

## PROCEEDINGS OF THE NUTRITION SOCIETY

*The Four Hundred and Forty-ninth Scientific Meeting was held at the Physics Lecture Theatre, Faraday Complex, University of Lancaster, Lancaster on 12/13 April 1988*

### SYMPOSIUM ON 'NUTRITION OF NON-RUMINANT HERBIVORES'

#### **Adaptations of digestive systems in non-ruminant herbivores**

By DAVID J. CHIVERS, *Sub-department of Veterinary Anatomy, University of Cambridge, Tennis Court Road, Cambridge CB2 1QS*

Early in the evolution of mammals some lineages veered away from small body size and insectivory, which characterized the earliest mammals, to become larger and herbivorous (e.g., Romer, 1966). Since plant matter is much more difficult to digest than animal matter, because of the high content of structural carbohydrates, such animals should be larger so as to be able to accommodate the more elaborate gastrointestinal tract required for the digestion (initially by bacterial fermentation) of such food. Such adaptations are worthwhile because of the great abundance of potential plant foods, especially the vegetative parts of plants (leaves of varying developmental stages and associated parts, such as stems).

While some mammalian orders have maintained the insectivorous habit, such as the Insectivora, Pholidota and Edentata, and others have become more specialized for *faunivory*, such as the Carnivora (feloids and cynoids), Pinnipedia and Cetacea, retaining small body size or simple gastrointestinal tract, or both, many mammalian orders have evolved to large body size and *folivory*, such as the Perissodactyla (hippomorphs and ceratomorphs), Artiodactyla (suines, tylopods and pecorans), Proboscidea and Sirenia. This has involved the dramatic enlargement of either the caecum and beginning of the colon or, more recently, as the quality of foliage improved, of the stomach, usually with some caeco-colic enlargement (e.g., Moir, 1968; Janis, 1976; Chivers & Hladik, 1980; Langer, 1987). Some folivores, such as the Rodentia, Lagomorpha and Hyracoidea, have mostly retained small body size with accompanying problems for digestion, such as the need for coprophagy (caecotrophy).

Much rarer has been occupancy of the ecological 'middle ground', in terms of abundance and digestibility, of *frugivory*. Among mammals, only the primates and some bats have competed with the successful avian consumers of plant reproductive parts, flowers and fruit. The success of primates seems to lie in their relative lack of specialization, and, while the majority are frugivorous, the smaller ones are faunivores and the larger ones are folivores (with either stomach or caeco-colic enlargement). None are exclusive frugivores, since certain amino acids do not occur in fruit; the smaller species supplement fruit with animal matter, the larger ones with foliage, in all cases showing convergence anatomically on the specialists in other orders.

Since no primate, or other mammal (to our current knowledge) consumes significant quantities of animal matter *and* foliage (because of anatomical and physiological incompatibility), and since mammals with such a variable diet based on fruit do not form

a distinct category, the widely-used concept of 'omnivory' is singularly inappropriate with our more detailed approaches and knowledge. For example, the varied diets of bears and pigs are based on fruit, as reflected by dental morphology, in the case of the latter including below-ground plant storage organs, such as tubers, bulbs and roots.

Herein we consider the gastrointestinal adaptations of non-ruminant herbivores; that is, mainly the adaptations of non-ruminant folivores, but with some reference to frugivores and the inevitable contrasts with ruminant folivores. Although there is a unifying herbivorous theme to their diets, and many species (especially primate) eat fruit and foliage (Fig. 1), the complexities of frugivory and folivory are sufficient to supersede the value of 'herbivory'. Among folivores we are concerned mainly with the contrasts between those mammals that break down cellulose by microbial fermentation in an expanded fore-stomach, and those that do so in an expanded caecum and colon (ascending or primitive right colon). It should be noted that this part of the large intestine is towards the end of the fetal mid-gut loop, which differs from the last part of the colon in blood supply, venous drainage and innervation, as well as in development. Thus, the term 'hind-gut fermentation', so widely used in the literature, is inaccurate.

