Oecologia (2001) 129:498–508
DOI 10.1007/s004420100768

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Phylogenetic analysis of stomach adaptation in digestive strategies in African ruminants

Received: 19 March 2001 / Accepted: 25 June 2001 / Published online: 31 July 2001

Abstract The stomach morphology of 28 species of artiodactyls that differ in feeding style (browser, mixed feeder, grazer) was analysed using a multivariate approach and phylogenetic correction in order to test whether stomach morphology was correlated with feeding style when body mass was controlled for. A total of 25 morphological traits of the stomach were used in the analysis. After the effects of body mass and phylogeny on stomach morphology were taken into account, there was no significant grouping of species according to feeding style. When information about the feeding style of each species was included in the analysis, the set of morphological traits separated the mixed feeders from the other two feeding styles, but grazers and browsers had similar morphological features. Most of the variance in stomach morphology was explained by body mass and a lesser proportion by phylogeny. The main morphological features that have previously been proposed as being adaptations in grazing species, namely, lengthening of the retention time of ingesta to achieve an increase in their fibre digestion capability by means of a larger relative stomach capacity, a greater subdivision of chambers and smaller openings, are not supported by the findings of this study. Thus, there is no consistent evidence to support a significant adaptive effect of stomach morphology to different diets in the Artiodactyla.

Keywords Allometry · Body mass · Comparative method · Feeding styles · Gut morphology

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Introduction

The feeding habits of some ungulates in a natural habitat were, to our knowledge, first defined by Van Zyl (1965), but it was Hofmann who classified African ruminants into three feeding styles according to morphological adaptations of the digestive system (Hofmann 1973, 1989), as related to differences in diet composition (Hofmann 1968, 1984, 1988; Hofmann and Stewart 1972; Hofmann et al. 1995). Hofmann's categorisation of feeding styles has been extensively used in grazing ecology (Owen-Smith 1982; Gordon and Illius 1988, 1994, 1996; McNaughton 1991; Van Wieren 1996). Differences in stomach morphology between species that differ in diet triggered subsequent studies on other parts of the digestive system, for example, morphological adaptations of the organs involved in the selection (lips, muzzle: Janis and Ehrhardt 1988; Pérez-Barbería and Gordon 2001a) and the processing of food (teeth, jaws, jaw muscles: Fortelius 1985; Axmacher and Hofmann 1988; Janis 1988; Pérez-Barbería and Gordon 1999a, 2001a) and also in behavioural variables (activity time: Mysterud 1998; Pérez-Barbería and Gordon 1999b; home range: Mysterud et al. 2001; habitat use: Pérez-Barbería et al. 2001b). Based on Hofmann's (1973) classification, it has been assumed that grazing species achieve a greater extent of digestion of fibre in comparison with browsing species by means of food retention in the rumen, large stomach capacity, higher degree of stomach compartmentalisation and smaller openings between the rumen and omasum. However, a statistical relationship between the differences in stomach morphology, described by Hofmann (1973), and diet composition has not yet been demonstrated.

A recurrent problem which arises when studying the differences in the morphology or function of the digestive system, in relation to Hofmann's classification, is the possible confounding effect of body mass (Gordon and Illius 1994; Robbins et al. 1995; Iason and Van Wieren 1998). After controlling for body mass, Gordon and Illius (1994) found that there were no differences in wet

or dry mass of the contents of the rumen, or in the fermentation rates or concentrations of volatile fatty acids in the rumen between species of African ruminants which consumed predominantly grass or browse diets.

It is important to control for the effect of sharing common ancestors, known as the phylogenetic effect (Felsenstein 1985; Harvey and Pagel 1991), when adaptive differences between species that differ in feeding styles are to be investigated. Non-phylogenetic cross-species analyses have come under considerable criticism because species do not represent independent samples of a statistical distribution and also because of similar morphological traits and behaviour variables owing to their common ancestry (Ricklefs 1996; Martins 2000).

It was Hofmann (1968) who observed that phylogeny could affect the differences observed between feeding styles. He stated that "[gut differences between feeding styles]... may be outnumbered or concealed by characteristics of genetic relation". However, he never separated this effect from the ones he considered adaptive and the phylogenetic effect has not been included in analyses of the comparative morphology of the stomach of ruminants.

In this paper we test for significant differences in the morphology of the alimentary tract for species with different feeding styles, (1) if, without previous knowledge of the feeding style of each species, there is any evidence of grouping using gut morphology traits, (2) once the species has been assigned into different feeding styles based on information about their diet, to establish the group of gut morphology traits which best defined each feeding style, and (3) to analyse the contribution of body mass and phylogeny to the analyses (1) and (2). We assume that the variables analysed have potential functional significance for digestion and, therefore, that they can be directly related to ecological differences between species that differ in the diet they consume.

Materials and methods

Our data set comes from Hofmann (1973) and Hofmann et al. (1995). Hofmann (1973) provides the most complete data set available in the literature about the stomach morphology of artiodactyls; the data set comprises some features that make it unique for the purpose of this study. Firstly, the most striking source of error in many comparative studies is that body masses and the morphological traits studied do not come from the same specimens (Gordon and Illius 1988; Janis 1988; Janis and Ehrhardt 1988; Spencer 1995; Pérez-Barbería and Gordon 1999a,b, 2000; Pérez-Barbería and Gordon 2001a). The variability in body mass between populations of artiodactyls can be of the same magnitude or greater than the variation shown between some species (Silva and Downing 1995). Hofmann (1973) provides information for a comprehensive data set of variables of the stomach morphology as well as body masses, both taken on the same specimens. Secondly, Hofmann's (1973) data set provides an almost complete data set for a number of stomach traits for approximately 27 species of artiodactyls (26 species of bovids and 1 member of Giraffidae, Fig. 1) which enable us to use a multivariate approach. To this data set we added a new species (*Antidorcas marsupialis*) from Hofmann et al. (1995); these authors provide information for the same variables provided by Hofmann (1973). We searched the literature in order to increase the number of species in our data set but most of the studies that deal with stomach morphology in ungulates give information for only a few of the traits in our initial data set, which prevents their inclusion in a multivariate analysis. The main drawbacks of Hofmann's (1973) data set are (1) the small number of animals sampled for some of the species, (2) the lack of information about age and sex of the individuals sampled and which season they were sampled; all of these could affect gut morphology.

