Oecologia (2003) 136:14–27
DOI 10.1007/s00442-003-1254-z

ECOPHYSIOLOGY

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The maximum attainable body size of herbivorous mammals: morphophysiological constraints on foregut, and adaptations of hindgut fermenters

Received: 22 July 2002 / Accepted: 1 March 2003 / Published online: 24 April 2003

Abstract An oft-cited nutritional advantage of large body size is that larger animals have lower relative energy requirements and that, due to their increased gastrointestinal tract (GIT) capacity, they achieve longer ingesta passage rates, which allows them to use forage of lower quality. However, the fermentation of plant material cannot be optimized endlessly; there is a time when plant fibre is totally fermented, and another when energy losses due to methanogenic bacteria become punitive. Therefore, very large herbivores would need to evolve adaptations for a comparative acceleration of ingesta passage. To our knowledge, this phenomenon has not been emphasized in the literature to date. We propose that, among the extant herbivores, elephants, with their comparatively fast passage rate and low digestibility coefficients, are indicators of a trend that allowed even larger hindgut fermenting mammals to exist. The limited existing anatomical data on large hindgut fermenters suggests that both a relative shortening of the GIT, an increase in GIT diameter, and a reduced caecum might contribute to relatively faster ingesta passage; however, more anatomical data is needed to verify these hypotheses. The digestive physiology of large foregut fermenters presents a unique problem: ruminant—and nonruminant—forestomachs were designed to delay ingesta passage, and they limit food intake as a side effect. Therefore, with increasing body size and increasing absolute energy requirements, their relative capacity has to increase in order to compensate for this intake limitation. It seems that the foregut fermenting ungulates did not evolve species in which the intake-limiting effect of the foregut could be reduced, e.g. by special bypass structures, and hence this digestive model imposed an intrinsic body size limit. This limit will be lower the more the natural diet enhances the ingesta retention and hence the intake-limiting effect. Therefore, due to the mechanical characteristics of grass, grazing ruminants cannot become as big as the largest browsing ruminant. Ruminants are not absent from the very large body size classes because their digestive physiology offers no particular advantage, but because their digestive physiology itself intrinsically imposes a body size limit. We suggest that the decreasing ability for colonic water absorption in large grazing ruminants and the largest extant foregut fermenter, the hippopotamus, are an indication of this limit, and are the outcome of the competition of organs for the available space within the abdominal cavity. Our hypotheses are supported by the fossil record on extinct ruminant/tylopod species which did not, with the possible exception of the *Sivatheriinae*, surpass extant species in maximum body size. In contrast to foregut fermentation, the GIT design of hindgut fermenters allows adaptations for relative passage acceleration, which explains why very large extinct mammalian herbivores are thought to have been hindgut fermenters.

Keywords Ruminants · Browsers · Grazers · Passage rate · Fermentation

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Introduction

Large body size provides a number of ecological advantages. The advantage cited most often is a reduced relative energy requirement for maintenance, and a relative increase in gastrointestinal capacity in relation to energy requirements (Parra 1978). This allows, but does not oblige, larger animals to use forage of lower

quality (Demment and Van Soest 1985) due to potentially longer passage rates and consequently more thorough digestion. Larger animals can facilitate larger movement ranges (Altman 1987). Large body size enables large species to successfully compete with smaller species for the same resource (e.g. elephants; Fritz et al. 2002) by means of interference (Persson 1985), or enables large species to use habitat resources unattainable for other species (e.g. the giraffe; Woolnough and du Toit 2001). Finally, large body size provides an organism with the ability to avoid predation (Owen-Smith 1988).

On the other hand, larger animals tend to have fewer offspring, mature sexually at a later age, and have longer gestation times (Peters 1983), all of which lead to long generation intervals, which drastically prolongs the evolutionary reaction time of larger species. In evolutionary terms, large mammalian species are "inert", and probably much more so than large dinosaurs in which the number of offspring was not as limited (Janis and Carrano 1992). Large animals obviously have high absolute energy requirements and therefore need abundant forage. Due to their low surface-to-volume ratio, they can have difficulties in dissipating heat, a fact that accounts for nocturnal habits and other adaptations of megaherbivores (Owen-Smith 1988); in fact, surface-to-volume ratio is considered a constraint on the potential upper body size of terrestrial mammals (Alexander 1989). Finally, larger animals are more conspicuous, a distinct disadvantage in the era of human predation. Humans have been held responsible for the extinction of very large animals like mammoths, giant ground sloths and temperate rhinoceroses. Economos (1981) demonstrated that due to the metabolic costs of gravity, 20 tons should be the maximum attainable body size of terrestrial mammals.

The relevance of body size for the morphophysiological design of different organ systems is well documented (e.g. Schmidt-Nielsen 1984; Damuth and MacFadden 1990). In this review, we want to draw attention to interactions between body size and particular digestive strategies. The omission of other factors important for the understanding of body size, such as resource availability, or allometric constraints on other organ systems, reflects the limitations of both the space available for this review and our own expertise, rather than the assumption that they have less significance.

Ecophysiological theories on the digestive relevance of body size

The influence of the body sizes of large herbivores has been a major area of ecophysiological research. Jarman (1968, 1974) and Bell (1969, 1971) focused attention on patterns of food selection among African ungulates of varying body size. They noted that, while specific metabolic rate decreases with increasing body weight, gut capacity remains a constant fraction of body weight; hence, larger ungulates should be able to tolerate a lower minimum dietary quality than smaller species. Geist (1974) labelled this concept the "Jarman-Bell Principle". This principle has since been applied to other animals (e.g. Gaulin 1979; Demment 1983), and has been used to explain the phenomenon of sexual dimorphism in ungulates (e.g. Barboza and Bowyer 2000). Parra (1978) supplied a quantitative verification of the concept by demonstrating that gut capacity, measured as gut contents, increases linearly with body weight. Demment and Van Soest (1985) postulated that the main effect of increasing body weight, and hence gut capacity, should be an increase in ingesta retention (mean retention time, MRT) and thus time available for digestion. Illius and Gordon (1992) finally provided the quantification of this influence, demonstrating that MRT (h) = 9.4 body weight$^{0.255}$ in hindgut fermenters and MRT (h) = 15.3 body weight$^{0.251}$ in ruminants.

Modifications to the general concept of the direct correlation of body weight and digestive potential were added, e.g. for small (rodent) herbivores (Justice and Smith 1992; Smith 1995), to include effects of differences in relative intake and food sorting; Owen-Smith (1988) and Van Soest (1996) also emphasized that larger ungulates can support their lower specific metabolic requirements either by accepting forage of lower quality, or by ingesting lesser amounts of regular quality forage per day, or some combination of both. Thus, larger animals should eat diets of lower nutritional quality than those selected by smaller herbivores, but the difference should be less marked than predicted simply on the basis of the body size-metabolic rate relationship.

Open questions in large herbivore digestive physiology

Why does the elephant deviate from the common body size scheme?

In recent studies on the digestive physiology of elephants (Clauss et al. 2003; Loehlein et al. 2003), we raised the question of why elephants so obviously deviate from the common digestive scheme postulated for herbivores of increasing body mass: they do not have long ingesta passage rates, and achieve only comparatively low digestibility coefficients. This is not only true in free-ranging animals, where one could be tempted to explain low digestibilities on the basis of a very low quality diet, but also in captive animals where food quality is higher.

Why is the largest ruminant smaller than the largest hindgut fermenter, and why is the largest ruminant a browser?

It has been repeatedly observed that browsing ruminants are mainly represented by smaller species, and grazing ruminants mainly by larger species (e.g. Case 1979; Owen-Smith 1988; Van Wieren 1996; Brashares et al. 2000; Gagnon and Chew 2000). This is not due to

physiological limitations but to forage abundance (Van Soest 1996). Large species cannot be as selective as small species, and the large amounts of forage necessary to supply large species are available mainly as grasses. If there is, however, an abundant food resource for browsers, they can also reach large body mass, e.g. the moose (*Alces alces*) or the giraffe (*Giraffa camelopardalis*; Renecker and Hudson 1992). The ruminant body weight range has been explained theoretically by Demment and Van Soest (1985). Whereas their explanation for the lower ruminant body weight limit is widely accepted (Prins and Kreulen 1991), their explanation for the upper body weight limit remains under debate (Van Soest 1994). By calculating the time necessary for optimum digestion of grass and browse forages, and using one correlation between body weight and passage rate for all feeding types, the authors demonstrate that above a certain body weight—600 kg for browse, 1,200 kg for grass forage—ruminants no longer have an advantage over hindgut fermenters in terms of digestive efficiency. The absence of ruminants in the larger body weight ranges is explained by this lack of digestive advantage. A "lack of digestive advantage", however, does not explain the complete absence of species from the higher body weight range. This absence needs to be explained in terms of a distinctive disadvantage or limitation.

Is the gastrointestinal capacity really a constant of body weight?