The caeco-colic expansion of rodents, lagomorphs, hyraxes, elephants, sirenians, horses and some strepsirhine primates (such as some galagos, indriids and sportive lemurs) appears to have evolved earlier, in relation to poor-quality foliage. Among haplorhine primates, species such as the howler and gorilla show comparable but more recent adaptations. In elongating and widening a 'tube' the surface area for absorption increases in relation to the volume for fermentation. By contrast, the expansion of the more spherical fore-stomach of macropod marsupials, sloths, peccaries, hippopotami, camels and colobine monkeys, as well as of ruminants, a later adaptation coincidental with the radiation of better-quality angiosperm foliage in the Miocene, is problematic in terms of inadequate surface area in relation to the volume of an expanded 'sac'. A final point for consideration is passage time, whether it relates to food quality or gut size.

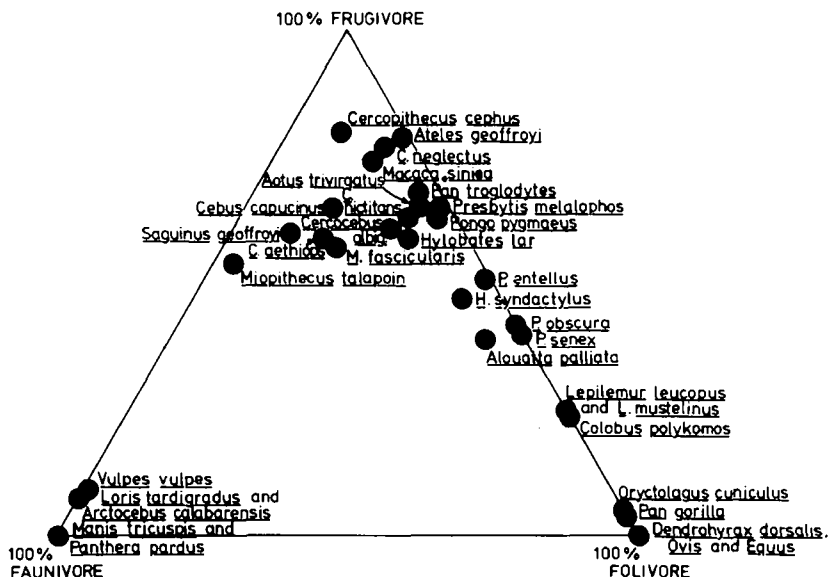


Fig. 1. Mean dietary characteristics of thirty-four mammal species, representing proportions of fruit, animal matter and foliage (from Chivers & Hladik, 1980).