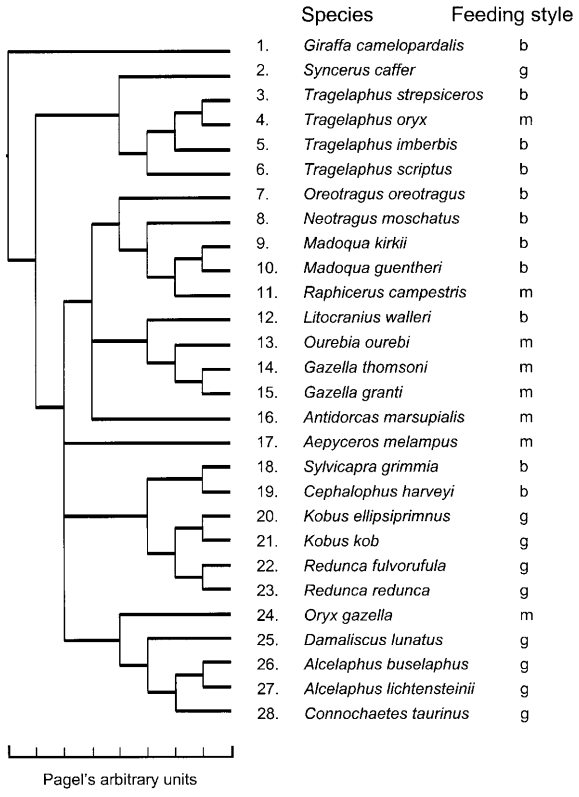

Fig. 1 Phylogenetic relationships and feeding styles amongst 28 artiodactyl species. *g* Grazer, *m* mixed feeder, *b* browser. The branch lengths are arbitrary units following Pagel's method (for details see Materials and methods)

In total, 25 traits of the stomach morphology were used (see Tables 1, 2). Feeding styles come from Pérez-Barbería and Gordon (1999a), which presents up-to-date information about ungulate diets. There are few differences between the feeding styles presented in Hofmann (1973) and those presented in Pérez-Barbería and Gordon (1999a). Hofmann (1973) classifies *Ourebia ourebi* and *Oryx gazella* as grazing species whilst Pérez-Barbería and Gordon (1999a) categorised them as mixed feeders based on Van Zyl (1965), Smithers (1971) and Kingdon (1979). When we repeated our analyses using Hofmann's (1973) feeding styles the results obtained were consistent with those presented in this paper.

All traits were $\log_{10}$-transformed prior to analysis. The data set had some missing values for some of the traits. Ten traits had one missing value, one trait had two missing values and three traits had four missing values. In order to include all traits in a multivariate analysis, we estimated the value of the missing values by using the least squares regression equation of the values of the particular trait against body mass prior to and after phylogeny had been controlled for (see Phylogeny and comparative method). This provides two models, one in which phylogeny was not taken into account (from now on called conventional) and a second one in which phylogeny was controlled for (phylogenetic). Since the main aim was to test whether differences between feeding styles were caused by adaptation or body mass, we considered the following approaches:

Table 1 Brief description of the traits used in this study (see Hofmann 1973 for details)

Variable no.	Units	Definition
2	kg	Body mass
27	cm	Abomasum: height of plicae spirales
15	cm	Abdomen: maximal height
26	Number	Abomasum: number of plicae spirales
14	cm	Abdomen: maximal width
8	Number/cm^2	Atrium ruminis: number of papillae
7	mm^2	Atrium ruminis papillae size: estimated as mean height × mean width
9	Number/cm^2	Dorsal blindsac: number of papillae
22	Number	Omasum: number of laminae I
24	Number	Omasum: number of laminae II
23	cm	Omasum: width of laminae I
25	cm	Omasum: width of laminae II
4	l	Omasum+abomasum: average capacity
21	cm	Omasum: total height
19	cm	Omasum: curvatura omasi
20	cm	Omasum: total length
13	cm^2	Ostium intraruminale area: estimated as maximum diameter×minimum diameter
5	cm^2	Ostium rumino-reticulare area: estimated as maximum diameter×minimum diameter
11	-	Maximal papillae surface enlargement factor: 2×papillary surface+basal surface over basal surface
6	mm	Reticulum: height of primary crests
16	cm	Reticulum: distance from cardia to fundus
18	cm	Reticulum: maximal length
17	cm	Reticulum: maximal width
12	cm	Rumino-reticulum: cranio-caudal length
3	l	Rumino-reticulum: average capacity
10	Number/cm^2	Rumen, ventral wall: number of papillae

1. A conventional approach: differences among feeding styles were carried out by comparing the results of two analyses, one without controlling for body mass and a second controlling for body mass. This approach does not allow a test of whether the differences detected are really caused by body mass, because it does not take into account the confounding effect of phylogeny, but we decided to include this as reference analysis for comparisons with previous studies which did not take phylogeny into account.
2. A phylogenetic approach: the same as the conventional approach but based on the phylogenetic model. This approach allows a test of whether differences were caused by body mass, adaptation or, both.

In order to check whether the estimates of the missing values affected the results, we performed several runs of the analyses whilst leaving out the traits with missing values. The results obtained in those analyses did not differ from the results of the full analysis presented in this paper.

Testing the phylogenetic independence

The effect of sharing common ancestors confers on a group of sister species a closer morphological or behavioural similarity than other groups of species that do not share the same ancestors (Maddison and Maddison 1992; Ridley 1996). This inflates the degrees of freedom of inter-specific statistical analysis and violates the requisite of statistical independence (Felsenstein 1985; Harvey and Pagel 1991). However, recently there has been a critical reappraisal of whether the use of comparative methods is always appropriate (Losos 1999; Harvey and Rambaut 2000). We used a diagnostic tool, proposed by Abouheif (1999), to test the assumption of phylogenetic independence before applying the comparative method to the data set (see below). The diagnosis is based on a measurement of the autocorrelation, in the form of a *C*-statistic, resulting from similarity between adjacent phylogenetic observations. This method requires the use of phylogenetic trees with fully resolved branching patterns (i.e. no polytomies are allowed). The phylogenetic tree used in this study had two polytomies. We solved these two polytomies using a random branching criterion, which generated six trees. As a result of the large number of morphological variables used in this study, we conducted all of our analyses on the variable body mass using these six trees. The results were independent of the different branching morphologies generated by the random criterion. Thus, we chose one of the trees on which to run the analyses for the rest of the variables. The diagnostic tool indicated that only three variables (namely 6, 8 and 27, see Table 1) were not phylogenetically related across species (*C*-statistics=0.184–0.269, $P \geq 0.124$ for the three variables), confirming the appropriateness of applying a comparative method analysis to our data set.

