The evolution of phylogenetic differences in the efficiency of digestion in ruminants

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This study investigates, for the first time (to our knowledge) for any animal group, the evolution of phylogenetic differences in fibre digestibility across a wide range of feeds that differ in potential fibre digestibility (fibre to lignin ratio) in ruminants. Data, collated from the literature, were analysed using a linear mixed model that allows for different sources of random variability, covariates and fixed effects, as well as controlling for phylogenetic relatedness. This approach overcomes the problem of defining boundaries to separate different ruminant feeding styles (browsers, mixed feeders and grazers) by using two covariates that describe the browser–grazer continuum (proportion of grass and proportion of browse in the natural diet of a species). The results indicate that closely related species are more likely to have similar values of fibre digestibility than species that are more distant in the phylogenetic tree. Body mass did not have any significant effect on fibre digestibility. Fibre digestibility is estimated to increase with the proportion of grass and to decrease with the proportion of browse in the natural diet that characterizes the species. We applied an evolutionary model to infer rates of evolution and ancestral states of fibre digestibility; the model indicates that the rate of evolution of fibre digestibility accelerated across time. We suggest that this could be caused by a combination of increasing competition among ruminant species and adaptation to diets rich in fibre, both related to climatically driven environmental changes in the past few million years.

Keywords: browser; grazer; phylogeny; evolution; digestibility; diet

1. INTRODUCTION

Despite considerable efforts in the analysis of the comparative anatomy of the digestive tract of ungulates, research has hitherto failed to demonstrate any relationship between differences in morphology and digestive efficiency between species, other than at a gross level (Robbins 1993). We offer a novel analysis that controls for confounding effects and highlights the flexibility of digestive adaptation in ruminants.

Previous research in this area demonstrates a number of weaknesses. The first weakness is the question of continuous versus discrete variables. Hofmann (1968, 1973) and Hofmann & Stewart (1972) described the stomach morphology of a number of species of African ruminants and using this information classified species into three groups (i.e. concentrate selectors, intermediate, and bulk and roughage eaters). Concentrate selectors (i.e. browsers) were the species whose diet mainly contained browse; bulk and roughage eaters (i.e. grazers) were species in which grass was the main component of the diet, and the third group, intermediate (i.e. mixed feeders), consumed a mixture of browse and grass, depending upon the habitat or season. Hofmann & Stewart (1972) and Hofmann (1973) pointed out that their stomach classification coincided with the main dietary habits of the

ruminant species. However, Hofmann's later papers (1985, 1988) established a composite criterion of species classification '...based on typical structures of the digestive tract ... and/or on feeding behaviour/forage selection' (Hofmann 1985, p. 398). This may be the cause of confusion in the literature as to the criteria used to classify species, almost entirely based on dietary habits but frequently linked with the stomach classification of Hofmann (1973) (see Iason & van Wieren 1999; Pérez-Barbería & Gordon 1999a, 2000, 2001; Brashares *et al.* 2000; Gagnon & Chew 2000; Pérez-Barbería *et al.* 2001a). As a result, the relationships that many studies find between the variables studied—dietary classification and stomach morphology—are confounded by circular argumentation (Pérez-Barbería *et al.* 2001a).

Hitherto, ruminant species have been classified into dietary groups using discrete boundaries based on information on stomach morphology or dietary habits (Axmacher & Hofmann 1988; Gordon & Illius 1988, 1994, 1996; Janis & Ehrhardt 1988; Spencer 1995; van Wieren 1996; Iason & van Wieren 1999; Pérez-Barbería & Gordon 1999a,b, 2000, 2001; Brashares *et al.* 2000; Gagnon & Chew 2000; Pérez-Barbería *et al.* 2001a). However, stomach morphology and dietary habits are continuous variables and they should be treated as such.

A second weakness of previous work has been an under-emphasis on phylogeny. Phylogeny has been demonstrated to be a significant factor in explaining the variability in a number of morphological traits (Pérez-Barbería & Gordon 1999a, 2001; Pérez-Barbería *et al.* 2001a) and behavioural variables (Pérez-Barbería &

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Gordon 1999b; Brashares *et al.* 2000; Myserud *et al.* 2001; Pérez-Barbería *et al.* 2001b, 2002) across a large number of ungulate species with different feeding styles.

