Constraints on feeding type in ruminants: a case for morphology over phylogeny

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Abstract. Ruminants were categorized into three feeding types: grazers, mixed feeders and browsers based on their food habits. We studied how phylogeny constrains the feeding types, the morphology of digestive organs, and their relationships in Cervidae and Bovidae. It is shown that species with different feeding types occur in the same phylogenetic group of the family, subfamily, and tribe. This suggests that phylogeny does not always reflect feeding type. Comparisons of three morphological indices of digestive organs (parotid gland size, rumino-reticulum capacity, and rumino-reticulum contents weight) among feeding types found that trends along the grazer-browser continuum were similar in both families. The index values of the same feeding types were similar in the two families. These results suggest that the morphology of digestive organs is closely related to feeding types, and that phylogenetic characteristics are less important. The species in the same feeding type also share other morphological characteristics of digestive organs, irrespective of phylogeny.

Key words: digestive organs, feeding type, morphology, phylogenetic constraint, ruminants.

The evolution of ruminants reflects changes in food quality and availability associated with changes in climate and vegetation during the Tertiary period (Romer 1966; Janis 1976). Adaptations were apparent in food habits, feeding behavior, morphology, and physiology of the digestive systems (Janis 1976; Hofmann 1989).

Studies on the feeding ecology of ungulates have revealed negative relationships between body mass and food quality (Bell 1971; Jarman 1974). These authors emphasized the importance of body weight for the evolution of ungulate feeding ecology. On the other hand, based on the comparative morphophysiology of digestive systems of 65 ruminant species (Hofmann 1968, 1989; Hofmann and Stewart 1972), Hofmann described the correspondence of feeding types and the morphology of digestive organs. Considering the evolution of ruminants, he concluded that changes in feeding ecology and diets were the primary adaptive factors in ruminant evolution while body weight was secondary (Hofmann 1989).

Hofmann (1989) has categorized ruminants into three feeding types. Of approximately 150 ruminants including six domestic species, about 25% fall into “grazers” which eat fibrous

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foods rich in cell wall, or structural carbohydrates. For example, cattle, sheep, water buffalo, *Bubalus* spp., and banteng, *Bos javanicus*, belong to this group.

More than 40% of ruminant species belong to "browsers". They thrive on high quality diets and are adapted to process forage that is rich in plant cell contents. For example, roe deer, *Capreolus capreolus*, moose, *Alces alces*, and dik-dik, *Madoqua kirki*, are representative browsers.

The other 35% of ruminant species are "mixed feeders" which have intermediate characteristics between grazers and browsers. They show short term or seasonal changes in anatomy in response to food quality. The domestic goat, *Capra hircus*, and red deer, *Cervus elaphus*, belong to this group.

Most ruminologists and animal ecologists gave little attention to phylogenetic relationships in comparative studies of ruminant feeding ecology. However, the importance of considering phylogeny in comparative biology has been stressed thoroughly by Harvey and Pagel (1991). One of the most important arguments is that similar characteristics shown by different species do not necessarily imply adaptation to a particular environment, because it is possible that they have resulted merely from the phylogenetic history. However, if similar correlation between feeding types and morphological characteristics of digestive organs are observed in several independently evolving lineages, this implies that the traits have evolved in a correlated fashion, and explanations associated with the phylogenetic history are less likely to apply (Harvey and Pagel 1991).

The objective of this study is to clarify the importance of phylogenetic constraints on the feeding types and the morphology of digestive organs of ruminants. We classify species of Bovidae and Cervidae according to their feeding types. We then compare parameters of the morphology of digestive organs among the feeding types in each family, and the same feeding types between the two families.

Materials and methods

Groups examined and their feeding types

Species-level information for the three ruminant feeding types (grazers, mixed feeders, and browsers) was collected from available literature (references in Tables 1 and 2). We limited our search to two families, Bovidae (115 spp) and Cervidae (53 spp), because they account for 91.3% of the true ruminants (184 spp), and quantitative information is more available for these two families.