Phylogenetic autocorrelation technique

We used the first-order autoregressive method (Cheverud et al. 1985; Gittleman and Kot 1990; Gittleman and Luh 1992) to separate the contribution of phylogenetic and adaptive components on the traits studied. This comparative method was applied to the phylogeny of Fig. 1. The group of species comprises mainly bovids, except one Giraffidae species (*Giraffa camelopardalis*); we used recent phylogenetic studies based on molecular techniques in order to derive information for the group of bovid species used in this analysis (Essop et al. 1997; Gatesy et al. 1997) and Garland and Janis (1993) provided phylogenetic information about giraffe. Since branch lengths were not available for all nodes, we used Pagel's (1992) arbitrary method to assign branch lengths. Branch lengths were calculated using Phenotypic Diversity Analysis Programs, PDAP 5.0 (Garland et al. 1993).

The autoregressive method has been thoroughly described in Cheverud et al. (1985) and Gittleman and Kot (1990). The method can be briefly described in two steps:

1. Computation of Moran's *I* statistic for each of the stomach traits. Moran's *I* test indicates which variable has a significant phylogenetic correlation and the distance in the phylogenetic tree where no phylogenetic correlation is observed for that

Table 2 The data set used in this study comes from Hofmann (1973). See Table 1 for the code of the variables (Variable no.) and units used

Variable no.	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Species name																										
Giraffa camelopardalis	750.0	105.0	16.0	144.1	2.0	104.5	24.5	24.0	19.0	30.0	94.0	1634.7	51.5	75.0	32.0	21.0	18.8	61.5	28.5	26.5	15.5	16.0	14.5	7.0	22.0	3.5
Syncerus caffer	750.8	107.0	12.0	176.0	12.0	156.8	16.5	49.5	23.5	35.0	86.0	1350.0	65.0	66.0	43.0	27.0	23.0	72.0	33.0	24.0	16.0	17.0	17.0	13.0	12.0	6.5
Tragelaphus strepsiceros	213.5	45.8	4.4	75.7	3.5	181.3	30.5	33.5	28.0	40.0	77.0	601.9	42.0	55.0	32.5	19.0	17.5	50.0	23.5	15.5	9.5	13.0	9.5	8.0	9.0	1.5
Tragelaphus oryx	420.0	53.0	6.5	171.0	2.3	80.0	40.0	42.5	44.0	45.0	67.0	952.0	47.5	47.5	37.0	20.5	21.0	43.0	24.5	16.0	11.0	12.5	12.5	7.0	13.0	3.0
Tragelaphus imberbis	98.0	13.2	1.9	50.8	2.5	59.5	28.0	28.5	29.5	32.0	51.5	255.0	32.0	37.0	18.5	11.5	12.0	25.5	15.5	9.0	9.5	6.0	8.5	3.8	5.0	0.5
Tragelaphus scriptus	55.5	7.7	1.1	49.5	2.5	12.3	51.0	49.0	58.5	25.0	31.0	93.5	25.5	23.5	15.3	8.3	9.8	17.3	9.8	6.8	11.0	4.5	9.0	2.5	7.5	1.0
Oreotragus oreotragus	11.4	2.6	0.2	30.0	1.8	18.0	57.5	81.5	50.5	18.0	26.3	85.0	17.3	16.5	10.8	8.3	7.8	7.3	4.3	3.0	6.5	1.4	5.5	0.9	12.5	1.1
Neotragus moschatus	6.2	1.0	0.1	12.0	1.5	9.2	93.5	49.5	56.0	12.0	15.3	30.3	13.3	12.8	7.2	4.5	4.9	8.9	4.9	2.5	6.5	2.1	11.0	0.9	11.0	0.9
Madoqua kirkii	5.2	0.9	0.1	14.3	1.0	10.5	75.5	82.0	115.0	18.0	16.0	30.3	12.0	11.0	7.9	5.4	5.3	9.4	4.3	2.9	8.0	1.8	7.0	0.6	13.5	0.8
Madoqua guentheri	4.1	0.8	0.1	11.3	1.0	11.4	97.5	75.0	82.0	20.0	16.0	25.0	12.0	10.0	7.4	4.5	5.5	10.3	5.3	3.5	8.5	1.5	7.5	0.5	12.0	0.6
Raphicerus campestris	10.5	2.5	0.2	24.5	0.8	13.0	72.0	68.5	74.5	18.0	18.5	63.0	18.0	16.0	8.5	7.0	6.5	6.3	4.3	2.5	8.5	1.1	2.5	0.3	9.5	1.4
Litocranius walleri	46.0	6.3	0.6	28.0	1.5	23.8	69.0	86.0	62.5	20.0	35.0	72.0	24.0	20.0	14.3	9.0	9.8	13.3	7.9	5.7	9.5	2.5	6.5	2.1	20.0	1.5
Ourebia ourebi	16.0	4.0	0.4	12.5	2.0	8.1	103.0	76.0	39.5	15.0	29.5	120.0	20.0	20.0	11.0	7.3	8.0	9.0	6.0	4.0	7.5	1.5	5.5	1.0	13.5	1.5
Gazella thomsoni	22.5	5.8	0.4	22.5	1.3	14.0	54.0	46.0	27.5	18.0	26.5	92.0	22.0	22.0	12.5	7.0	7.5	10.3	6.3	4.5	8.0	3.0	5.0	1.2	15.5	2.0
Gazella granti	64.0	12.8	1.3	45.0	2.5	57.5	41.0	46.5	42.5	20.0	39.5	247.0	30.5	28.0	17.0	10.8	10.3	14.8	9.8	5.8	11.0	3.0	4.0	0.8	19.5	3.8
Antidorcas marsupialis	42.7	4.8	0.4	33.2	2.1	14.0	50.6	58.6	51.6	20.2	35.6	195.0	26.0	25.5	14.4	8.7	9.7	14.8	8.6	5.5	14.5	3.9	13.5	2.0	18.5	2.5
Aepyceros melampus	62.6	11.9	1.2	28.0	3.5	12.0	49.0	52.5	44.0	15.0	40.5	187.0	33.0	29.0	16.5	11.0	11.0	19.5	11.5	6.5	11.0	5.0	11.5	3.5	17.0	2.5
Sylvicapra grimmia	14.0	3.2	0.2	18.0	1.2	18.8	103.5	97.0	93.0	24.0	28.3	67.5	20.0	15.3	10.0	6.8	7.8	7.8	4.8	2.7	8.5	1.7	6.9	1.0	9.0	1.2
Cephalophus harveyi	16.0	5.0	0.5	13.5	1.2	12.3	79.5	52.5	65.0	12.0	25.0	52.0	16.0	18.0	11.8	10.5	10.3	11.0	7.3	4.0	7.5	2.3	5.5	0.9	10.5	1.1
Kobus ellipsiprimnus	226.0	41.0	3.7	84.0	6.0	37.5	52.0	57.0	32.5	32.0	60.5	629.8	44.0	54.0	20.5	12.5	14.0	33.5	18.0	11.3	14.5	10.0	12.0	6.0	14.8	5.0
Kobus kob	96.0	9.8	1.1	66.0	6.0	10.0	98.0	90.5	60.0	20.0	47.0	532.0	40.0	35.0	14.5	7.5	9.5	23.5	12.0	8.3	14.5	5.2	13.5	3.0	13.0	2.5
Redunca fulvorufula	26.0	7.3	0.7	21.0	3.0	12.0	84.5	52.5	30.0	13.0	32.0	143.0	23.0	24.0	12.5	8.5	8.0	15.5	9.5	5.0	11.5	3.2	11.5	1.6	13.0	2.0
Redunca redunca	45.0	9.7	0.9	28.0	3.0	15.8	76.0	65.5	33.5	20.0	36.0	238.0	27.0	25.0	11.5	7.8	8.8	17.5	8.8	6.8	12.0	4.5	12.5	2.0	12.5	1.9
Oryx gazella	203.0	35.5	3.6	60.0	5.0	26.3	31.5	22.0	16.0	12.5	55.0	609.0	44.0	41.0	22.0	15.0	14.0	42.5	21.0	14.5	16.5	10.5	14.5	4.5	21.0	3.5
Damaliscus lunatus	130.0	31.0	3.0	45.0	4.0	9.4	76.0	47.0	43.5	16.0	60.0	729.0	40.0	44.0	18.0	13.0	12.5	34.5	15.0	11.0	14.5	8.5	12.5	6.0	17.5	3.0
Alcelaphus buselaphus	138.0	23.0	2.6	45.0	4.0	12.8	82.5	49.5	31.0	20.0	64.0	494.0	40.0	43.0	17.5	14.0	14.0	35.0	17.5	13.5	15.5	10.0	14.0	6.0	21.0	3.0
Alcelaphus lichtensteinii	174.0	40.0	4.6	72.0	3.7	13.5	73.0	44.0	33.3	25.3	69.0	511.5	42.0	45.0	21.0	15.0	15.0	38.5	19.5	13.5	13.5	12.0	13.0	7.0	22.5	3.5
Connochaetes taurinus	201.0	40.0	4.3	72.0	5.0	56.3	52.5	47.5	51.0	38.0	59.0	648.0	47.0	49.0	27.5	14.5	16.0	49.0	24.0	16.5	15.0	14.0	12.5	9.0	15.0	2.5