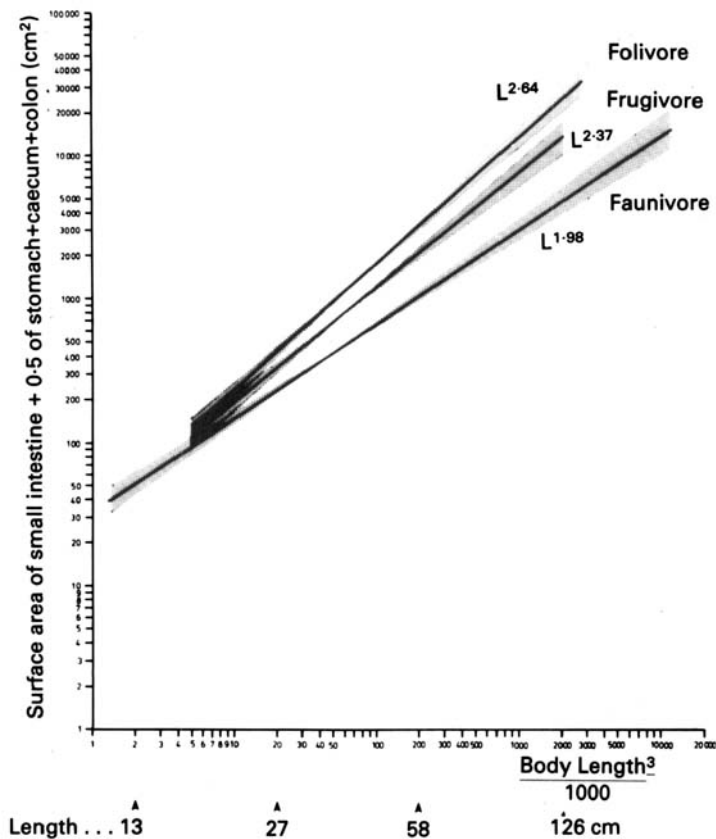


Fig. 2. The relation between the potential surface areas for absorption and body size in faunivores, frugivores and folivores, demarcating the 95% confidence limits for the slopes (from Chivers & Hladik, 1980). L, length.

While caeco-colic fermenters rely on the rapid passage of digesta, fore-stomach fermenters retain the better-quality food for much longer, but, unlike caeco-colic fermenters, they are less able to alter retention time (Langer, 1987).

#### *Gastrointestinal anatomy*

The gastrointestinal tracts of about 200 individuals of eighty mammalian species (forty-two primate species) have been measured and analysed quantitatively in relation to body size (Chivers & Hladik, 1980; Martin *et al.* 1985; MacLarnon *et al.* 1986; Stark *et al.* 1987). The surface areas of stomach, small intestine and caecum and colon were measured, in relation to absorptive ability; from these measurements were calculated the volumes of each gut compartment, in relation to the fermentative capacity of fore-stomach or caecum and colon, or both. Each compartment was weighed, giving an indication of differences in muscular activity associated with digestion.

Surface area of the small intestine was found to scale with metabolic body size (Kleiber, 1961), but larger faunivores had less absorptive area than expected, and larger folivores had more, especially the fore-stomach fermenters (Chivers & Hladik, 1980). Better resolution was obtained by adding half the stomach, caecum and colon areas to the area of small intestine as a more accurate indicator of absorptive ability (Fig. 2).

Similarly, the volumes of stomach, caecum and colon, the potential fermenting chambers, were found to scale with actual body size, closely for faunivores with no

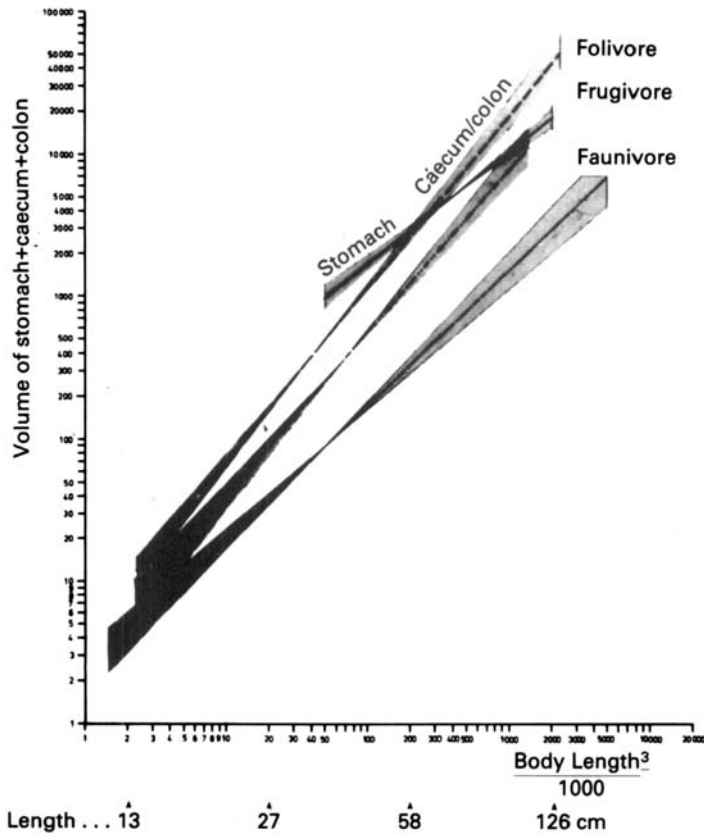


Fig. 3. The relation between the volumes of potential fermenting chambers and body size in faunivores, frugivores and fore-stomach and caeco-colic fermenting folivores, demarcating 95% confidence limits (from Chivers & Hladik, 1980).