The Jarman-Bell Principle (see above) is based on the observation that gastrointestinal capacity remains a constant proportion of body weight. The correlation between body weight and gastrointestinal capacity determined by Parra (1978) for all herbivores of gut capacity = 0.0936 body weight$^{1.0768}$ is generally interpreted as an indication that the "true" exponent is 1. If that was the case, gastrointestinal capacity of herbivores of all body sizes would always be 9.36% of body weight. If Parra's exponent, however, is taken literally, we can deduce that gut capacity, expressed as a percentage of body weight, increases with increasing body weight, and the increase becomes less as body size increases.

Given the fact that the largest extant and probably all larger extinct mammalian herbivores were hindgut fermenters (Langer 1994), we intended to elucidate the reason and possible morphophysiological correlates of these observations. We hypothesize that buffaloes, giraffes, and the common hippopotamus (*Hippopotamus amphibious*) represent, in general, the maximum attainable body size limits for grazing and browsing ruminants and non-ruminant foregut fermenters, respectively, and that the elephant indicates a digestive trend all other, even larger, extinct hindgut fermenters would have had to follow (Colbert 1993). In order to test the hypothesis on the limiting effect of foregut fermentation as we know it in large ungulates, we surveyed the existing data on fossil ungulates, looking for potentially larger ruminant species.

Body sizes of herbivores

Although various, and at times incredibly high, body weights have been reported for some ruminant species, for the purpose of this review we will follow Owen-Smith (1988) in his allocation of body weight ranges to ruminant species and hippos (cf. Table 1). The most notable

Table 1 Body weights for large ruminant species and the hippopotamus from different sources

Species	Body mass range (kg)	Average/maximal body mass (female)	Average/maximal body mass (male)	Source
Grazers				
Bison bison	361–1,000	495	808/907	Silva and Downing (1995) Owen-Smith (1988)
Bos gaurus	650–1,000	590/700	880/940	Silva and Downing (1995) Owen-Smith (1988)
Bos javanicus	400–800			Silva and Downing (1995)
Bos sauveli	700–900			Silva and Downing (1995)
Bubalus arnee	248–1,200			Silva and Downing (1995)
Syncerus caffer	295–667	520/636	650/860	Silva and Downing (1995) Owen-Smith (1988)
Browsers				
Giraffa camelopardalis	680–1,400 550–1,900	825/1,125	1,200/1,400	Silva and Downing (1995) Owen-Smith (1988) Kingdon (1979)
Nonruminant				
Choeropsis liberiensis	200–270	160	200	Silva and Downing (1995) Owen-Smith (1988)
Hippopotamus amphibius	600–2,000	1,350/2,352	1,500/2,669	Silva and Downing (1995) Owen-Smith (1988)

Table 2 Body weights for large herbivore species from different sources

Species	Body mass range (kg)	Average/maximal body mass (female)	Average/maximal body mass (male)	Source
Wild equids	136–410	220–380/242–450	250–400/284–450	Silva and Downing (1995) Owen-Smith (1988)
Tapirus indicus	250–375	160	275	Silva and Downing (1995) Owen-Smith (1988)
Tapirus terrestris	77–300	135	160	Silva and Downing (1995) Owen-Smith (1988)
Dicerorhinus sumatrensis	900–1,000	800	800	Silva and Downing (1995) Owen-Smith (1988)
Rhinoceros sondaicus	1,500–2,000	1,300	1,300	Silva and Downing (1995) Owen-Smith (1988)
Diceros bicornis	816–1,300	932–1,080/1,134–1,316	931–1,124/1,022–1,316	Silva and Downing (1995) Owen-Smith (1988)
Ceratotherium simum	1,400–2,300	1,600/1,800	2,200/2,400	Silva and Downing (1995) Owen-Smith (1988)
Rhinoceros unicornis	1,410–2,000	1,600	2,100	Silva and Downing (1995) Owen-Smith (1988)
Loxodonta africana	1,700–6,100	2,800/4,000	5,000/8,000	Silva and Downing (1995) Owen-Smith (1988)
Elephas maximus	1,810–5,000	2,500/4,160	4,000/5,400	Silva and Downing (1995) Owen-Smith (1988)
(*Indricotherium transouricalium*†)		11,000/15,000	11,000/15,000	Fortelius and Kappelman (1993)

difference is that giraffes are, for both sexes, generally about 400 kg heavier than the respective buffaloes. Body weights for extant very large hindgut fermenters are summarized in Table 2. Additionally, probably the most accurate weight estimate for *Indricotherium transouralicum*, the "largest land mammal ever imagined", is given (Fortelius and Kappelman 1993). This extinct giant is considered to represent the actual upper size limit ever attained by terrestrial mammals. Its body weight is thought to not have exceeded 20 tons. In contrast, the largest dinosaurs, the sauropods, are thought to have weighed 10–75 tons (Farlow 1987).

Limits to forage fermentation

All mammalian herbivores depend on the fermentation of plant cell walls by gastrointestinal bacteria. Within the body size range usually studied, the efficacy of this fermentation is directly correlated to fermentation time, i.e. to passage rates. The longer passage rates that larger animals can achieve is regarded as the main digestive advantage of large body size (Demment and Van Soest 1985). However, the usefulness of ingesta passage delay is clearly limited: there will be a point at which any forage is completely digested, and retention beyond this point will not yield further benefit. Demment and Van Soest (1985) demonstrated that, after 60–70 h, digestion of plant material was complete. Interestingly, this limit, though recognized by many scientists, has never been understood as an actual limitation. Demment and Van Soest (1985) state that at a certain body size "a point is reached at which complete digestion of the potentially digestible cell wall will occur even without selective delay of ingesta"; they leave open the question of what will happen if a species surpasses this body size limit. Farlow (1987), speculating on the digestive physiology of large dinosaurs, cited Demment and Van Soest and stated there would "come a time when an animal could not accomplish any more by retaining digesta in its fermentation chamber". Prins and Kreulen (1991) and Van Soest (1994) introduced another variable to these considerations—the fact that with increasing passage times, methanogenes could grow in increasing proportions. Methanogenes are bacteria that convert acetic acid—the dominant volatile fatty acid in both fore- and hindgut fermenters, and the major energy source of large herbivores—to methane and carbon dioxide, thus causing severe energy losses. Prins and Kreulen (1991) actually used methanogene growth rates to calculate a ruminant upper body size threshold, without considering the same consequences for hindgut fermenters. Van Soest (1994) stated that "very large herbivores [...] have no need to reduce passage to optimize the yield of metabolizable energy". To our knowledge, the consequence of these concepts, namely that very large herbivores *not only have no need* for an increased passage delay, but are actually *obliged* to accelerate passage rate relative to their body mass, has not been emphasized.

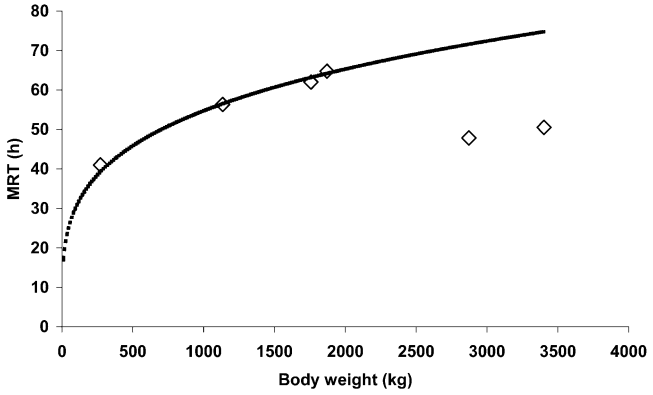

Fig. 1 Passage rates of large hindgut fermenters. Average data for wild equids, rhinos and elephants from Foose (1982); regression line according to Illius and Gordon (1992). Elephants do not match the common pattern of increased mean retention times (MRT) with increasing body weight

Ingesta passage in large hindgut fermenters

The most comprehensive comparative study of herbivore passage rates is the one by Foose (1982, Fig. 1). This dataset was the major source for the quantification of herbivore passage rates by Illius and Gordon (1992). The equation for hindgut fermenters given by these authors is MRT (h) = 9.4 body weight$^{0.255}$. Thus, the MRT of a 3 ton elephant or a hypothetical 15 ton *Indricotherium* therefore should be 72 or 109 h, respectively. But, according to Foose (1982), an elephant of this size has an MRT below 50 h, and an MRT of 109 h for *Indricotherium* would have surpassed the 4-day threshold that Van Soest (1994) postulates for the disproportionate growth of methanogene bacteria. We therefore suggest that the comparatively fast ingesta passage in elephants indicates the trend that must have also been present in past very large herbivore faunas.

The main limitation of Foose's dataset is that the experimental set-up allowed only one pooled faecal sample to be taken per day. If other studies with frequent daily sampling are compared to Foose's data (Hackenberger 1987; Kiefer 2002; Clauss et al. 2002a; Polster, in preparation), lower absolute values for MRTs result, but the pattern does not change qualitatively for hindgut fermenters (in contrast to the ruminant data, for which differences between browsers and grazers become evident, Clauss and Lechner-Doll 2001). These lower MRTs indicate that the trade-off between a fibre fermentation and methanogene growth on the one hand, and ingestion of fresh material on the other hand, might not lie as close to the absolute time necessary for complete fibre digestion as suggested by Foose's data.