variable (i.e. the cut off distance). We detected a significant phylogenetic correlation in all traits.

2. The second step consists of removing the phylogenetic relatedness by generating a group of standardised residuals free of phylogenetic correlation. The method partitions the total variance of a trait (y) into the variance attributable to the phylogenetic effect (W_y) and the variance related to the independent evolution or adaptation of a species (ε; the model is $y=\rho W_y+\varepsilon$). The autocorrelation coefficient (ρ) represents the correlation between the observed value of the variable (y) and its strictly phylogenetic value (W_y). W describes the relative phylogenetic distance of all pairs of species included in the analysis (n=28; Fig. 1). We used the cut-off distance for each variable to exclude uncorrelated data from the analysis. The cut-off distances varied between 2 and 6 units (mode=5). Then a maximum likelihood procedure was applied to estimate ρ and r^2, where r^2 is the variance explained by the phylogeny (Cheverud et al. 1985). By following this procedure we obtained a data set of standardised ε values (mean zero and unit variance) associated with each trait and species which represented the variance caused by only hypothetical adaptation.

Statistical analysis

Body mass was controlled for by using the residuals from the regression of standardised body mass against the stomach traits (Model I regression, Rayner 1985; McArdle 1988) in the conventional and phylogenetic models (see above). Altogether four models were applied to the data set: (1) when neither body mass nor phylogeny were taken into account; (2) when body mass was taken into account but phylogeny was not; (3) when the phylogenetic effect was accounted for but the body mass effect was not; (4) when both the phylogeny and body mass effects were accounted for.

Firstly, since our aim was to verify, a priori, differences between feeding styles, principal component analysis (PCA) was applied to the correlation matrices of the above data set separately for each of the four models (see above). We used the scores of the PCA to plot species and check for any evident clustering pattern of species belonging to different feeding styles. The number of principal components retained was determined by optimising the percentage of explained variance and the most parsimonious solution. This was also consistent with the inspection of the residual correlation matrix, which in all cases showed small residual values. This matrix represents the partial correlations between pairs of variables when the effects of the factors have been removed (Tabachnick and Fidell 1989). The loadings of the PCA were used to investigate the contribution of the traits to each principal component in order to characterise them, since the size of the loadings reflects the extent of the relationship between traits and factors (Tabachnick and Fidell 1989). Multivariate analysis of variance (MANOVA, using approximate χ^2 test) was applied to the scores of PCA to test for significant differences between feeding styles. Once MANOVA detected significant differences between feeding styles in gut morphology, restricted maximum likelihood (REML, Genstat 5 Committee 1993) was applied to the scores of each of the two first principal components, using species as a random term and feeding style as a fixed factor, in order to determine which of the principal components was contributing to the largest extent to the total variance. Finally, comparisons among feeding styles were assessed by inspection of the standard errors of the predicted means of the REML analysis.

Secondly, to assess differences a posteriori in gut morphology among species, that is, after the species had been assigned to their feeding style using the information available on their diet from the literature, a canonical variates analysis (CVA) was applied to each of the four models (see above). The significance of the contribution of each canonical variate in explaining the variance between feeding styles was estimated using the χ^2 test (Genstat 5 Committee 1993). As above, CVA loadings were used to characterise each canonical variate.

The assumptions of normality and homoscedasticity were verified by inspection of the normal residual plots. Statistical analyses were performed using GENSTAT 5 (v. 4.1.) for Windows statistical package (Genstat 5 Committee 1993).