fermentation occurring; larger frugivores had more voluminous chambers than expected, and larger caeco-colic fermenters even more so, but larger fore-stomach fermenters had smaller chambers than expected (Fig. 3). The latter can be explained by the absorptive inefficiency of larger stomachs, and so larger animals have relatively reduced volumes despite the elaboration of folds and papillae to increase surface area (Chivers & Hladik, 1980).

Allometric analyses were taken further by Martin *et al.* (1985), MacLarnon *et al.* (1986) and Stark *et al.* (1987), using the surface areas for each compartment. Having confirmed that these findings conformed with Kleiber's (1961) Law by scaling with metabolic body size (a slope of 0.75), compartmental quotients were calculated according to deviations from the expected (distance above or below the slope of 0.75, Fig. 4) for each species and subjected to multi-variate analysis. Dendograms were found to be too labile, with the addition or subtraction of values, and, although caeco-colic and fore-stomach fermenters were clearly separated, the rest (frugivores and faunivores) were not. By contrast, multi-dimensional scaling was found to be sufficiently robust and informative.

Mammal species separated into a central cluster of frugivores, with outlying groups of caeco-colic and fore-stomach fermenters (both with some compartments larger than

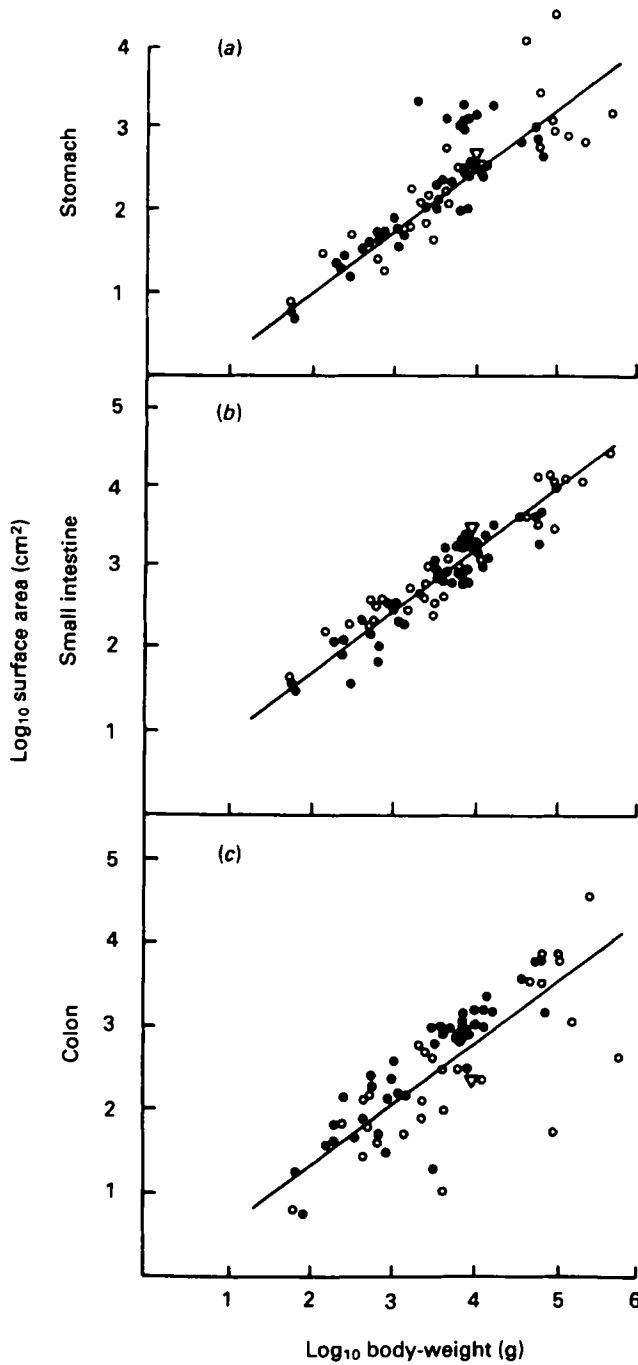


Fig. 4. Logarithmic plots of surface areas of (a) stomach, (b) small intestine and (c) colon for eighty mammal species, in relation to the best-fit line of slope 0.75 (from Stark *et al.* 1987). (●), Primates; (○), mammals; (▽) *Meles meles*.

expected) and of faunivores (with some compartments smaller than expected) (Fig. 5). Having eliminated the effects of body size, it can be shown that degrees of similarity between species reflect dietary adaptation rather than phylogeny. While the horse is the most distinctive caeco-colic fermenter, and the ruminants show the most extreme fore-stomach elaboration, primates fall in both groups, and, through humans, squirrel and capuchin monkeys, among the faunivores as well. Otherwise, primates form the bulk of the frugivore cluster, with contrasting positions towards the periphery according to the proportions of foliage or animal matter supplements in the diet.

### *Non-ruminant herbivores*

Thus, we have a quantitative structural basis from which to discuss herbivory in mammals. Distinctions can be made (but not always easily) between frugivores and folivores and, in the latter, between fore-stomach (mostly ruminants) and caeco-colic fermenters. Milton (1980), in distinguishing between frugivorous and folivorous primates and referring to the gradation between them, compares anatomical and behavioural folivores. The relative lack of gut specialization, among primates in particular, confers the abilities to eat fruit, especially seeds, with a more elaborate gut, and to eat leaves, mainly young ones, with a less elaborate tract. Thus, such primates can and do respond very effectively to environmental fluctuations, especially the less predictable ones.