Morphological correlates of MRT acceleration

When investigating potential morphological correlates for the comparatively fast passage in large herbivores, the

Table 3 Length of the gastrointestinal tract (*GIT*) in metres. *DFC* Distal fermentation chamber (caecum + colon ascendens)

Source	[a]	[b]	[b]	[c]	[d]	[e]	[a]	[f]	[g]	[a]	[h]	[i]	[j]	[k]	[k]	[a]	[l]	[m]	[n]
	Pony	Am. tapir		Malayan tapir	Horse		Zebra	Sumatran rhino	Javan rhino	Black rhino			White rhino	Indian rhino		Elephant			
Stomach	0.2	–	–	0.5	(0.25)	(0.25)	0.2	–	–	0.9	1.2	0.8	(1)	1.2	0.8	1.1	1.2	1.0	1.2
Small intestine	7.9	–	–	21.0	22.5	26.7	11.4	11.0–16.6	8	12.0	8.0	11.6	13.8	19.8	15.2	13.8	20.0	10.0	11.0
Caecum	0.7	–	–	0.3	1.0	1.0	0.8	0.8–0.9	0.4–0.6	0.7	1.1	–	0.8	0.9	0.6	0.8	0.5	0.5	1.0
Colon total + rectum	4.2	–	–	5.9	7.5	7.0	4.7	–	–	4.9	2.9	–	7.2	9.1	6.4	8.5	5.8	6.0	6.0
DFC total	3.0	–	–	–	4.5	4.5	3.4	–	–	3.7	–	–	–	–	–	6.1	–	–	–
Total GIT	13.1	16.8	27.4	27.8	31.3	35.0	17.2	–	–	18.5	13.2	16.9	22.8	31.1	23.1	24.2	27.5	17.5	19.0

[a] Stevens and Hume (1995), measured from the graph, [b] Anon. (1872), [c] Home (1821), [d] Bourdelle and Lavocat (1955), [e] Frewein et al. (1999), [f] Home (1821) and Garrod (1873), [g] Garrod (1877) and Beddard (1887), [h] De Bouveignes (1953), [i] Wilson and Edwards (1965), [j] Kiefer (2002), [k] Owen (1862), [l] Mullen (1682), [m] Frade and Vanfrey (1955), [n] Sikes (1971)

Table 4 Proportion of different GIT sections in percent of total GIT length. For sources, see notes to Table 3

Source	[a]	[c]	[d]	[e]	[a]	[a]	[h]	[i]	[j]	[k]	[k]	[a]	[l]	[m]	[n]
	Pony	Tapir	Horse		Zebra	Black rhino			White rhino	Indian rhino		Elephant			
Stomach	2	2	1	1	1	1	9	5	–	4	4	5	4	6	6
Small intestine	61	76	72	76	66	66	61	68	61	64	66	57	73	57	58
Caecum	5	1	3	3	5	5	8	–	4	3	3	3	2	3	5
Colon and rectum	33	21	24	20	28	28	22	–	32	29	28	35	21	34	32
DFC total	23	–	14	13	20	20	–	–	–	–	–	25	–	–	–

Table 5 The diameter of the small intestine in different hindgut fermenters

	Species	Small intestine diameter (cm)
Frewein et al. (1999)	Horse	5–7
Garrod (1873)	Sumatran rhino	5–6
Kiefer (2002)	White rhino	5–6
Owen (1862)	Indian rhino	5–8
Sikes (1971)	Elephant	13–20

Table 6 The diameter of the caecum in different hindgut fermenters

	Species	Caecum diameter (cm)
Bourdelle and Lavocat (1955)	Horse	15–18
Garrod (1877), Beddard (1887)	Javan rhino	38–51
Home (1821), Garrod (1873)	Sumatran rhino	46–91
Endo et al. (1999), Kiefer (2002)	White rhino	21–30
Owen (1862)	Indian rhino	24–44
Mullan (1682), Sikes (1971)	Elephant	25–57

Table 7 Capacities (measured as wet contents, kg) of GIT sections of different hindgut fermenters. *DFC* Distal fermentation chamber

Source	[a]	[b]	[c]	[d]	[c]
	Pony		Black rhino	Elephant	
Stomach	3	4	37	51	58
Small intestine	2	3	9	38	28
Caecum	4	5	40	86	75
Colon total	19	18	87	312	254
DFC	22	22	113	–	279
Total tract	29	31	173	487	415

[a] Meyer et al. (1993)
[b] Coenen et al. (1990)
[c] Clemens and Maloiy (1982)
[d] Van Hoven et al. (1981)

paucity of existing data is striking, especially in view of the fact that these animals have lived and died in captivity for centuries. A great proportion of the data we draw upon stems from the nineteenth century. All elephant data refers to the African species, *Loxodonta africana*. The data from Stevens and Hume (1995) were derived by measurements from the drawings in their monograph.

There are two basic ways to accelerate passage through a tubular system, namely either a shortening of the tube, or an increase of its diameter. Data on the length of the GIT of large hindgut fermenters (Table 3) do not seem to indicate an increase in GIT length as would be expected from body size alone. Not only domestic horses—whose long small intestine could well be interpreted as an adaptation to concentrate feeding throughout their domestication period—but also a Malayan tapir (*Tapirus indicus*) seems to have a generally longer GIT than an elephant. The proportions of the different GIT sections, based on length measurements (Table 4), do not indicate any systematic shifts in GIT design, maybe with the exception of the caecum which seems to be shorter in larger species. Several authors have commented upon a comparatively short but wide caecum in rhinos (Owen 1862; Mitchell 1903/6; Bourdelle and Lavocat 1955; Endo et al. 1999) and elephants (Mullen 1682).

The few available measurements on the diameter of the small intestine (Table 5) seem to indicate a drastic increase in this parameter in elephants. A wide small intestine could account for low digestibility values of protein and nitrogen-free extracts (Clauss et al. 2003) due to unfavourable proportions of absorptive surface and ingesta volume; similarly, a voluminous small intestine with potentially incomplete mixing of ingesta and GIT secretions could account for the fact that GIT bacteria are regularly found in the small intestine of elephants (Eloff and Van Hoven 1980; Van Hoven et al. 1981). Existing data on the diameter of the base of the caecum does not indicate a particular trend, except that this organ seems to be wider in rhinos and elephants than in horses (Table 6).

The existing data on GIT capacity, measured as GIT contents (Table 7), emphasizes the need for measurements that can be correlated to the body weight of the same individual. The absolute values do not allow any conclusive observation. The average body weights of the ponies were 154 (Coenen et al. 1990) and 213 kg (Meyer et al. 1993). If we assume a body weight of 1000 kg for the black rhinoceros (*Diceros bicornis*), then we can create regression lines and adjust the elephant body weights accordingly (Fig. 2): if the body weights for the elephants are chosen to match expected values for small intestinal and colonic capacity, then caecal and total GIT capacity of these elephants would be less than expected (Fig. 2A). This finding is in accord with the postulate that elephants must show morphological adaptations for comparatively faster passage rates. If, however, the body weights are chosen so that the total GIT capacity is in accord with the pony-rhino regression line (Fig. 2B), then