Results

Conventional approach

Not controlling for body mass

The first two principal components explained 84% of the total variance; the first axis explained 75% and the second only 9%. The first principal component was mainly defined by two groups of variables; in the positive part of the axis there was a compact cluster of variables related to the volume and dimensions (length, height, width) of the rumen, reticulum, abomasum, omasum and the two variables related to ostium apertures (Fig. 2 a). The negative part of the first component was characterised by variables related to the density of papillae in different parts of the rumino-reticulum. The second axis contrasted the surface area of the mucosa in the negative part of the axis and the number of plicae spiralis in the positive

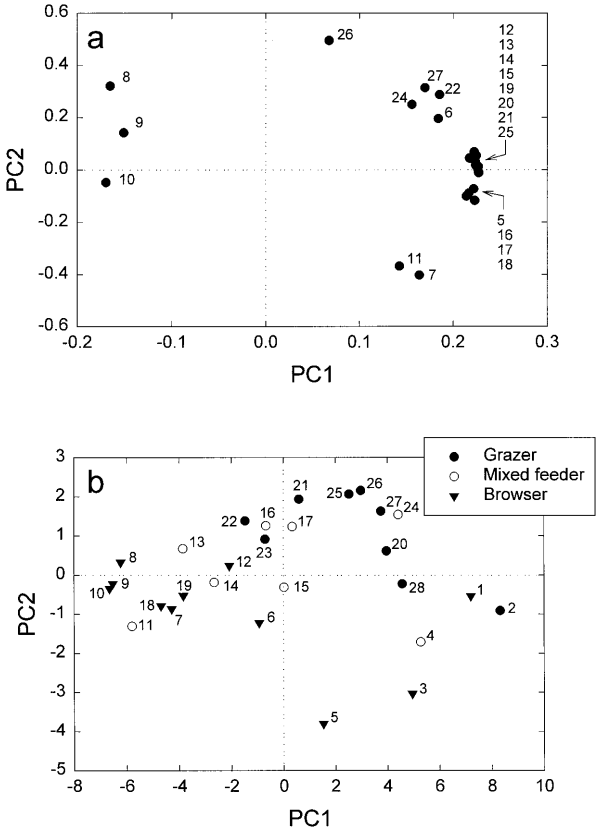

Fig. 2 Loadings (**a**) and scores (**b**) of the principal component analysis of some stomach morphology traits on the first two principal components (PC1, PC2) when body mass and phylogeny were not taken into account. Loadings are coded following Table 1. Percentage of variance explained by each principal component is in Table 3. Scores of species are coded following Fig. 1

Table 3 Principal component analysis (PCA), multivariate analysis of variance (MANOVA) and restricted maximum likelihood analysis (REML) of the PCA scores of 25 traits of the stomach morphology of 28 species of Artiodactyls. Two approaches were used, conventional and phylogenetic (see Materials and methods). Predicted means (from REML) and standard errors of difference between $\log_{10}$-transformed predicted means of different feeding styles are shown. PC1 and PC2 are the first and the second principal components of PCA. The percentage of variance explained for either of the first two principal components is shown. Predicted means of feeding styles (grazers, mixed feeders, browsers) with a different superscript differ at α=0.05

Approach	PCA			MANOVA		REML		Predicted means			
	Control for body mass		Variance explained	χ^2 (*df*=4)	*P*	Wald statistic (*df*=2)	*P*	Grazer	Mixed	Browser	SE (*df*=4)
Conventional	No	PC1	74.99	21.11	0.0001	11.5	0.003	3.902[a]	–0.611[ab]	–3.245[b]	1.961
		PC2	8.51			2.1	0.350	0.456	0.276	–0.318	0.539
	Yes	PC1	22.24	18.13	0.001	4.6	0.100	–1.170	0.657	0.089	0.863
		PC2	20.25			5.4	0.067	–0.523	–1.022	1.165	1.015
Phylogenetic	No	PC1	69.48	10.60	0.031	9.9	0.007	3.470[a]	–0.333[ab]	–3.125[b]	1.937
		PC2	8.37			0.6	0.741	0.335	0.152	–0.201	0.664
	Yes	PC1	25.24	8.07	0.089	2.5	0.287	1.095	–0.792	–0.325	1.199
		PC2	16.72			1.9	0.387	–0.725	0.557	–0.033	0.951

part of the axis. Most of the other variables were widely scattered along the second axis, with a group of loadings related to dimensions of the stomach compartments centred around the origin (Fig. 2a).

The species distribution along the first component axis showed a slight pattern of aggregation in relation to some feeding styles (Fig. 2b). Most of the browsing species were located on the negative part to the first axis, although two species in the browser category lay on the positive part of the first component (i.e. *Giraffa camelopardalis* and *Tragelaphus strepsiceros*) and one species lay closer to the origin (i.e. *Tragelaphus imberbis*). Grazing species lay along the positive part of the first component, although two species were located in the negative part. Along the first principal component the most polarised location was shown by *Syncerus caffer* in the positive part of the axis and *Madoqua guentheri* in the negative part, suggesting a marked effect of body mass on this axis. Mixed feeders could not be distinguished using the information provided by the two principal components. Accordingly, the scores of the two principal components distinguished between feeding styles (MANOVA, P=0.0001, Table 3). The univariate analysis indicated that differences between feeding styles were caused by the first principal component (P=0.003). Grazers could be distinguished from browsers (P<0.05, Table 3), whilst mixed feeders could not be distinguished from either grazers or browsers (P>0.05, Table 3). No significant differences were detected between feeding styles in the second principal component (Table 3).

Two canonical variates discriminated between feeding styles (χ^2=95.5, *df*=50, P=0.0001). However, after removal of the first canonical variate there was no significant association between the feeding styles and the gut morphology traits (χ^2=32.9, *df*=24, P=0.106), which indicates that only the first canonical variate contributed to feeding style discrimination. The first canonical variate accounted for 91% of the variability among feeding styles. As shown in Fig. 3a the first canonical variate separated browsers from the other two feeding styles, mixed feeders and grazers. The loadings matrix suggested that the best gut morphological variables for distinguishing browsers from mixed feeders and grazers were the presence, in browsers, of the small area of the ostium rumino-reticulum and low reticulum primary crests, a short cranio-caudal length of the rumino-reticulum and small number of papillae in the atrium ruminis.

Controlling for body mass

After body mass was controlled for in the analysis, the variance explained by the two first principal components was only 42%, and three additional dimensions were necessary to explain 70% of the total variance. The loadings of the variables were scattered along both of the first two axes creating difficulty in characterising each principal component, although a number of variables related to stomach compartment dimensions were in the negative part of the first principal component (Fig. 4a). The scores of the species were more scattered across the two axes than in the previous approach (not controlling for body mass) and grazers were in the negative part of the first component and browsers in the positive part (Fig. 4b). Significant differences were detected among feeding styles using the scores of the PCA (MANOVA, P=0.001, Table 3), but differences were not detected using a univariate analysis on any of the two principal components (PC1: P=0.100; PC2: P=0.067, Table 3).

Only the first canonical variate was significant (χ^2=80.2, *df*=50, P<0.004) and accounted for 97% of the variability among feeding styles. The first canonical variate discriminated mixed feeders from the other two feeding styles (Fig. 3b). The loadings indicated that mixed feeders were characterised by a small omasum-abomasum capacity, short cranio-caudal length of the rumino-reticulum and a narrow laminae II of the omasum.