The dietary flexibility of primates contrasts with other herbivores, especially the folivores. Apart from the ungulates, the stomach is elaborated in rodents (e.g., cricetids, sciurids and some caviomorphs), sloths, lagomorphs, some marsupials, sirenians and proboscids and, in most cases the caecum and colon even more so; the tree hyrax (*Dendrohyrax*), apart from having a much elongated, sacculated stomach, has a pair of extra caeca 200 mm along the colon from the main one (Chivers & Hladik, 1980).

It is the ungulates, however, which show the most distinctive adaptations, along with a marked increase in body size. Their evolution is well documented and reviewed by Langer (1987) in terms of increasing or decreasing numbers of species in each time period for each continent. This reveals that Perissodactyla (caeco-colic fermenters) peaked in the Eocene and Oligocene outside Africa, with a large secondary peak in the Miocene in North America, and a late, low-key appearance in Africa. Among the Artiodactyla, caeco-colic fermenters flourished in the Eocene and Oligocene of Europe and North America, but then faded out, increasing somewhat in Asia and Africa since the Miocene. Fore-stomach fermenters, by contrast, flourished on all continents from the Miocene (much later in Africa). Today ruminants are expanding everywhere but North America, whereas caeco-colic fermenting artiodactyls are contracting in Europe, expanding in Africa and are in balance in Asia (possibly expanding) and North America (possibly contracting). The caeco-colic fermenting perissodactyls are expanding in Africa, in balance in North America (and Europe), but contracting in Asia.

Despite their specializations, there are distinctive variations within and between species, mainly with regard to food retention time in relation to food quality and body size, as well as in anatomy. Ruminants, for example, are subdivided into (1) 'browsers', of necessity from their small body size seeking higher-quality foods (even fruit, some species exclusively so), (2) 'intermediate feeders' and (3) 'grazers', exclusive folivores of large body size and high biomass, seeking quantity of food rather than quality (Hofmann, 1973; Jarman, 1974). An important limiting factor is that the passage of digesta through the ruminant stomach cannot be regulated in the way that it can be through the large intestine of non-ruminants (Langer, 1987). Fermentation in the caecum and colon of ruminants is likely to be a secondary adaptation (Janis, 1976), but it