Taxonomic relationships of the species were used instead of phylogenetic relationships because the phylogenetic tree for all ruminant species is not available. The standard taxonomies of Spinage (1986) for Bovidae and Walker (1975) for Cervidae were adopted. For the classification of feeding types according to food habits, the results of Kay et al. (1980), Kay (1987), and Hofmann (1973, 1982, 1984) were used. Species not included in these studies were categorized according to food habit studies, i.e., the oryx, *Oryx basia* (Maloiy et al. 1982), bighorn sheep, *Ovis canadensis* (Belovsky 1986), Pere-David's deer, *Elaphurus davidianus* (Axmacher and Hofmann 1988), and Roosevelt elk, *Cervus elaphus roosevelti* (Church and Hines 1978). Based on feeding types, the taxonomic classifications of the ruminant species were rearranged.

Indices of digestive organs

Quantitative data on digestive organs of ruminants with different feeding types were collected from available literature (Tables 1 and 2). Three quantitative indices were derived: 1) ratio of parotid weight (g) to body weight (kg) (6 species of Cervidae and 14 species of Bovidae); 2) ratio of rumino-reticulum capacity (l) to body weight ($\text{kg}^{0.75}$) (6 species of Cervidae and 30 species of Bovidae); and 3) ratio of weight of rumino-reticulum contents to body weight ($\text{kg}^{0.75}$) (11 species of Cervidae and 36 species of Bovidae). Indices with inadequate sample size or otherwise unsuitable for quantitative comparison were used to describe qualitative differences between grazers and browsers (Table 3).

Data related to feeding type was available for 50 species and subspecies of Bovidae and 15 species and subspecies of Cervidae, including domestic species. For these subspecies and species, we could obtain data related to the three indices for 43 species and subspecies of Bovidae and 13 species and subspecies of Cervidae. Index values are expressed as mean $\pm$ SD.

Results

Feeding types

Tables 1 and 2 show that both Bovidae and Cervidae include species belonging to different feeding types. Different feeding types were found not only in the two families, but also in lower taxonomic levels. In Bovidae, for example, the buffalo, *Syncerus caffer*, European bison, *Bison bonasus*, and greater kudu, *Tragelaphus strepsiceros*, in the subfamily Bovinae belonged to the grazers, mixed feeders, and browsers, respectively. Different feeding types were also found in subfamilies Antilopinae and Caprinae, and also at tribe levels, such as in Bovini, Antilopini, Neotragini, and Caprini. In Cervidae also, the subfamily Cervinae and the tribe Cervini included grazers and mixed feeders, and the subfamily Odocoilinae included both mixed feeders and browsers. There were, however, fewer species classified as grazers in Cervidae than in Bovidae.

Morphology of digestive organs

a. Parotid gland

In Bovidae, the relative weights of parotid glands were lower in grazers than those of mixed feeders and browsers, but no obvious difference was found between mixed feeders and browsers (Fig. 1, Table 1). In Cervidae, data were not available for grazers. The mean value for browsers was higher than that for mixed feeders, but variation was great (Fig. 1, Table 2).

Index values for each feeding type were similar in Bovidae and Cervidae. Index values showed a similar increasing tendency from grazers to browsers in both Bovidae and Cervidae (Fig. 1).

b. Rumino-reticulum capacity

In Bovidae, the relative capacities of rumino-reticula were greater in grazers than in mixed feeders and browsers (Fig. 1, Table 1). The mean value for mixed feeders was greater than that for browsers, but variation was great. Although only one datum was available for Cervidae browsers and grazers, respectively, relative capacity was larger in the grazer (Fig. 1,

Table 1. Parameters of digestive organs of species belonging to different feeding types in Bovidae.