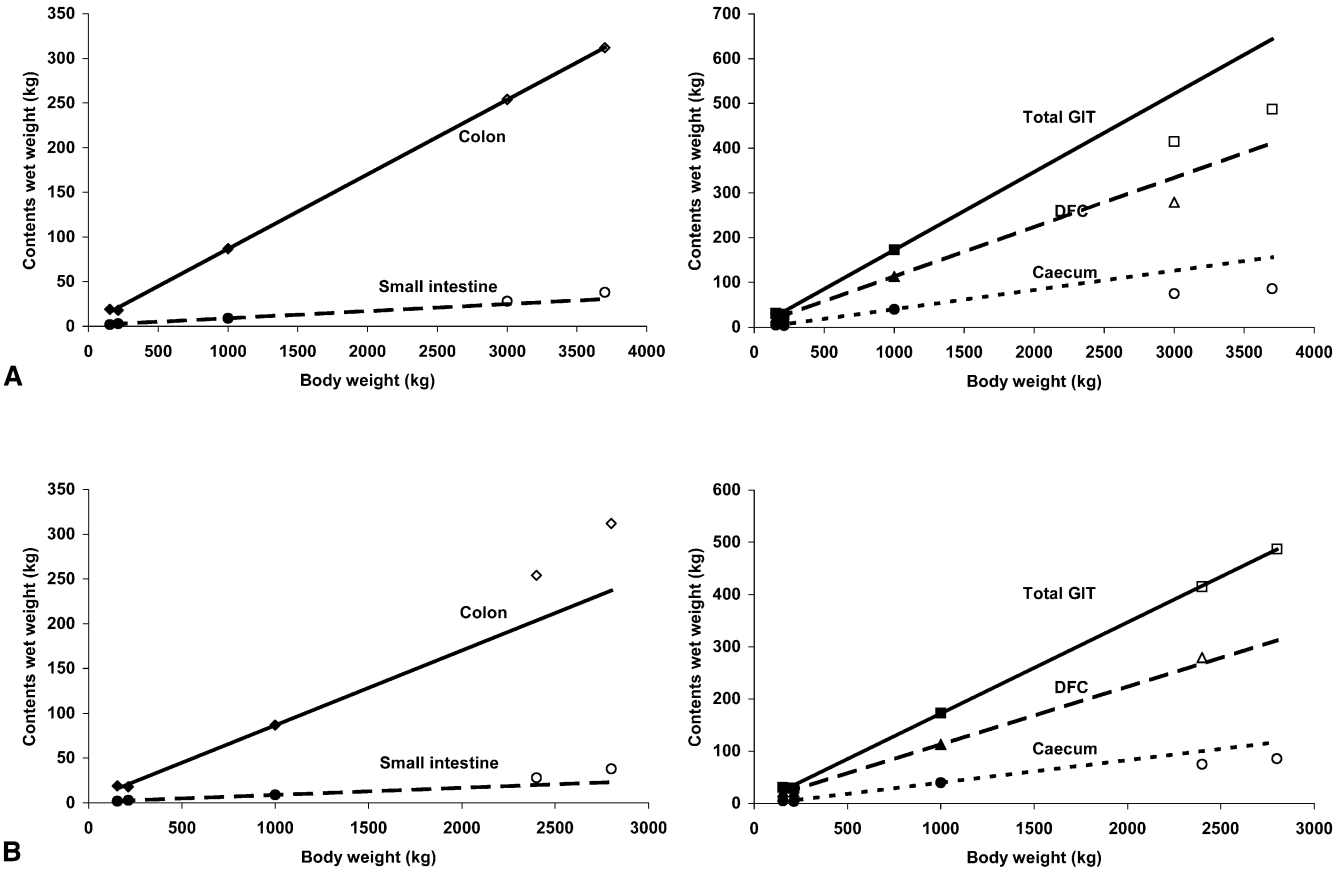

Fig. 2A, B Capacities (measured as wet contents, kg) of different gastrointestinal tract (GIT) sections of ponies, black rhinos and elephants. Data from references listed in Table 6, including pony body weights. Black rhino body weight was assumed to be 1,000 kg. The body weights of the elephants were adjusted to match either: **A** the regression lines on small intestinal and colonic capacity; or **B** the regression lines on total GIT capacity

these elephants would have higher small intestinal and colonic capacities than expected. As long as comprehensive measurements are lacking, this second, albeit seemingly unlikely, interpretation cannot be ruled out. It is notable, however, that for either solution, the caecal capacity remains below the regression line.

A last qualitative observation can be made on the drawings of the GIT of hindgut fermenters from Stevens and Hume (1995, Fig. 3). The transition from the dorsal layer of the colon ascendens to the colon transversum is relatively abrupt in equids—the diameter of the large, "stomach-like" colonic fermentation chamber is reduced without transition to the small tube of the colon transversum (Frewein et al. 1999). The same abrupt change of diameter at this point can be deduced for the Malayan tapir from Home (1821). For the Indian rhino, however, Owen (1862) observed that this transition is a gradual one, as can be deduced from Fig. 3 for the black rhino. In the elephant, it seems that at the colonic localization there is hardly any reduction in diameter. These differences in morphological design might also contribute to a comparatively faster ingesta passage in the larger species.

Ruminant forestomach capacity

We propose that the most important (and mostly overlooked) feature of ruminant morphophysiology, with respect to the subject of this review, is the fact that not only the absolute but also the relative proportion of reticulorumen contents increases linearly with body size for both grazers and browsers (Fig. 4). As the ruminoreticulum delays the passage of ingesta and thereby limits intake, larger ruminants need to increase their ruminoreticulum capacity in order to compensate for intake limitation and accommodate higher energy requirements. If the regressions of Fig. 4 are used, one can theoretically calculate that at a body weight of 12 tons, a ruminant would consist of nothing but rumen contents. Obviously, such a calculation has little practical relevance, but it stresses the point that there must be either: (1) a certain body weight threshold at which the relative ruminoreticulum capacity does not increase further, a fact for which there is currently no evidence; or (2) a certain threshold of ruminoreticulum capacity that cannot be surpassed, and therefore limits the maximum attainable body weight of ruminants. The different intercept

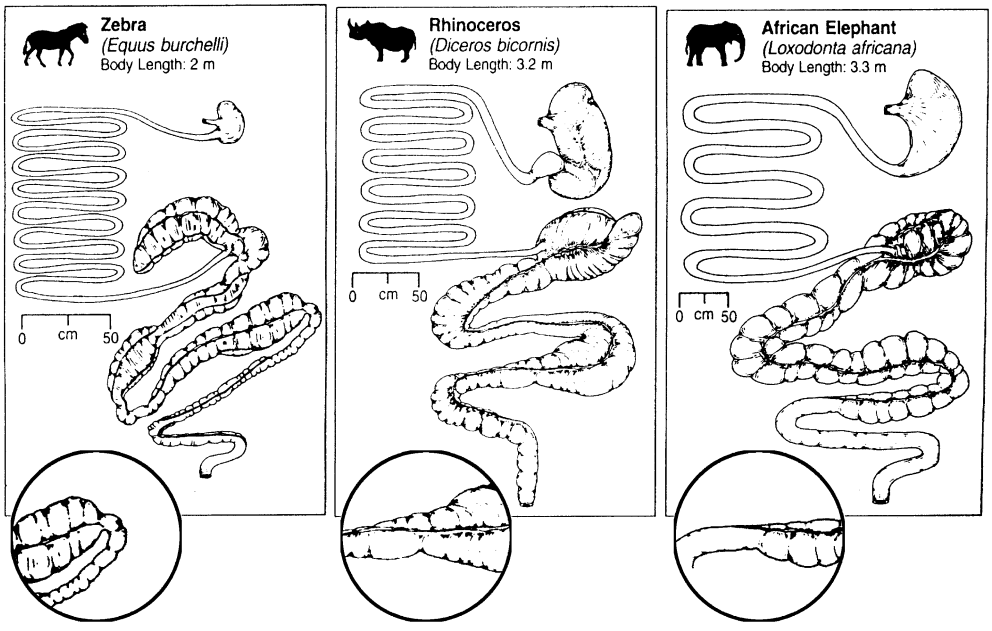

Fig. 3 Digestive tracts of large hindgut fermenters, with special emphasis on the transition from the colon ascendens to the colon transversum. Adapted from Stevens and Hume (1995)

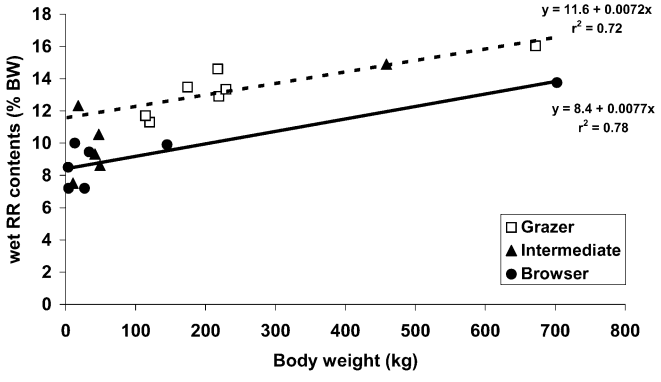

Fig. 4 The correlation of body weight and relative weight of the reticulo-rumen contents (wet weight as % of body weight) for free-ranging ruminant species of different feeding types. Data from Giesecke and Van Gylswyk (1975), Hoppe (1977) and Maloiy and Clemens (1982)

(P<0.001) [1] of the two regression lines of Fig. 4 suggests that such a maximum body weight should be reached earlier by grazers than by browsers. The slopes of the regression lines for grazers and browsers do not differ (P=0.843). This allows the calculation of a common slope for both equations which amounts to 0.00753. Based on this common slope, we can adjust the intercepts yielding

y_{grazer} = 0.00753body $weight_{grazer}$ + 11.46 and
$y_{browser}$ = 0.00753body $weight_{browser}$ + 8.43.

The scope of the theoretical size difference between maximum grazers and browsers can then be estimated from:

0.00753body
$weight_{grazer}$ + 11.46=0.00753body $weight_{browser}$ + 8.43
which yields
body $weight_{grazer}$ + 402 = body $weight_{browser}$

This means that, at any threshold for the relative ruminoreticulum capacity, a browser could be about 400 kg bigger than the largest possible grazer. This difference is in good accord with the observed difference between species maxima for large male and female Bovinae and giraffes according to Owen-Smith (1988) of 940 versus 1,400 and 700 versus 1,125 kg, respectively (Table 1).