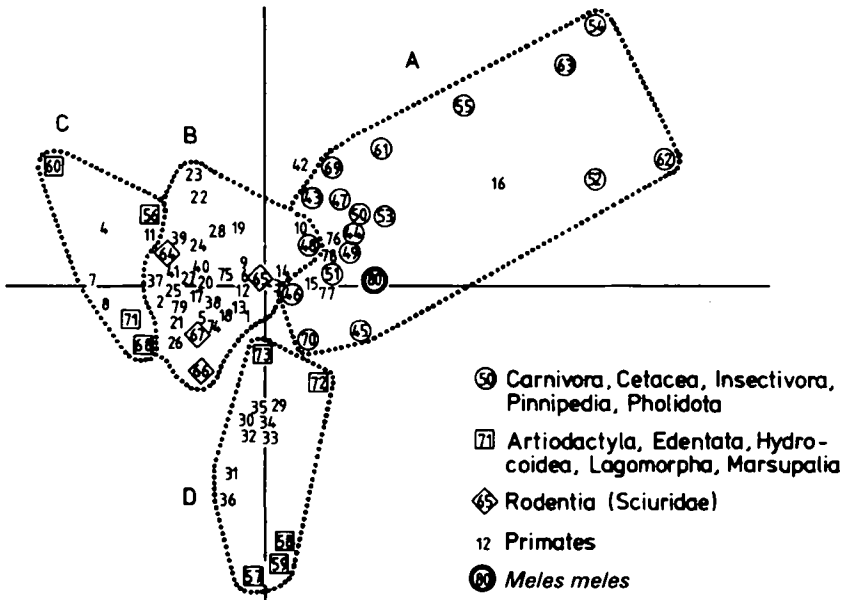


Fig. 5. Multi-dimensional scaling plot using log indices for three gut compartment surface areas (stomach, small intestine, caecum plus colon) for eighty mammal species: clusters A, faunivores; B, frugivores; C, caeco-colic fermenting folivores; D, fore-stomach fermenting folivores (from MacLarnon *et al.* 1986; Stark *et al.* 1987).

Key	Key	Key
1 <i>Arctocebus calabarensis</i>	28c <i>Erythrocebus patas</i>	55c <i>Panthera tigris</i>
2 <i>Avahi laniger</i>	29 <i>Colobus polykomos</i>	56c <i>Sus scrofa</i>
3 <i>Cheirogaleus major</i>	30 <i>Presbytis entellus</i>	57c <i>Capra hircus</i>
4 <i>Euoticus elegantulus</i>	31 <i>Presbytis cristata</i>	58c <i>Ovis aries</i>
5 <i>Galago alleni</i>	32 <i>Presbytis obscura</i>	59 <i>Cervus elaphus</i>
6 <i>Galago demidovii</i>	33 <i>Presbytis melalophos</i>	60c <i>Equus caballus</i>
7c <i>Lepilemur mustelinus</i>	34c <i>Presbytis rubicunda</i>	61c <i>Halichoerus grypus</i>
8 <i>Lepilemur leucopus</i>	35c <i>Nasalis larvatus</i>	62* <i>Phocaena phocaena</i>
9 <i>Loris tardigradus</i>	36c <i>Pygathrix nemaeus</i>	63* <i>Tursiops truncatus</i>
10 <i>Microcebus murinus</i>	37c <i>Hylobates pileatus</i>	64 <i>Sciurus vulgaris</i>
11 <i>Perodicticus potto</i>	38c <i>Hylobates syndactylus</i>	65 <i>Epixerus ebii</i>
12 <i>Sanguinus geoffroyi</i>	39c <i>Pongo pygmaeus</i>	66 <i>Heliosciurus rufobrachium</i>
13 <i>Aonon trivirgatus</i>	40 <i>Pan troglodytes</i>	67 <i>Sciurus carolinensis</i>
14c <i>Ateles belzebuth</i>	41 <i>Gorilla gorilla</i>	68 <i>Oryctolagus cuniculus</i>
15 <i>Saimiri oerstedii</i>	42c <i>Homo sapiens</i>	69* <i>Potamogale velox</i>
16 <i>Cebus capucinus</i>	43c <i>Felis domestica</i>	70* <i>Manis tricuspis</i>
17 <i>Alouatta palliata</i>	44c <i>Canis familiaris</i>	71 <i>Dendrohyrax dorsalis</i>
18c <i>Lagothrix lagothericha</i>	45* <i>Mustela nivalis</i>	72* <i>Bradypus tridactylus</i>
19 <i>Miopithecus talapoin</i>	46 <i>Vulpes vulpes</i>	73c <i>Macropus rufus</i>
20 <i>Cercopithecus cephus</i>	47 <i>Atilax paludinosus</i>	74 <i>Cacajao calvus</i>
21 <i>Cercopithecus neglectus</i>	48* <i>Nandinia binotata</i>	75 <i>Cacajao melancephalus</i>
22 <i>Cercopithecus nictitans</i>	49 <i>Poiana richardsoni</i>	76 <i>Cebus apella</i>
23 <i>Cercocebus albigena</i>	50 <i>Genetta servalina</i>	77 <i>Saimiri sciureus</i>
24 <i>Macaca sylvanus</i>	51* <i>Mustela sp.</i>	78 <i>Saimiri vanzolinii</i>
25 <i>Macaca sinica</i>	52*c <i>Ailurus fulgens</i>	79 <i>Alouatta seneculus</i>
26 <i>Macaca fascicularis</i>	53*c <i>Nasua narica</i>	80* <i>Meles meles</i>
27 <i>Papio sphinx</i>	54c <i>Genetta sp.</i>	