Species		Body weight		Parotid	R-R capacity	R-R contents	Reference
English name	Scientific name	kg	kg ^{0.75}	g/kg	% l/kg ^{0.75}	% kg/kg ^{0.75}	No.
Grazers							
Subfamily Bovinae							
Tribe Bovini							
Buffalo	<i>Syncerus caffer</i>	807.5	151.5		88.4	85.3	3, 4, 6
American bison	<i>Bison bison</i>	800.0	150.4			69.3	6, 12
European ox	<i>Bos taurus</i>	600.0	121.2	0.6		69.8	6, 13
Zebu	<i>Bos indicus</i>	400.0	89.4			63.3	6
Cow	<i>Bos taurus</i>	400.0	89.4		136.7	61.5	1, 2
Subfamily Reduncinae							
Mountain reedbuck	<i>Redunca fulvorufula</i>	23.5	10.7		68.4		3
Bohor reedbuck	<i>Redunca redunca</i>	45.0	17.4		55.8	20.1	3, 6
Laikipia waterbuck	<i>Kobus ellipsiprymnus</i>	220.0	57.1		76.9	52.5	3, 6, 9
Waterbuck	<i>Kobus defassa</i>	229.0	58.9			51.9	8
Nile lechwe	<i>Kobus megaceros</i>	80.0	26.7				6
Uganda kob	<i>Kobus kob</i>	79.0	26.5		36.8		3
Subfamily Hippotraginae							
Roan antelope	<i>Hippotragus equinus</i>	250.0	62.9				6
Sable antelope	<i>Hippotragus niger</i>	200.0	53.2				6
Oryx	<i>Oryx basia</i>	174.3	48.0			48.9	8
Oryx (Wild)	<i>Oryx gazella</i>	181.5	49.5		71.8	49.1	3, 4, 6
Oryx (Domesticated)	<i>Oryx gazella</i>	200.0	53.2			42.9	6
Subfamily Alcelaphinae							
Blue wildebeest	<i>Connochaetes taurinus</i>	182.0	49.6		80.7	57.3	3, 4, 5, 6
Hartebeest	<i>Alcelaphus buselaphus</i>	156.0	44.1		70.3	38.5	3, 5, 6
Topi	<i>Damaliscus lunatus</i>	119.0	36.0		86.0	44.2	3, 5, 6
Subfamily Antilopinae							
Tribe Antilopini							
Black buck	<i>Antilope cervicapra</i>	40.9	16.2	0.7			13
Tribe Neotragini							
Oribi	<i>Ourebia ourebi</i>	16.0	8.0		49.4		3
Subfamily Caprinae							
Tribe Caprini							
Ibex	<i>Capra ibex</i>	36.0	12.8				11
European sheep	<i>Ovis aries</i>	50.0	18.8	0.5	64.8	37.1	2, 5, 6, 13
Mouflon	<i>Ovis ammon musimon</i>	33.5	13.9	0.7	68.2	34.2	6, 11, 13
Mean ± SD				0.6 ± 0.1	73.4 ± 23.8	51.6 ± 16.1	
Mixed Feeders							
Subfamily Bovinae							
Tribe Bovini							
European bison	<i>Bison bonasus</i>	800.0	150.4			44.1	6
Tribe Tragelaphini							
Eland (Wild)	<i>Taurotragus oryx</i>	700.0	136.1		52.9	57.6	3, 6
Eland antelope (Pofu)	<i>Taurotragus oryx</i>	519.0	108.7		57.0	51.0	3, 7
Subfamily Aepycerotinar							
Impala	<i>Aepyceros melampus</i>	62.6	22.3		53.5	29.7	3, 4, 5, 6

Table 1. (continued)