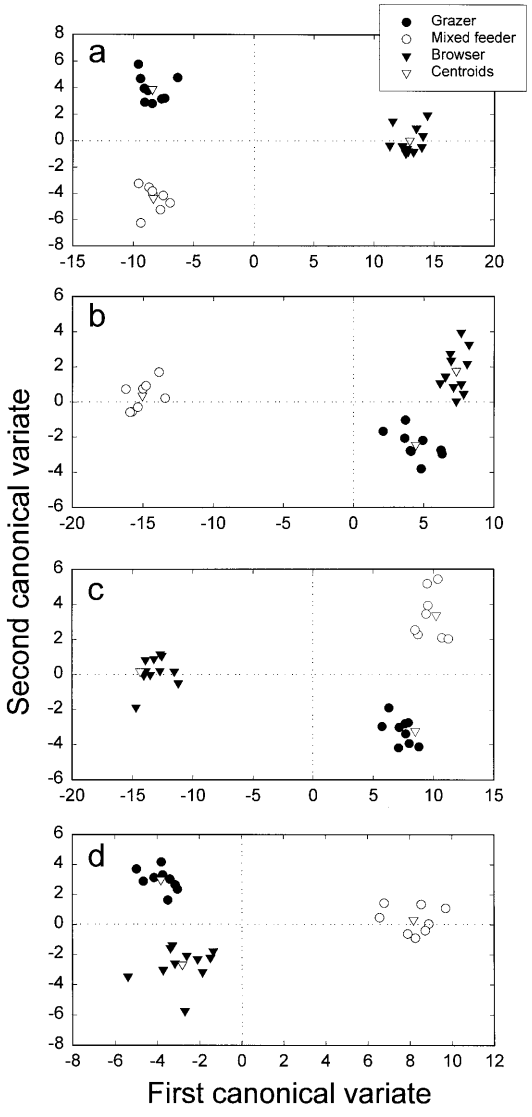

Fig. 3 Scores of the canonical variate analysis on the first two axes when **a** body mass and phylogeny were not controlled for, **b** controlling only for body mass, **c** controlling only for phylogeny,and **d** controlling for body mass and phylogeny. Also the centroids of each feeding style are shown

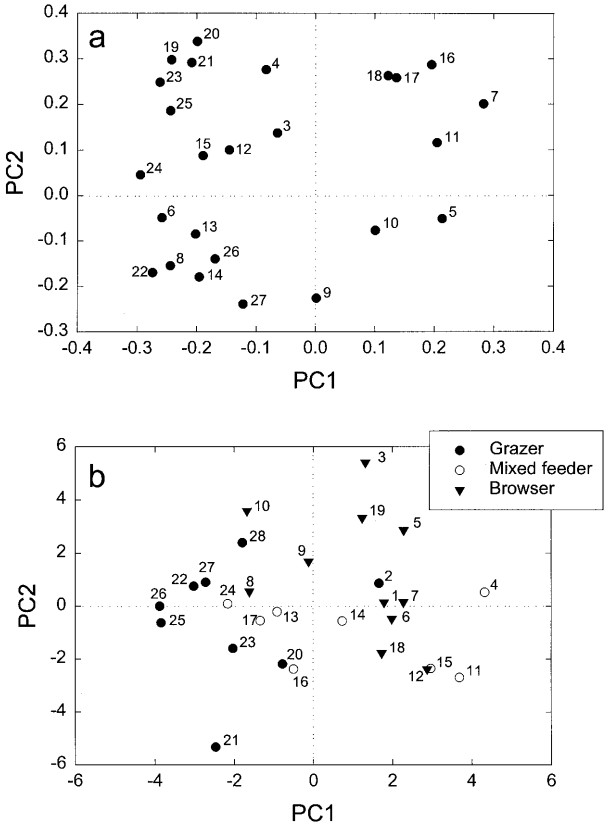

Fig. 4 Loadings (**a**) and scores (**b**) of the principal component analysis on the first two principal components when body mass was controlled for but phylogeny was not. (For explanation of abbreviations see Fig. 2)

Phylogenetic approach

Not controlling for body mass

When only phylogeny was taken into account, the results obtained (i.e. characterisation of the principal components and distribution of the species' scores, Fig. 5a, b) were similar to the ones obtained when phylogeny was not taken into account (Conventional approach), although the total variance explained by the two first components was slightly less (78%, Table 3). The visual clustering pattern of some species in relation to the feeding styles was corroborated by statistical analyses; the scores of the two principal components discriminated between different feeding styles significantly (MANOVA, P=0.031). REML analysis detected differences among feeding styles in the first principal component (P=0.007, Table 3) but not in the second component (P=0.741, Table 3). Grazers could be distinguished from browsers in relation to the first component (P<0.05, Table 3), whilst mixed feeders could not be distinguished from grazers or browsers (Table 3).

Only the first canonical variate was significant (χ^2=92.9, df=50, P=0.0002) and it accounted for 95% of the variability between feeding styles. The first canonical variate separated browsing species from the other two feeding styles (Fig. 3 c). Browsing species were defined by having a small ostium rumino-reticulum area, short cranio-caudal length of the rumino-reticulum, narrow laminae I of the omasum and large size of papillae of the atrium ruminis.

Controlling for body mass

When both phylogeny and body mass were controlled for, the two principal components only retained 42% of the total variance, and it was necessary to include another three dimensions to explain 70% of the variance. The first principal component maintained the same characterisation described in the previous approach, when only phylogeny had been controlled for (i.e. with the stomach

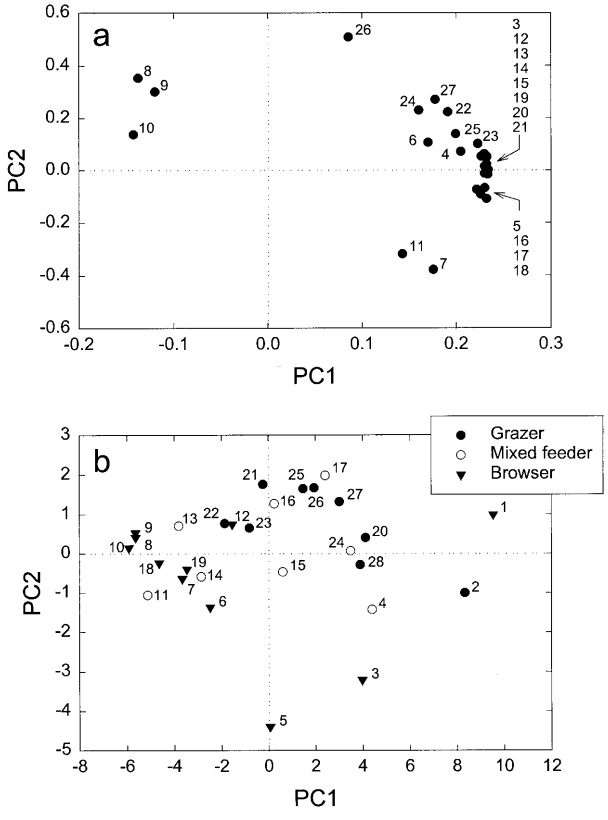

Fig. 5 Loadings (**a**) and scores (**b**) of the principal component analysis on the first two principal components when phylogeny was controlled for but body mass was not. (For explanation of abbreviations see Fig. 2)