The reason for the larger ruminoreticulum in grazers was put forward by Owen-Smith (1982) and elaborated further by Clauss et al. (2002b): the forage of a browser does not form a "fibrous raft" and a stratification of ruminoreticulum contents, and can therefore be passed through the ruminoreticulum comparatively fast. This permits a selective particle retention that is nearly constant across a wide range of body sizes. The forage of grazers, however, automatically induces a stratification of rumen contents, and is thus responsible for longer passage rates and a selective particle retention that might increase with body weight (c.f. Clauss and Lechner-Doll 2001). In order to meet their energetic demands, grazers therefore had to increase their forestomach fermenting capacity more than browsers in order to compensate for the increase in particle retention and food intake limitation (Owen-Smith 1982).

[1] Regression lines were calculated and compared according to Sachs (1997) using the SSS software (Rubisoft software GmbH, Puchheim, Germany, 1998).

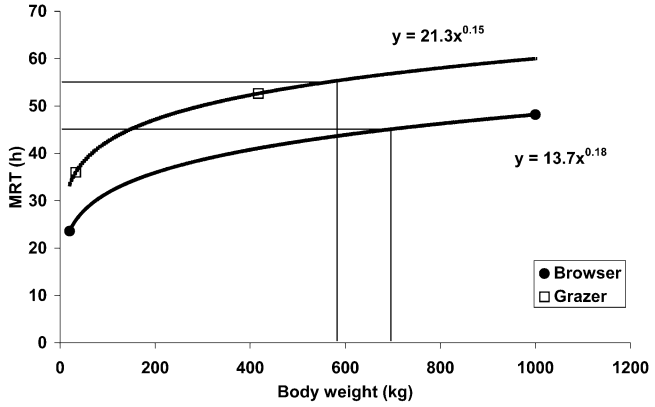

Fig. 5 A qualitative model of ruminant mean MRT for grazers and browsers. Data from Bartocci et al. (1997), Clauss et al. (1998) and Behrend (2000). Demment and Van Soest (1985) calculated optimal energy gains from grass and browse forages for a rumen MRT of 45 and 35 h, respectively. 10 h were added for passage through the rest of the alimentary tract

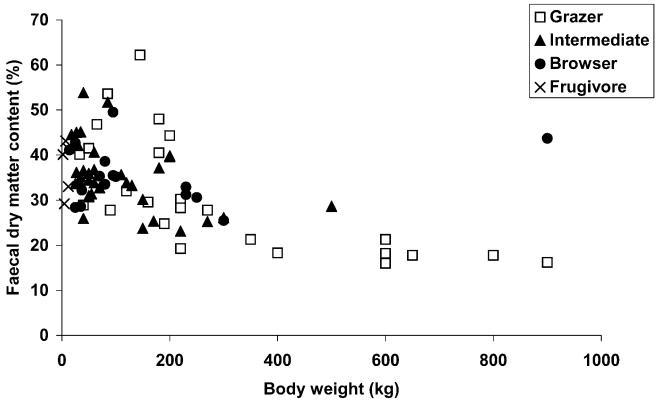

Fig. 6 The correlation of body weight and faecal dry matter content for captive ruminant species of different feeding types. Data from Clauss et al. (2002c)

Ruminant passage rates

One of the consequences of increased particle retention in a larger ruminoreticulum should be longer ingesta retention times in grazers. The question of potential differences in passage rates between grazers and browsers has already been addressed in Clauss and Lechner-Doll (2001). If we use four data points on the MRT of particles of a defined size to create Fig. 5—a small and a large grazer (mouflon *Ovis ammon musimon*: body weight 33 kg/MRT 36.0 h, Behrend 2000; Asian buffalo *Bubalus bubalus*: 417 kg/52.7 h, Bartocci et al. 1997) and a small and a large browser (roe deer *Capreolus capreolus*: 20 kg/23.6 h, Behrend 2000; giraffe *Giraffa camelopardalis*: 1,000 kg/48.2 h, Clauss et al. 1998)—it becomes obvious that a potential difference in ingesta MRT between the feeding types is of particular importance. Given the difference in the time necessary to attain a reasonable energy gain from the fermentation of the different forages as described by Demment and Van Soest (1985, see above), the browsers can, due to their faster passage rates, still function economically at larger body sizes than the grazers. Thus, both the difference in forestomach capacity and in ruminoreticulum ingesta retention can explain the observed tendency for the largest extant browsers to be bigger than grazers.

Limitations to forestomach capacity increase

The question remains, however, how the maximum ruminant body weight, determined by the maximum attainable relative ruminoreticulum capacity, can be defined. We propose that the first limiting factor for an increase in ruminoreticulum capacity is the available space in the abdominal cavity for which all abdominal organs compete. This concept is rarely addressed in the literature (Roux 1881; Gutmann 1989). As the ruminoreticulum reduces the space available to other organs, one or several of these organs should become significantly affected in their physiological function (Demment and Longhurst 1987). Mitchell (1903/6, p 523) and Langer (1991, Table 7) pointed out that herbivores with a complex forestomach generally tend to have small caeca, but did not interpret this fact as an outcome of intra-abdominal space competition.

A suggestion of what physiological function could be the first to be affected by a decrease in available intra-abdominal space can be deduced from Clauss et al. (2002c). In that work, the authors presented faecal dry matter data for 81 captive wild ruminant species from temperate zone zoos during the winter, and concluded that, as the animals investigated were not subjected to heat stress and had ad libitum access to drinking water, the resulting faecal water content should directly reflect the length of the colon descendens (see also Woodall and Skinner 1993). Clauss et al. (2002c) reported a monotonous decrease in faecal dry matter content with increasing body weight for ruminants. In our recent studies, we found a negative monotonous trend for grazers (Spearman coefficient = –0.80, $P<0.001$) and intermediate feeders (Spearm. coeff. = –0.44, $P=0.008$), but not for browsers (Spearm. coeff. = –0.10, $P=0.708$) or frugivores (Spearm. coeff. = 0.21, $P=0.741$). From Fig. 6 it is obvious that grazers have a general tendency to increase their faecal water content with body size. If data on free-ranging animals is collated (Clemens and Maloiy 1983; Woodall and Skinner 1993), a similar trend can be observed. These results are in accordance with the observation that all large grazers defecate "pies", not "pellets". Clemens and Maloiy (1983, 1984) stated the curious fact that the African buffalo (*Syncerus caffer*) is the only ruminant species in its habitat that does not produce a faecal pellet. In their study, the buffalo had the lowest value for colonic water absorption of all species investigated. Accordingly, African buffalo depend on the availability of drinking water (Sinclair 1974; Field 1976).

In an earlier work, Maloiy and Clemens (1980) had shown that among five species of eastern African herbivores the zebu cattle—another large ruminant that does not produce faecal pellets—was the least efficient in colonic water re-absorption. The data from Clauss et al. (2002c) show that African buffalo and zebu share a high faecal water content with all other representatives of the Bovinae. This family represents the largest grazers, and the question arises why there is not one species among them with a higher faecal dry matter content—an option so evidently open to other ruminants.

We hypothesize that the larger ruminoreticulum of grazers leads to an obligatory size reduction in other organs, e.g. the colon descendens. Therefore for very large grazers, a "regular" faecal water absorption as in other ruminant species is no longer possible. This hypothesis could also explain the observed differences in hindgut anatomy between the feeding types. Hofmann (1988) states that grazers have a smaller caecum and a shorter spiral colon with fewer coils than browsers, and Gordon and Illius (1994) found that the difference in hindgut contents between Hofmann's feeding types was significant. The largest existing grazers could therefore represent the largest possible increase in ruminoreticulum capacity that can be achieved without risking the integrity of colonic function.

The case of the hippopotamus

Our hypothesis on the abdominal space limitation gains support from the only other very large, non-ruminant foregut-fermenting herbivore, the hippopotamus. The hippo feeds on grass and has a complex forestomach; however, in contrast to grazing ruminants, and similar to other foregut fermenters, a stratification of contents has not been demonstrated (Langer 1976) and a distinct selective particle retention seems unlikely. Langer (1988) quotes different sources that give a range of stomach capacity of 11–26.6% of body weight, which is higher than that of any ruminants investigated; accordingly, hippos seem to achieve particularly long ingesta retention times (Foose 1982). If the equation for browsers (i.e. animals not impeded by an intake limitation due to forestomach content stratification) from Fig. 4 on relative ruminoreticulum capacity is used, then the hippo body weight range from Table 1 would yield values of 18.8% and 20.0% for average females and males (Owen-Smith 1988) and 26.5% for the maximum female body weight. Such an enormous foregut capacity in the hippo comes at a price: Stevens and Hume (1995) state that the hippo, while having one of the most complex forestomachs, has the simplest and shortest hindgut of the Artiodactyla. A caecum is absent, the colon is undifferentiated (Van Hoven 1978; Clemens and Maloiy 1982), and the dry matter concentration of hindgut contents measured by Clemens and Maloiy (1982) was low (10.7%). It could be hypothesized that the hippo can only tolerate high faecal water losses due to its amphibious lifestyle, and is limited to this habitat niche by its gastrointestinal morphology. For the pygmy hippo (*Choeropsis liberiensis*), data on the relative capacity of the forestomach is lacking (Langer 1988).