Species		Body weight		Parotid	R-R capacity	R-R contents	Reference
English name	Scientific name	kg	kg ^{0.75}	g/kg	% l/kg ^{0.75}	% kg/kg ^{0.75}	No.
Subfamily Antilopinae							
Tribe Antilopini							
Grant's gazelle	<i>Gazella granti</i>	64.0	22.6	2.0	56.6	23.9	3, 5, 6, 13
Thomson's gazelle	<i>Gazella thomsoni</i>	22.5	10.3	1.0	56.1	26.0	3, 5, 6, 13
Springbok	<i>Antidorcas marsupialis</i>	42.0	16.5	1.4	28.4	23.2	4, 6, 15
Tribe Neotragini							
Steinbok	<i>Raphicerus campestris</i>	10.5	5.8	2.2	42.9	13.5	3, 5, 6, 13
Subfamily Caprinae							
Tribe Ovibovini							
Musk ox	<i>Ovibos moschatus</i>	350.0	80.9				6
Tribe Rupicapriini							
Chamois	<i>Rupicapra rupicapra</i>	33.5	13.9	1.8	53.1		11
Tribe Caprini							
Goat	<i>Capra hircus</i>	40.0	15.9			44.6	5, 6
Dall's sheep	<i>Ovis dalli</i>	80.0	26.7				6
Bighorn sheep	<i>Ovis canadensis</i>	72.0	24.7			18.8	12, 14
Sheep	<i>Ovis aries</i>	30.0	12.8			44.9	6
Mean $\pm$ SD				1.7 $\pm$ 0.5	50.1 $\pm$ 9.8	34.3 $\pm$ 13.9	
Browsers							
Subfamily Bovinae							
Tribe Tragelaphini							
Greater kudu	<i>Tragelaphus strepsiceros</i>	250.0	62.9			36.9	4, 6
Lesser kudu	<i>Tragelaphus imberbis</i>	90.5	29.3		45.0		3
Bushbuck	<i>Tragelaphus scriptus</i>	60.0	21.6		37.4	18.1	3, 5, 6
Bongo	<i>Taurotragus eurycerus</i>	200.0	53.2				6
Subfamily Cephalophinae							
Red duiker	<i>Cephalophus harveyi</i>	16.0	8.0	2.2	62.5	29.6	3, 6
Grey duiker	<i>Sylvicapra grimmia</i>	14.3	7.4		43.5	19.2	3, 5, 6
Subfamily Antilopinae							
Tribe Antilopini							
Gerenuk	<i>Litocranius walleri</i>	40.0	15.9	2.0	39.3	22.7	3, 6, 8, 13
Tribe Neotragini							
Klipspringer	<i>Oreotragus oreotragus</i>	12.0	6.4		26.1	12.1	6
Dik-dik	<i>Madoqua spp.</i>	5.2	3.4	1.6		10.2	3, 5, 6, 13
Gunther's dik-dik	<i>Madoqua quentheri</i>	4.1	2.9		26.0		3
Kirk's dik-dik	<i>Madoqua kirki</i>	5.2	3.4	1.5	27.4	10.8	1, 6, 10, 13
Suni	<i>Nesotragus moschatus</i>	4.5	3.1	1.6	25.5	12.3	3, 5, 6, 10, 13
Mean $\pm$ SD				1.8 $\pm$ 0.3	37.0 $\pm$ 12.4	19.1 $\pm$ 9.2	

R-R: Rumino-reticulum. Reference No. 1. Short et al. (1965), 2. Prins and Geelen (1971), 3. Hofmann (1973), 4. Giesecke and Van Gylswyk (1975), 5. Hoppe et al. (1977), 6. Kay et al. (1980), 7. Demment (1982), 8. Maloiy et al. (1982), 9. Clemens and Maloiy (1983), 10. Hoppe et al. (1983), 11. Hofmann (1984), 12. Belovsky (1986), 13. Kay (1987), 14. Gordon and Illius (1988), 15. Hofmann et al. (1995).

Table 2). Index values for each feeding type were similar in Bovidae and Cervidae.

Table 2. Parameters of digestive organs of species belonging to different feeding types in Cervidae, Tragulidae, Camelidae and Giraffidae.