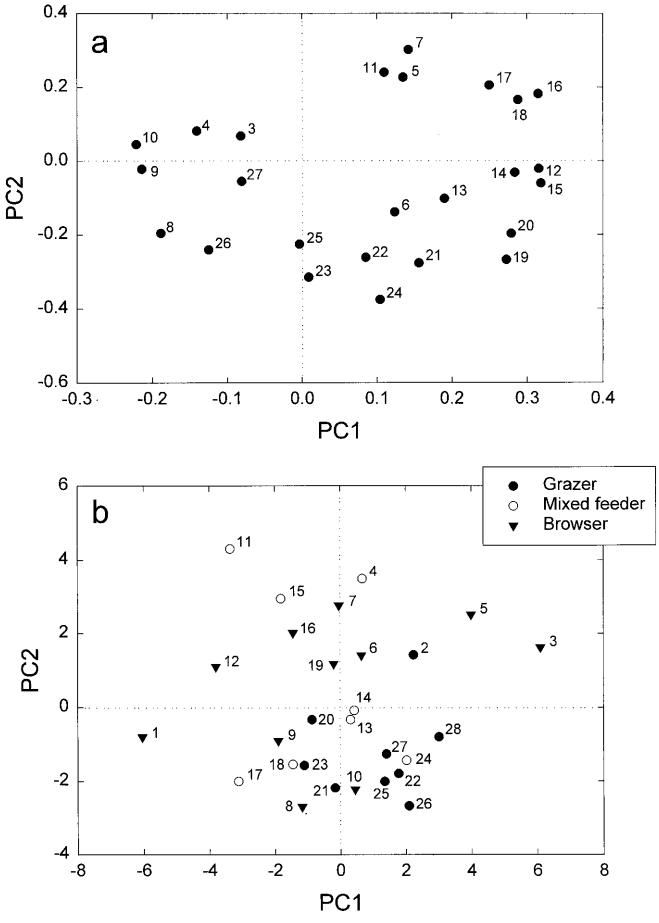

Fig. 6 Loadings (**a**) and scores (**b**) of the principal component analysis on the first two principal components when phylogeny and body mass were controlled for. (For explanation of abbreviations see Fig. 2)

compartments dimensions in the positive part and the density of papillae of the rumino-reticulum in the negative part but clearly more scattered, Fig. 6 a). Most of the variables were broadly scattered along the second component which contrasted the surface area of the mucosa (variables 7, 11) in the positive part and the number and width of omasum laminae in the negative part (variables 22–25).

The species distribution along the two first principal components in relation to feeding styles was confused (Fig. 6b). The browser category suffered the greatest loss of discrimination in relation to the first two principal components. Browsing species were distributed almost proportionally between the four sectors defined by the two principal components. Most of the grazers were in the negative part of the second principal component but the discrimination of this group was weak. The pattern described in this approach is similar to the one obtained when only body mass had been controlled for, but now no significant differences were detected among feeding styles (MANOVA, p=0.089, Table 3).

Only the first canonical variate contributed significantly to the discrimination between feeding styles (χ^2=92.9, *df*=50, *P*<0.005). Although the variance explained was not as high as in the previous approaches, it was still considerable (83%). Mixed feeders were separated from the other two feeding styles (Fig. 3d), but no significant differences were detected between browsers and grazers. A narrow reticulum and abdomen, short rumino-reticulum cranio-caudal length and high rumino-reticulum capacity distinguished mixed feeders from the other two feeding styles.

Discussion

The phylogenetic effect and functionality of morphological variables

Whether phylogeny-based comparative methods can or cannot separate adaptive evolution from the contribution of sharing common ancestry is an arguable issue (Ricklefs 1996). This is especially important when supposed adaptive changes in a trait occur only a few times within the phylogeny (Vanhooydonck and Van Damme 1999). The main point of the latter discussion is how to weigh the effect of ecology on adaptive evolution and shared ancestry on a particular trait. We addressed our discussion using the same approach as adopted in sequential statisti-

cal analyses. That is, we controlled for different terms, body mass and phylogeny (as explained in Materials and methods) and discussed the effect that each of these terms has on the rest of the model.

Many variables of the data set were strongly correlated with each other because they represented different measurements of the same organ or part of the organ. This is not a problem for multivariate analysis, because correlated variables contribute equally to the explained variance although no-correlated variables can also contribute equally to different components of a PCA (Gaillard et al. 1989). We decided to use all of the variables presented by Hofmann (1973) in an attempt to statistically analyse the morphological differentiation in the ruminant stomach observed by Hofmann, which has been the baseline for many comparative studies in the Artiodactyla (see Introduction). The variables analysed in our study do not give complete information about all the morphological features of the ruminant stomach described by Hofmann (1973, 1989), but they all present measurable features. Although the functionality of all variables measured has not been shown in the literature, we consider that these variables provide a measure of function. Functional differences among feeding styles can be achieved if differences in (1) quantity of stored food in the stomach (stomach volume), (2) time that the food is retained in the stomach (shape of compartments, pillars size, diameters of orifices), and (3) absorptive surface (stomach surface, density of papillae, papillae surface) occur. We have found differences between feeding styles based on the macroscopic morphological variables analysed in this study, but, as discussed below, these differences do not support the traditional classification.

Which traits characterise morphological differences between feeding styles?

Our analysis clearly demonstrates that differences between species in alimentary tract morphology pointed out in the literature (Hofmann 1968, 1973, 1984, 1988, 1989; Demment and Longhurst 1987; Hofmann et al. 1995; Yamamoto et al. 1998) do exist, but, contrary to previous suggestions, the adaptive effect between feeding styles is undetectable. This is because differences in stomach morphology detected between feeding styles are caused by the combined effects of body size and phylogeny. Most of the differences obtained when phylogeny and body mass were not taken into account remained when body mass was controlled for, but no differences were detected between feeding styles when both body mass and phylogeny were accounted for. Stomach morphology features are shared by related species, which implies a close link between feeding style and speciation within the same clade. After accounting for body mass but not phylogeny, the differences between feeding styles were not easily defined. MANOVA detected differences between feeding styles when the first and second principal components were both analysed together, but the differences did not remain when only one of the two principal components was used.