The fossil evidence

If we assume our hypothesis on abdominal space limitation to be universally valid, then we would expect to find no ruminants (or tylopods) in the fossil evidence that exceed the largest extant Bovinae or giraffe in body size.

The super-buffaloes (*Pelovoris* ssp.)

We used the data from Gentry (1967) and from Gentry and Gentry (1978) on skeletal measurements of *Pelovoris* to calculate body weight estimates, using the regression equations from Janis (1990) and Scott (1990). This resulted in a body weight estimate of 660 kg based on femur length, and a range of 827–1,205 kg (mean 1,016 kg) based on dental measurements. From the same sources, the estimated body weight of *Homoioceras* spp. and *Bos primigenus* were 940 and 906 kg based on femur length and 731 and 700 kg based on dental measurements, respectively. These calculations indicate that these extinct large bovids did not significantly surpass the largest extant buffaloes in size.

The giraffids

Giraffa camelopardalis is the largest ruminant that is listed in the Neogene of the Old World database (NOW 2002). For the grazer *Samotherium*, body weight estimates of 600 kg are given. The Sivatheriinae could represent the only detectable deviation from the trend that fossil ruminants did not exceed extant forms in body size. No quantitative body size estimate has, to our knowledge, been published for this group. According to Solounias et al. (2000), the Sivatheriinae comprised mainly intermediate feeders or grazers. Applying the equation for total skull length from Janis (1990) to the data provided by Harris (1991), we estimate a body weight of 1,230 kg. Using maximum bone length measurements from Geraads (1996) and Singer and Boné (1960) and the equations from Scott (1990), we estimate a mean of 937 kg (range 529–1,739 kg). However, length measurements are not considered very reliable predictors (Scott 1990); calculations with length measurements on the extant giraffe yield a mean estimate of 3,013 kg (range 2,100–4,467 kg). If data on the breadth of the metacarpal/metatarsal bones are used from the same sources, the estimate for the giraffe is more realistic with 1,522 kg (range 1,215–1,829 kg), and gives 2,018 kg (range 1,727–2,310 kg) for Sivatheriinae. Data on maximal tooth measurements (Singer and Boné 1960; Geraads 1996), transformed according to Janis

(1990), yield even higher body weight estimates of 1,020–3,720 kg (for extant giraffe 530–1,880 kg). All these estimates confirm the qualitative interpretation of Singer and Boné (1960) that the Sivatheriinae have larger teeth and shorter but thicker bones than the extant giraffe. One could, on the one hand, speculate that the data—short but very strong limb bones—suggest a rather stout animal with a potentially fundamentally more capacious abdominal cavity. One could doubt that an extrapolation of estimates based on measurements that distinctively exceed the range of values that were used for the establishment of the predictive equations (Janis 1990) is methodologically sound, or speculate that the Sivatheriinae deviate from the general body design of those groups from which the predictive equations were derived. Either way, the Sivatheriinae remain the most likely candidates for an exception to our hypothesis.

The giraffe camel (*Aepycamelus major*)

The estimated body weight of this giant browsing tylopod is discussed extensively by MacFadden and Hulbert (1990), who conclude that an estimate of 1,026 kg is realistic. Scott (1990) gives a range of estimates of 501–1,013 kg based on different techniques.

Thus, with the exception of the Sivatheriinae, the ungulate fossil record supports the notion that the delayed ingesta passage, the thereby necessitated increase in forestomach capacity, and the space limitation of the abdominal cavity, prevented any larger ruminant life forms from evolving. The ruminant digestive tract does not allow a relative acceleration of ingesta passage. Any larger fossil herbivorous ungulates (giant rhinos, mammoths, etc.) belonged to modern taxa that are hindgut fermenters. Interestingly, it has been suggested that, due to the intake-limiting effect of a rumen-like forestomach, dinosaurs should have been hindgut fermenters (Farlow 1987). In this context, we suggest that from their body size alone one could argue that the fossil giant ground sloths were, unlike their rather distant relatives, the extant and comparatively small arboreal sloths[2], hindgut fermenters (cf. Guthrie 1984). This is in contrast to Naples (1987, 1989) who claims that ground sloths, too, possessed a foregut fermentation chamber.

Macropods

The largest extant macropodid herbivores, the red and grey kangaroos (*Macropus giganteus* and *Macropus rufus*), achieve a relative capacity of their foregut (wet contents in kg) of 5.4–6.0% body weight (Langer 1988), and are thus even below the intercept for browsing ruminants (Fig. 3). Macropodid marsupials have evolved foregut fermentation based on a stomach anatomy that resembles, anatomically, a large intestine, and are not as intake-limited as ruminants of comparable size on high-fibre diets (Hume 1999, Fig. 6). The interesting question remains why other herbivore taxa did not evolve a comparable foregut that would potentially have allowed them to achieve a larger body weight than the existing foregut fermenters. A potential answer is that foregut development was initiated and perfected in species of small body weight (cf. Pérez-Barberìa et al. 2001). This allowed very efficient systems to evolve, whose body size-limiting effects came to play a role, if at all, only much later.

Primates

In his fundamental publication, Parra (1978) could not include any data on wild equids, tapirs, rhinos or elephants (for elephants, only a measurement for the capacity of the distal fermentation chamber was available but no measurement of total gut capacity). In contrast to his work, in which he did not find a difference in the capacity of the fermentation chambers between hindgut and foregut fermenters, Chivers and Hladik (1980) reported that in their sample of 27 small folivores, the capacity of the hindgut fermentation chamber in hindgut fermenters scaled to body weight$^{1.20}$, whereas the capacity of the forestomach in foregut fermenters scaled to body weight$^{0.78}$ (unfortunately, these authors did not measure actual body weight but an extrapolation from body length). The fact that foregut fermenters actually reduce their relative forestomach capacity in folivorous primates indicates that, in this group, different retention- and intake-limiting mechanisms must be operating than in the larger ungulates.

Palaeoecology

We hypothesize that one reason for the success of hindgut fermenters, in terms of attainable body size, is the fact that their gastrointestinal design allowed for modifications that accelerated relative ingesta passage. Compared to foregut fermenters, hindgut fermenters are, however, at a disadvantage when having to deal with secondary plant compounds. These potentially dangerous substances can be detoxified by forestomach bacteria, but reach the intestinal absorption sites unmodified in hindgut fermenters. This fact could suggest a digestive contribution to the decline of very large herbivorous species. Janis et al. (1994, 2000) noted a decrease in browsing hindgut fermenters in the Miocene, and in the latter work it is demonstrated that this could be due to a decline in productivity of dicotyledonous forage. Guthrie (1984) is,

[2] The proportionally largest forestomach occurs in sloths, in which its capacity can be up to 30% of body weight (Langer 1988). Sloths have, if at all, only rudimentary caeca and a short large intestine (Stevens and Hume 1995). These animals have very low metabolic rates (McNab 1978), a low food intake (Nagy and Montgomery 1980), long retention times, and defecate only about once per week (Montgomery and Sunquist 1978)—options obviously not available for large ungulates.

to our knowledge, the first to speculate in detail on the consequences of an increase in antiherbivore defences by dicotyledonous plants that could have accompanied their biomass decline. As hindgut fermenters are regarded as less well adapted to the potentially toxic effects, they should have suffered more losses than foregut fermenters and ruminants. With respect to large body masses, Freeland (1991) proposed that, due to their relatively lower metabolic turnover, larger animals should be less well adapted to fast metabolic de-toxification rates, and therefore cannot ingest the same amount of any particular toxin as small animals. This author demonstrated that the number of plant species included in a natural diet increases with the size of the herbivore. These findings are in accord with Guthrie's (1984) hypothesis that a reduction in available plant variety caused the decline of very large animals, a case he exemplifies with the well recorded decline in variety of diet that preceded the extinction of the Shasta ground sloth (*Nothrotheriops shastense*), which he assumes to have been a hindgut fermenter. Thus, while morphophysiological constraints alone could limit the potential body size in foregut fermenters, ecological constraints might limit that of the morphophysiologically unconstrained hindgut fermenters.

Acknowledgements We thank M. Clauss and V. Margerie for support in literature acquisition, and A.W. Milewski and T.J. Foose for comments upon the manuscript. A.W. Milewski provided the spark for this review.