Species		Body weight		Parotid	R-R capacity	R-R contents	Reference
English name	Scientific name	kg	kg ^{0.75}	g/kg	% l/kg ^{0.75}	% kg/kg ^{0.75}	No.
Cervidae							
Grazers							
Cervinae							
Pere-David's deer	<i>Elaphurus davidianus</i>	190.5	51.3				14
Cervini							
Sika deer	<i>Cervus nippon</i>	61.2	21.9		56.7	48.6	10, 16
Mixed feeders							
Cervinae							
Cervini							
Wapiti	<i>Cervus canadensis</i>	318.0	75.3			28.1	9, 12
Wapiti (Elk)	<i>Cervus elaphus roosevelti</i>	272.5	67.1				8
Red deer	<i>Cervus elaphus</i>	150.0	42.9	0.6	71.8	40.1	4, 7, 9, 13, 18
Fallow deer	<i>Dama dama</i>	70.0	24.2		35.2	29.0	4, 7, 9
Odocoilinae							
Odocoileini							
Mule deer	<i>Odocoileus hemionus</i>	120.0	36.3		28.5	22.6	2, 3, 9
White-tailed deer	<i>Odocoileus virginianus</i>	66.6	23.3		32.0	25.3	1, 9, 13
Caribou	<i>Rangifer tarandus acticus</i>	120.0	36.3			32.6	6, 9
Reindeer, Norwegian	<i>Rangifer tarandus tarandus</i>	90.0	29.2	0.6		41.5	9, 13, 17
Reindeer, Svalbard	<i>Rangifer t. platyrhynchus</i>	71.0	24.5	1.6		38.9	9, 13, 17
Mean ± SD				0.9 ± 0.6	41.9 ± 20.1	32.3 ± 7.2	
Browsers							
Odocoilinae							
Alcini							
Moose	<i>Alces alces</i>	400.0	89.4			43.4	9
Capreolini							
Roe deer	<i>Capreolus capreolus</i>	20.7	9.7	2.2	15.5	15.9	4, 7, 9, 13
Hydropotinae							
Chinese water deer	<i>Hydropotes inermis</i>	12.0	6.4	1.4			9, 13, 15
Muntiacinae							
Reeves' muntjac	<i>Muntiacus reevesi</i>	10.4	5.8	1.4			9, 13
Mean ± SD				1.7 ± 0.5	15.5	29.7 ± 19.4	
Other families:							
Mixed feeder							
Camelidae							
Arabian camel	<i>Camelus dromedarius</i>			0.5			13
Antilocapridae							
Pronghorn	<i>Antilocapra americana</i>	50.0	18.8			33.8	6, 12
Browsers							
Tragulidae							
Larger mousedeer	<i>Tragulus napu</i>	4.0	2.8				9
Lesser mousedeer	<i>Tragulus javanicus</i>	1.5	1.4				9
Giraffidae							
Giraffe	<i>Giraffa camelopardalis</i>	750.0	143.3		73.2	70.3	5, 11

R-R: Rumino-reticulum. References No. 1. Short (1964), 2. Short et al. (1965), 3. Hakonson and Whicker (1971), 4. Prins and Geelen (1971), 5. Hofmann (1973), 6. Hobson et al. (1975), 7. Nagy and Regelin (1975), 8. Church and Hines (1978), 9. Kay et al. (1980), 10. Hofmann (1982), 11. Maloiy et al. (1982), 12. Belovsky (1986), 13. Kay (1987), 14. Axmacher and Hofmann (1988), 15. Hofmann et al. (1988), 16. Takatsuki (1986), 17. Staal and White (1991), 18. Fraser (1996).

Fig. 1. Three indices of digestive organs of Bovidae and Cervidae. Top: weight contributions of parotid glands to body weight (g/kg), middle: ratios of capacity of rumino-reticulum (l) to metabolic body weight ($\text{kg}^{0.75}$), and down: ratio of content weight (kg) of rumino-reticulum to metabolic body weight ($\text{kg}^{0.75}$). GR: grazers, MF: mixed feeders and BR: browsers. Numbers in parentheses indicate sample size and vertical lines indicate *SD*. For data sources, see Tables 1 and 2.

c. Weight of rumino-reticulum contents

In Bovidae, the relative weight of rumino-reticulum contents was highest in grazers, followed by mixed feeders and lowest in browsers (Fig. 1, Table 1). A similar tendency was noted among the three feeding types in Cervidae, but only two data were available for browsers and one for grazers, respectively (Fig. 1, Table 2). Obvious difference was not found between mixed feeders and browsers (Fig. 1). Index values for each feeding type were similar in Bovidae and Cervidae.

Table 3. Characters of the digestive organs of grazers and browsers.

	Grazers	Browsers	Reference No.
Total salivary gland W (g)/Body W (kg)	1.8	3.6	5
Rumen structure	Subdivided	Simple	1
Rumen pillar	Powerful	Weak	1
Pappilla density in rumen wall	Low, uneven	High, even	2, 4
Rumen dorsal wall SEF	Low	High	2, 4
Average rumen SEF	Low	High	2, 4
Reticulum	Small, deeply cellululated	Large, lightly cellululated	1, 2
Omasum	Large, high SEF	Small, low SEF	1, 2
Orifice between reticulum and omasum	Small	Large	1, 2, 3
Abomasum	Large	Small	1, 2
Intestine L/Body L (time)	25–30	12–15	5
Small intestine L/Total intestine L (%)	80–82	65–73	5
Large intestine L/Total intestine L (%)	18–20	27–35	5
Capacity ratio of DFC/R-R	1/15–13	1/6–10	5

SEF: Surface enlargement factor of inner surface, L: Length, W: Weight, R-R: Rumino-reticulum. DFC: Distal fermentation chamber. Reference No. 1. Hofmann and Stewart (1972), 2. Hofmann (1973), 3. Kay et al. (1980), 4. Hofmann et al. (1988), 5. Hofmann (1989).