In order to test whether diet composition, gastrointestinal morphology or digestive function vary between feeding styles as proposed by Hofmann (1973), many studies have categorised species according to feeding style and tested for differences between categories (e.g. Gordon and Illius 1994; Robbins et al. 1995; Iason and Van Wieren 1998). However, we did not detect any difference in stomach morphology between feeding styles, after both body mass and phylogeny were taken into account. There is no doubt that classification of ruminants into dietary habits is useful in the study of their ecology and there is superficial agreement that the classification attributed to Hofmann correlates with the feeding styles and feeding habits used in this and other studies (Iason and Van Wieren 1998). However, we have found that, after adjusting for phylogeny and body mass, stomach morphology provides no basis for the classification of ruminant herbivores into feeding styles.

It has been suggested that the main difference in stomach morphology between feeding styles lies in the larger absorptive surface of the stomach of browsers versus grazers or mixed feeders (Hofmann 1984; Demment and Longhurst 1987). However, some concerns arise when these studies are analysed in detail. Van Wieren (1996) analysed five of Hofmann's (1973) stomach traits using a univariate approach and found that the only difference between feeding styles was due to the density of papillae in the ventral rumen wall (grazers and mixed feeders had lower density of papillae than browsers), but differences between feeding styles disappeared when the three smallest species (*Madoqua kirki*, *Madoqua guentheri* and *Neotragus moschatus*) were removed from the analysis. Demment and Longhurst (1987) stated that there were no differences between feeding styles in the surface area of the rumen but that browsers had a greater total absorptive area in the rumen (i.e. estimated as rumen surface area × papillae density × papillae surface area). This result was derived by comparing the regression lines of the absorptive area against body mass between browsers and grazers plus mixed feeders, finding differences between the slopes. This conclusion is unjustified, because the heterogeneity of slopes between feeding styles means that the average of the response variable (i.e. total absorptive area) in any of the feeding styles depends on the value of the explanatory variable, in this case body mass. Van Wieren (1996) also analysed the maximum surface enlargement factor from Hofmann's (1973) data set and found no differences between feeding styles.

We found that the density of papillae in different stomach regions contributes significantly to the characterisation of the first principal component, but only when body mass was not taken into account (Figs. 2a, 5a). After body mass was accounted for, the density of papillae did not explain any more of the variance than the rest of the variables studied (Fig. 4a, 6a).

The caecum and large intestine (i.e. hindgut) of some mammals (e.g. proboscids, perissodactyls, hyraxes) play an important role in the fermentation of plant fibre and soluble plant matter and also in the absorption of electrolytes, ammonia, volatile fatty acids, amino acids and bacterial vitamin synthesis (Robbins 1993). However, the functional significance of the hindgut in ruminant digestion is considerably less than that of the stomach (Prins et al. 1984; Gordon and Illius 1994). It is, therefore, unlikely that ruminants that differ in feeding style present more conspicuous morphological differences in hindgut morphology than in stomach morphology.

In conclusion, the stomach traits studied did not allow us to distinguish between species that differed in feeding style. Most of the variability in stomach morphology was caused by body mass and a small fraction by phylogeny. Thus, there is no consistent evidence to support a significant adaptive effect of stomach morphology on different diets.

An a posteriori classification of gut morphology

The gut morphology of species that differ in feeding style could be characterised using a multivariate approach based on a previous definition of their feeding styles using information about their diets. When we did not control for body mass or phylogeny, the gut morphology of browsing species could be distinguished from that of mixed feeders and grazers but these two latter groups of species could not be separated from each other. Similar results were obtained when we controlled only for phylogeny. Surprisingly, the grouping changed radically when body mass was controlled for: mixed feeders were clearly separated from the other two feeding styles, which did not differ from each other. Mixed feeders were characterised by a small omasum-abomasum capacity, short cranio-caudal length of the rumino-reticulum and narrow laminae II of the omasum. Hofmann (1989) characterised mixed feeders as a group that had a morphology which was transitional between the grazer and the browser types, although closer to the latter type. This is not borne out by this study. Mysterud (1998) analysed differences in activity time between feeding styles and found that mixed feeders were more active than both grazers and browsers, which did not differ in activity time from each other, but these results did not hold when phylogeny was controlled for (Pérez-Barbería and Gordon 1999b). Although the results found by Mysterud (1998) are in agreement with what we have found in this study, it is not known whether activity time and the stomach morphological traits analysed here are functionally related.

When both body mass and phylogeny were controlled for, again grazers and browsers were indistinguishable and mixed feeders formed a separate group. Now mixed feeders were characterised by having high rumino-reticulum capacity, a short rumino-reticulum cranio-caudal length and narrow reticulum. The results of this analysis show that browsers and grazers form a homogeneous group in terms of gut morphology when body mass and phylogeny are taken into account.

The main morphology features which have been hypothesised to be adaptive traits in grazing species that increase the retention time of ingesta (namely, a larger relative stomach capacity, more subdivision of chambers and smaller openings) cannot be supported by the results of this study. Mixed feeders cannot be classified as a transitional group that have a stomach morphology in between that of browsing and grazing species, because mixed feeders seem to constitute a well-defined group in relation to their stomach morphology.

It is advisable not to pay too much attention to the final group of variables that defines each feeding style on the grounds that the functional meaning of some of these traits is unknown when they are considered in isolation. It is more useful to try to understand the general process that separates the gut morphology of one feeding style from another. From our analysis of gut morphology it is clear that body size is the main trait which determines the morphological characteristics of the gut in the Artiodactyla. This effect is far more important that variation in stomach morphology associated with phylogenetic branching pattern or feeding style. This is consistent with the fact that mixed feeders are able to shift their feeding style, so they should have evolved a stomach morphology which is able to cope with both grass and browse dominated diets independent of body mass, exactly as our analysis indicates.

Acknowledgements We thank Glenn Iason, John Milne, Atle Mysterud, Jean-Michelle Gaillard and an anonymous referee for their comments on this manuscript and Carlos Nores from the Instituto de Recursos Naturales y Ordenación del Territorio for his support in the initial stages of this study. This paper was supported by funding from The Scottish Executive Rural Affairs Department and Training and Mobility of Researchers of the European Communities.

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