References

Alexander RM (1989) Dynamics of dinosaurs and other extinct giants. Columbia Univesity Press, New York

Altman SA (1987) The impact of locomotor energetics on mammalian foraging. J Zool (Lond) 211:215–225

Anonymous (1872) Bairds Tapir. Zool Garten 13:58–59

Barboza PS, Bowyer RT (2000) Sexual segregation in dimorphic deer: a new gastrocentric hypothesis. J Mammal 81:473–489

Bartocci S, Amici A, Verna M, Terramoccia S, Martillotti F (1997) Solid and fluid passage rate in buffalo, cattle and sheep fed diets with different forage to concentrate ratios. Livestock Prod Sci 52:201–208

Beddard FE (1887) A note on the visceral histology of ceratotherium. J R Microsc Soc 78:120–122

Behrend A (2000) Kinetik des Ingestaflusses bei Rehen und Mufflons im saisonalen Verlauf. Dissertation Thesis Biology, Humboldt-University of Berlin, Germany

Bell RHV (1969) The use of herbaceous layers by grazing ungulates in the Serengeti. In: Watson A (ed) Animal populations in relation to their food resources. Symp Br Ecol Soc. Blackwell, Oxford, pp 111–124

Bell RHV (1971) A grazing ecosystem in the Serengeti. Sci Am 225:86–93

Bourdelle E, Lavocat R (1955) Ordre des Périssodactyles. In: Grassé JP (ed) Traité de zoologie. Anatomie, systématique, biologie. Tome XVII vol I. Paris, pp 1002–1167

Brashares JS, Garland T, Arcese P (2000) Phylogenetic analysis of coadaptation in behavior, diet, and body size in the African antelope. Behav Ecol 4:452–463

Case TJ (1979) Optimal body size and an animal's diet. Acta Biotheor 28:54–69

Chivers DJ, Hladik CM (1980) Morphology of the gastrointestinal tract in primates: comparisons with other mammals in relation to diet. J Morphol 166:337–386

Clauss M, Lechner-Doll M (2001) Differences in selective reticuloruminal particle retention as a key factor in ruminant diversification. Oecologia 129:321–327

Clauss M, Deutsch A, Lechner-Doll M, Flach EJ, Tack C (1998) Passage rate of fluid and particle phase in captive giraffe. Adv Ethol [Suppl Ethol] 33:98

Clauss M, Fröschle T, Lechner-Doll M, Dierenfeld ES, Hatt JM (2002a) Fluid and particle passage rate in captive black rhinoceros. Abstract Book of the Joint Nutrition Conference, August 2002, Antwerp, p 88

Clauss M, Lechner-Doll M, Streich WJ (2002b) Ruminants: why browsers are non-grazers. Abstract Book of the Joint Nutrition Conference, August 2002, Antwerp, p 126

Clauss M, Lechner-Doll M, Streich WJ (2002c) Faecal dry matter content in captive wild ruminants: implications for the browser/grazer-dichotomy. Abstract Book of the Joint Nutrition Conference, August 2002, Antwerp, p 128

Clauss M, Loehlein W, Kienzle E, Wiesner H (2003) Studies on feed digestibilities in captive Asian elephants. J Anim Physiol Anim Nutr 87:1-14

Clemens ET, Maloiy GMO (1982) Digestive physiology of three East African herbivores, the elephant, rhinoceros and hippopotamus. J Zool (Lond) 198:141–156

Clemens ET, Maloiy GMO (1983) Digestive physiology of East African ruminants. Comp Biochem Physiol 76A:319–333

Clemens ET, Maloiy GMO (1984) Colonic absorption and secretion of fluids, electrolytes and organic acids in East African ruminants. Comp Biochem Physiol 77A:51–56

Coenen M, Meyer H, Stadermann B (1990) Amount and composition of the GIT content according to type of feed and exercise. In: Meyer H (ed) Contributions to water and mineral metabolism of the horse. Parey, Berlin; Adv Anim Physiol Anim Nutr 21:7-20

Colbert EH (1993) Feeding strategies and metabolism in elephants and sauropod dinosaurs. Am J Sci 293A:1–19

Damuth J, MacFadden BJ (eds) (1990) Body size in mammalian paleobiology: estimation and biological implications. Cambridge University Press, Cambridge

De Bouveignes O (1953) Sparrmann et les rhinoceros. Zooleo 21:85–97

Demment MW (1983) Feeding ecology and the evolution of body size of baboons. Afr J Ecol 21:219–233

Demment MW, Longhurst WH (1987) Browsers and grazers: constraints on feeding ecology imposed by gut morphology and body size. In: Santana OP, da Silva AG, Foote WC (eds) Proceedings of the 4th International Conference on Goats, Departamento de Difusao de Tecnologia, Brazil, pp 989–1004

Demment MW, Van Soest PJ (1985) A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. Am Nat 125:641–672

Economos AC (1981) The largest land mammal. J Theor Biol 89:211–215

Eloff AK, Van Hoven W (1980) Intestinal protozoa of the African elephant. S Afr J Zool 15:83–90

Endo H, Morigaki T, Fujisawa M, Yamagiwa D, Sasaki M, Kimura J (1999) Morphology of the intestinal tract in the White rhinoceros. Anat Hist Embryol 28:303–305

Farlow JO (1987) Speculations about the diet and digestive physiology of herbivorous dinosaurs. Paleobiology 13:60–72

Field CE (1976) Palatability factors and nutritive value of the food of buffalo (*Syncerus caffer*) in Uganda. E Afr Wildl J 14:181–201

Foose TJ (1982) Trophic strategies of ruminant versus nonruminant ungulates. PhD thesis, University of Chicago, Chicago, Ill., USA

Fortelius M, Kappelman J (1993) The largest land mammal ever imagined. Zool J Linn Soc 107:85–101