\*, Caecumless species; c, captive specimens—only wild-caught specimens used for all other species.



accounts for up to 20% of the volatile fatty acids absorbed in some species (N. Tyler, personal communication).

Although they are ecologically similar (perhaps not so similar when studied in detail), the independent evolution of artiodactyls and perissodactyls is based on the former passing high-quality food slowly, and the latter passing low-quality food rapidly through the gastrointestinal tract (Janis, 1976). Langer (1987) shows that, relative to their body size, while the passage of digesta is rapid through the small intestine of the pig, slowing down markedly in the caecum and colon, in the horse passage is slower than expected through the stomach, but not particularly slow in the caecum. By contrast, in ruminants, after a long stay in the stomach (not so long in sheep) and rapid transit through the small intestine, passage is at the expected rate through the large intestine of cattle (slower in sheep).

In contrasting small and large caeco-colic fermenting ungulates with small and large fore-stomach fermenting ones, Langer (1987) further shows that (1) retention time is shorter in smaller species, especially in non-ruminants, (2) retention time in the whole gut is proportionately longer in ruminants and (3) retention time in the fermenting chamber is longest in ruminants (Tables 1 and 2). Furthermore, non-ruminants generally fail to make digestive use of microbial metabolites and cells, relying for their nourishment on the absorption of fermentation products. Janis (1976) refers to the urea cycle in ruminants which boosts, in terms of growth and breeding, the microbial population, in contrast to the lower rate of urea use in non-ruminants, especially the larger ones that are not coprophagous.

In conclusion, smaller folivores eat a higher-quality diet because they need more nutrients/kg body-weight per d; so too do fore-stomach fermenters, especially the smaller ones. Fermenting volume is proportional to body-weight, and absorptive area to metabolic body size, but passage time varies according to gut structure. For example, the taenia, haustra and folds of the large intestine of caeco-colic fermenters both retain digesta and vary the balance between retention and passage. Anti-peristalsis is common in the large intestine, but rare in the small intestine, hence the rapid passage through the small intestine of all species. Digestion and absorption are much more thorough in fore-stomach than caeco-colic fermenters.