Other morphological characteristics of digestive organs

Other characteristics of digestive organs were compared for grazers and browsers (Table 3). The weight contribution of total salivary glands was higher in browsers than in grazers. The rumens of grazers were more subdivided, more capacious, and had more powerful muscle pillars for contraction than those of browsers (Hofmann 1968; Hofmann and Stewart 1972). Within the stomach, various shapes and sizes of papillae were more unevenly distributed in grazers than in browsers. Furthermore, papillae were less dense in grazers than in browsers (Hofmann 1968, 1973). In the dorsal regions of the stomachs of grazers, extensive unapillated zones existed, while in browsers the papillae were evenly distributed. Consequently, the degree of rumen surface enlargement was smaller in grazers than in browsers (Hofmann 1973; Hofmann et al. 1988). The reticula of grazers were relatively smaller and more deeply cellululated than in browsers, and exhibited distinct subdivisions in the secondary and the tertiary crests (Hofmann 1973; Church and Hines 1978). The omasa were larger with more pronounced mucosal surface enlargement in grazers than in browsers, because of many laminae of several orders in size in grazers. The abomasa were larger and more spacious in grazers than in browsers. Orifices between reticula and omasa were smaller in grazers than in browsers (Hofmann 1973, 1989). Total intestinal length of grazers were relatively longer, but the large intestines were relatively shorter than those of browsers (Hofmann 1989). The distal fermentation chambers of grazers were relatively less spacious than those of browsers. The digestive systems of grazers can pass foods more slowly through the gut and digest them more thoroughly than those of browsers (Kay et al. 1980; Van Soest 1982; Hofmann 1989).

Discussion

In this analysis, species relationships were derived from the traditional taxonomic

classification of ruminants based mainly on morphology (Walker 1975; Spinage 1986). In spite of considerable advances in studies on the phylogenetic relationships of ruminants (Miyamoto et al. 1990; Gatesy et al. 1992; Wall et al. 1992; Chikuni et al. 1995; Cronin et al. 1996), a phylogenetic tree for all ruminants has not been established. However, phylogenetic studies have confirmed close relationships within genera as defined by traditional taxonomic categories. We assume that the use of traditional taxonomic relationships does not affect our results.

The indices analyzed are closely related to food habits and digestive physiology. The salivary gland and rumino-reticulum are the most important organs for ruminants to digest fibrous foods (Hofmann 1973). The amount of the saliva secreted by the parotid gland is closely related to the size of the glands, and the quick turnover and fermentation of ingesta in the stomach of browsers need more saliva to buffer the rumen's volatile fatty acid and pass the digesta (Kay 1987; Hofmann 1989). Therefore, browsers possess larger parotid glands than do grazers. In contrast to the salivary glands of the browsers, grazers possess a larger rumino-reticulum, which ferments and digests fibrous food efficiently by its long retention time (Hofmann 1973, 1989).

The result that different species in the same phylogenetic group (Bovidae or Cervidae) appear in different feeding types suggests that the feeding types are not constrained strongly by phylogenetic relations. The average values for each index showed a similar tendency from grazers to browsers in both Bovidae and Cervidae (Fig. 1). In addition, other morphological characteristics of the digestive organs of ruminants are similar in species of the same feeding type irrespective of the phylogenies (Table 3). This further suggests that the morphologies of digestive organs associated with different feeding types are likely consistent in different phylogenetic groups, and are not strongly constrained by phylogeny. These results suggest that the correlation among characteristics reflects independently evolving lineages in ruminants. It is, however, noteworthy that Cervidae contains fewer grazers, suggesting that species numbers are affected by phylogeny.

Two conclusions arise from this study: 1) phylogenetic relations did not strongly constrain feeding types and morphology of digestive organs of ruminants, and 2) there exists an underlying principle that feeding types of ruminants are closely related to the morphology of their digestive organs even in different phylogenetic groups.

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