Frade F, Vanfrey R (1955) Ordre de Proboscidiens. In: Grassé JP (ed) Traité de zoologie. Anatomie, systématique, biologie. Tome 17, vol 1. Paris, pp 715–875
Freeland WJ (1991) Plant secondary metabolites: biochemical coevolution with herbivores. In: Palo RT, Robbins CT (eds) Plant defenses against mammalian herbivory. CRC Press, Boca Raton, pp 61–81
Frewein J, Gasse H, Leiser R, Roos H, Thomé H, Vollmerhaus B, Waibl H (eds) (1999) Lehrbuch der Anatomie der Haustiere, vol 2. Eingeweide, 8th edn. Parey, Berlin
Fritz H, Duncan P, Gordon IJ, Illius AW (2002) Megaherbivores influence trophic guilds structure in African ungulate communities. Oecologia 131:620–625
Gagnon M, Chew AE (2000) Dietary preferences in extant African bovidae. J Mammal 81:490–511
Garrod AH (1873) On the visceral anatomy of the Sumatran rhinoceros. Proc Zool Soc Lond, pp 92–104
Garrod AH (1877) On some points in the visceral anatomy of the rhinoceros of the Sunderbunds (*Rhinoceros sondaicus*). Proc Zool Soc Lond, pp 707–711
Gaulin SJC (1979) A Jarman/Ball model for primate feeding niches. Hum Ecol 7:1-20
Geist V (1974) On the relationship of social evolution and ecology in ungulates. Am Zool 14:205–220
Gentry AW (1967) *Pelovoris oldowayensis* Reck, an extinct bovid from East Africa. Bull Br Mus Nat Hist Geol Ser 14:243–299
Gentry AW, Gentry A (1978) Fossil Bovidae of Olduvai Gorge, Tanzania. Bull Br Mus Nat Hist Geol Ser 29:289–446; 30:1-83
Geraads D (1996) Le *Sivatherium* du Pliocène final d'Ahl al Oughlam et l'évolution du genre en Afrique. Paläont Z 70:623–629
Giesecke D, Van Gylswyk NO (1975) A study of feeding types and certain rumen functions in six species of South African wild ruminants. J Agric Sci (Camb) 85:75–83
Gordon IJ, Illius AW (1994) The functional significance of the browser-grazer dichotomy in African ruminants. Oecologia 98:167–175
Guthrie RD (1984) Mosaics, allelochemics and nutrients. In: Martin PS, Klein RG (eds) Quaternary extinctions. A prehistoric evolution. University of Arizona Press, Tucson, pp 259–298
Gutmann WF (1989) Die Evolution hydraulischer Konstruktionen: Organismische Wandlung statt altdarwinistischer Anpassung. Kramer, Frankfurt/Main, Germany
Hackenberger MK (1987) Diet digestibilities and ingesta transit times of captive Asian and African elephants. MS thesis, University of Guelph, Canada
Harris JM (1991) Giraffidae. In: Harris JM (ed) Koobi Fora research project 3. Clarendon Press, Oxford, pp 93–138
Hofmann RR (1988) Morphophysiological evolutionary adaptations of the ruminant digestive system. In: Dobson A, Dobson MJ (eds) Aspects of digestive physiology in ruminants. Cornell University Press, Ithaca, N.Y., USA, pp 1–20
Home E (1821) An account of the skeletons of the dugong, two-horned rhinoceros, and tapir of Sumatra. Philos Trans R Soc Lond 11:268–274
Hoppe PP (1977) Rumen fermentation and body weight in African ruminants. In: Peterle TJ (ed) 13th Congress of Game Biology. The Wildlife Society, Washington, DC, pp 141–150
Hume ID (1999) Marsupial nutrition. Cambridge University Press, Cambridge
Illius AW, Gordon IJ (1992) Modelling the nutritional ecology of ungulate herbivores: evolution of body size and competitive interactions. Oecologia 89:428–434
Janis CM (1990) Correlation of cranial and dental variables with body size in ungulates and macropodoids. In: Damuth J, MacFadden BJ (eds) Body size in mammalian paleobiology: estimation and biological implications. Cambridge University Press, Cambridge, pp 255–299
Janis CM, Carrano M (1992) Scaling of reproductive turnover in archosaurs and mammals: why are large terrestrial mammals so rare? Ann Zool Fenn 28:201–216
Janis CM, Gordon IJ, Illius AW (1994) Modelling equid/ruminant competition in the fossil record. Hist Biol 8:15–29
Janis CM, Damuth J, Theodor JM (2000) Miocene ungulates and terrestrial primary productivity: where have all the browsers gone? Proc Natl Acad Sci 97:7899–7904
Jarman PJ (1968) The effect of the creation of Lake Kariba upon the terrestrial ecology of the middle Zambezi valley. PhD thesis, University of Manchester
Jarman PJ (1974) The social organization of antelope in relation to their ecology. Behaviour 48:215–267
Justice KE, Smith FA (1992) A model of dietary fiber utilization by small mammalian herbivores, with empirical results for Neotoma. Am Nat 139:398–416
Kiefer B (2002) Quality and digestibility of white rhinoceros food—a comparison of field and experimental studies. Diss thesis, University of Munich, Germany
Kingdon J (1979) East African mammals, vol 3, part B. Large mammals. Academic Press, London
Langer P (1976) Functional anatomy of the stomach of *Hippopotamus amphibius*. S Afr J Sci 72:12–16
Langer P (1988) The mammalian herbivore stomach. Fischer, Stuttgart
Langer P (1991) Evolution of the digestive tract in mammals. Verh Dtsch Zool Ges 84:169–193
Langer P (1994) Food and digestion of Cenozoic mammals in Europe. In: Chivers DJ, Langer P (eds) The digestive system of mammals: food, form, and function. Cambridge University Press, Cambridge, pp 9–24
Loehlein W, Kienzle E, Wiesner H, Clauss M (2003) Investigations on the use of chromium oxide as an inert external marker in captive Asian elephants (*Elephas maximus*): passage and recovery rates. In: Fidgett A, et al. (eds) Zoo animal nutrition, vol 2. Filander, Fürth, Germany (in press)
MacFadden BJ, Hulbert, RC (1990) Body size estimates and size distribution of ungulate mammals from the Late Miocene Love Bone Bed of Florida. In: Damuth J, MacFadden BJ (eds) Body size in mammalian paleobiology: estimation and biological implications. Cambridge University Press, Cambridge, pp 337–363
Maloiy GMO, Clemens CT (1980) Colonic absorption and secretion of electrolytes as seen in five species of East African herbivorous mammals. Comp Biochem Physiol 67A: 21–25
Maloiy GMO, Clemens ET, Kamau JMZ (1982) Aspects of digestion and in vitro rumen fermentation rate in six species of East African wild ruminants. J Zool (Lond) 197:345–353
McNab B (1978) Energetics of arboreal folivores: physiological problems and ecological consequences of feeding on an ubiquitous food supply. In: Montgomery GG (ed) Ecology of arboreal folivores. Smithsonian Institution Press, Washington, DC, pp 153–162
Meyer H, Stadermann B, Radicke S, Kienzle E, Nyari A (1993) Investigations on amount and composition of the gastrointestinal tract and postprandial parameters in blood and urine according to type of feed. Pferdeheilkunde 9:15–25
Mitchell PC (1903/6) On the intestinal tract of mammals. Trans Zool Soc Lond 17:437–536
Montgomery GG, Sunquist ME (1978) Habitat selection and use by two-toed and three-toed sloths. In: Montgomery GG (ed) Ecology of arboreal folivores. Smithsonian Institution Press, Washington, DC, pp 329–359
Mullen A (1682) An anatomical account of the elephant accidentally burnt in Dublin on Fryday, June 17. in the year 1681. Smith, London
Nagy KA, Montgomery GG (1980) Field metabolic rate, water flux and food consumption in three-toed sloths. J Mammal 61:465–472
Naples VL (1987) Reconstruction of cranial morphology and analysis of function in the Pleistocene ground sloth *Nothrotheriops shastense*. Nat Hist Mus Los Angeles Cty Contrib Sci 389:1-21

Naples VL (1989) The feeding mechanism in the Pleistocene ground sloth, *Glossotherium*. Nat Hist Mus Los Angeles Cty Contrib Sci 415:1-23
NOW (2002) Neogene of the Old World. http://www.helsinki.fi/science/now. Cited June 2002
Owen TR (1862) On the anatomy of the Indian rhinoceros. Trans Zool Soc Lond 4:31–58
Owen-Smith N (1982) Factors influencing the consumption of plant products by large herbivores. In: Huntley BJ, Walker BH (eds) Ecology of tropical savannas, Springer, Berlin Heidelberg New York, pp 359–404
Owen-Smith N (1988) Megaherbivores. The influence of very large body size on ecology. Cambridge University Press, Cambridge
Parra R (1978) Comparison of foregut and hindgut fermentation in herbivores. In: Montgomery, GG (ed) The ecology of arboreal folivores. Smithsonian Institution Press, Washington, DC, pp 205–230
Pérez-Barberìa FJ, Gordon IJ, Nores C (2001) Evolutionary transitions among feeding styles and habitats in ungulates. Evol Ecol Res 3:221–230
Persson L (1985) Asymmetrical competition: are larger animals competitively superior? Am Nat 126:261–266
Peters RH (1983) The ecological implications of body size. Cambridge UniversityPress, Cambridge
Prins RA, Kreulen DA (1991) Comparative aspects of plant cell wall digestion in mammals. In: Hoshino S, Onodera R, Minoto H, Itabashi H (eds) The rumen ecosystem: the microbial metabolism and its regulation. Japan Scientific Soc Press, Tokyo, pp 109–121
Renecker LA, Hudson RJ (1992) Thermoregulatory and behavioral response of moose: is large body size an adaptation or constraint? Alces [Suppl] 1:52–64
Roux W (1881) Der Kampf der Theile im Organismus. Engelmann, Leipzig, Germany
Sachs L (1997) Angewandte Statistik, vol 8. Springer, Berlin Heidelberg New York
Schmidt-Nielsen K (1984) Scaling. Why is animal size so important? Cambridge UniversityPress, Cambridge
Scott KM (1990) Postcranial dimensions of ungulates as predictors of body mass. In: Damuth J, MacFadden BJ (eds) Body size in mammalian paleobiology: estimation and biological implications. Cambridge UniversityPress, Cambridge, pp 301–335
Sikes SK (1971) The natural history of the African elephant. Weidenfeld and Nicolson, London, UK
Silva M, Downing JA (1995) CRC handbook of mammalian body masses. CRC Press, Boca Raton, Fla.
Sinclair ARE (1974) The natural regulation of buffalo population in East Africa. IV. The food supply as a regulating factor and competition. E Afr Wildl J 10:77–89
Singer R, Boné E (1960) Modern giraffes and the fossil giraffids of Africa. Ann S Afr Mus 45:375–548
Smith FA (1995) Scaling of digestive efficiency with body mass in Neotoma. Funct Ecol 9:299–305
Solounias N, McGraw WS, Hayek LA, Werdelin L (2000) The paleodiet of the Giraffidae. In: Vrba ES, Schaller GB (eds) Antelopes, deer, and relatives. Fossil record, behavioral ecology, systematics, and conservation. Yale University Press, New Haven
Stevens CE, Hume ID (1995) Comparative physiology of the vertebrate digestive system. Cambridge UniversityPress, Cambridge
Van Hoven W (1978) Digestion physiology in the stomach complex and hindgut of the hippopotamus. S Afr J Wildl Res 8:59–64
Van Hoven W, Prins RA, Lankhorst A (1981) Fermentative digestion in the African elephant. S Afr J Wildl Res 11:78–86
Van Soest PJ (1994) Nutritional ecology of the ruminant, 2nd edn. Cornell UniversityPress, Ithaca
Van Soest PJ (1996) Allometry and ecology of feeding behavior and digestive capacity in herbivores: a review. Zoo Biol 15:455–479
Van Wieren SE (1996) Browsers and grazers: foraging strategies in ruminants. In: Van Wieren SE (ed) Digestive strategies in ruminants and nonruminants. Thesis, Landbouw Universiteit, Wageningen, pp 119–145
Wilson VJ, Edwards PW (1965) Data from a female rhinoceros and foetus from the Fr. Jameson district. Puku 3:179–180
Woodall PF, Skinner JD (1993) Dimensions of the intestine, diet and faecal water loss in some African antelope. J Zool (Lond) 229:457–471
Woolnough AP, du Toit JT (2001) Vertical zonation of browse quality in tree canopies exposed to a size-structured guild of African browsing ungulates. Oecologia 129:585–590