyaena,* in Israel. *Palaeont. afr.* 23: 99 – 104.

SMITHERS, R.H.N. & WILSON, V.J. 1979. Check list and atlas of the mammals of Zimbabwe/Rhodesia. National Museums and Monuments, Salisbury.

TODD, J.B. 1927. Winter food of cottontail rabbits. *J. Mammal.* 8: 222 – 228.

VAN JAARSVELD, A.S. 1983. Aspects of the digestion in the Cape porcupine. *S. Afr. J. Anim. Sci.* 13: 31 – 33.

VORONTSOV, N.N. 1962. The ways of food specialization and the evolution of the alimentary system in Muroidea. In: Symposium Theriologicum. *Publ. House. Czeck. acad. Sci.* 360 – 377.

Reproduced by Sabinet Gateway under licence granted by the Publisher (dated 2010).