Caeco-colic fermentation (or non-ruminant folivory) has been related to the earlier evolutionary efforts to exploit lower-quality foliage. It is perhaps a reflection of the versatility of the system, despite its lower efficiency in some respects, that non-ruminant folivores, with a much broader taxonomic base, have not been eclipsed by ruminants.

Table 1. *Fermenting volume (FV) and mean retention time (MRT) in parts of the gastrointestinal tract of various ungulates (from Langer, 1987)*

Fermenting system	Species	Body-wt (kg)	Reticulo-rumen		Omasum		Abomasum, stomach		Small intestine		Caecum		Colon	
			FV	MRT	FV	MRT	FV	MRT	FV	MRT	FV	MRT	FV	MRT
Caeco-colic	Pig	190	-	-	-	-	8	8	9	2	1	3	9	27
Fore-stomach	Cattle	800	125	55	20	8	15	2	65	2	10	3	25	5
	Sheep	112	17	38	1	3	2	2	6	2	1	5	3	14
Caeco-colic	Horse	450	-	-	-	-	8	16	27	4	14	10	41	36



Table 2. *Functional adaptations of the gastrointestinal tracts in domestic ungulates (from Langer, 1987)*

Fermenting system . . .	Caeco-colic		Fore-stomach	
	Horse	Pig	Cattle	Sheep
Species . . .	Horse	Pig	Cattle	Sheep
Body-wt (kg)	450	190	800	112
Nutritional needs (/kg body-wt (BW))	Low	High	Low	High
Food quality	Low	High	Low	Low
Fermenting chamber:				
Volume (/kg BW)	Proportional	Smaller	Larger	Larger
MRT (/kg BW)	Shorter	Shorter	Shorter	Longer
Overall MRT (/kg BW)	Shorter	Proportional	Longer	Longer
Nutrient origin:				
From digesta	Sufficient	Sufficient	Metabolized	Metabolized
Microbial metabolites	Sufficient, little	Little	Sufficient, little	Sufficient
Microbial cells	Very little	Very little	Sufficient, little	Sufficient
Small quantities	Deleterious	-	Deleterious	-

MRT, mean retention time.

This paper is based mainly on work done in collaboration with Dr C. M. Hladik of the Museum National d'Histoire Naturelle, Brunoy, Paris and then with Prof. R. D. Martin and Dr Ann MacLarnon of the Department of Anthropology, University College London. The author thanks all those who helped provide material.

#### REFERENCES

- Chivers, D. J. & Hladik, C. M. (1980). *Journal of Morphology* **166**, 337–386.
- Hofmann, R. R. (1973). *The Ruminant Stomach*. Nairobi: East African Literature Bureau.
- Janis, C. (1976). *Evolution* **30**, 757–774.
- Jarman, P. (1974). *Behaviour* **58**, 215–267.
- Kleiber, M. (1961). *The Fire of Life: An Introduction to Animal Energetics*. New York: Wiley.
- Langer, P. (1987). *Zeitschrift für Zoologisches Systematik und Evolutionforschung* **25**, 212–236.
- MacLarnon, A. M., Chivers, D. J. & Martin, R. D. (1986). In *Primate Ecology and Conservation*, pp. 75–85 [J. G. Else and P. C. Lee, editors]. Cambridge: Cambridge University Press.
- Martin, R. D., Chivers, D. J., MacLarnon, A. M. & Hladik, C. M. (1985). In *Size and Scaling in Primate Biology*, pp. 61–89 [W. L. Jungers, editor]. New York: Plenum.
- Milton, K. (1980). *The Foraging Strategy of Howler Monkeys*. New York: Columbia University Press.
- Moir, R. J. (1968). In *Handbook of Physiology*, vol. 5, sect. 6, pp. 2673–2694 [C. F. Code, editor]. Washington, DC: American Physiological Society.
- Romer, A. S. (1966). *Vertebrate Paleontology*. Chicago: Chicago University Press.
- Stark, R., Roper, T. J., MacLarnon, A. M. & Chivers, D. J. (1987). *Zeitschrift für Säugetierkunde* **52**, 88–96.