Finally, studies dealing with differences in fermentation rates and fibre digestibility between ruminant species specialized to feed on different diets are based on meta-analyses of data collated from the literature (e.g. Robbins 1993; Gordon & Illius 1994, 1996; Robbins *et al.* 1995; van Wieren 1996; Jason & van Wieren 1999). Thus, these datasets involve a number of sources of variability that need to be controlled for to detect the main effects.

There is palaeoecological evidence that the ancestral ruminant was a small and forest-dwelling species (Janis 1982) and, therefore, a consumer of parts of the vegetation rich in intracellular carbohydrates (Pérez-Barbería *et al.* 2001b, 2002). As the area of forest decreased through the Late Oligocene, giving way to vast tracts of grasslands throughout the Late Miocene (Leopold 1969; Janis *et al.* 2000; Jernvall & Fortelius 2002), mixed feeders and grazing species radiated, and it is presumed that ruminants evolved adaptations to increase their efficiency in digesting fibre (Pérez-Barbería *et al.* 2001b, 2002). Within this evolutionary scenario, a number of questions arise about the evolution of the efficiency of fibre digestion. These questions stem from the interpretation of the neo-Darwinism concept; that is, was the transition rate between two traits constant (i.e. phyletic gradualism) or did the new trait emerge suddenly (punctuated evolution, *sensu* Eldredge & Gould 1972)? In the case of fibre digestion in ruminants, has the efficiency of fibre digestion increased over time? Has the efficiency of digesting fibre gradually changed across species (i.e. species-specific adaptation) or was it subjected to an intense period of evolution that then decelerated (i.e. adaptive radiation)?

This study analyses an updated dataset on fibre digestibility in ruminants and controls for a number of confounding components, namely, data source, food type, fibre content, body mass and phylogeny. The aims are: (i) to estimate the contribution of each component in explaining variation in the digestion of fibre (i.e. neutral detergent fibre digestibility) between species adapted to consuming different diets and (ii) to trace the evolution of the efficiency of fibre digestion through the phylogeny. We expect that:

- (i) phylogenetically related species will have similar digestion efficiencies, after accounting for body mass;
- (ii) body mass and digestive efficiency will be positively correlated, since larger ungulates have longer retention times of food through the digestive tract (Illius & Gordon 1991);
- (iii) species adapted to consuming different diets will differ in the efficiency with which they digest fibre when body mass has been taken into account;
- (iv) ancestral species were less efficient at digesting forages of high fibre content than are extant ruminants; and
- (v) species will have developed flexible adaptive strategies to digest fibre in response to changes in vegetation composition and availability.

2. MATERIAL AND METHODS

(a) Selection of variables and data collection

We collated data from experiments in which ruminant species had been fed on single forages, classified as either gramineous, herbaceous dicotyledonous or woody dicotyledonous plants (i.e. grass, forbs or browse, respectively), without supplements. We excluded experiments where a mixture of grass, forbs and browse was fed. We found 37 published papers, a total of 139 feeding trials, on 24 ruminant species containing complete information for the following parameters: neutral detergent fibre digestibility (NDFD, %), type of forage fed, the lignin and neutral detergent fibre (NDF) content of the forage fed and body mass of the animals used in the trials. (A breakdown of the number of records for each species is given in electronic Appendix A.) Data are available from A. W. Illius. One of the covariates used in this study was the log_e-transformed ratio of lignin to NDF (LLigNDF) in the forage fed to the animals. We used LLigNDF as a covariate to control for potential variations in the digestibility of the forage used in the digestibility trials in the literature (Robbins *et al.* 1987a,b).

The percentages of the major components in the diet of each species in the wild (grass, browse, fruit; electronic Appendix A) were averaged from information presented in van Wieren (1996), Gagnon & Chew (2000), N. Owen-Smith (personal communication) and Pérez-Barbería & Gordon (1999a). We found no quantitative figures for the diets of two species, *Tragulus javanicus* and *Boselaphus tragocamelus*; therefore, we used arbitrary values that were suggested by qualitative comments on their diets recorded in the literature (Novak 1999). *Tragulus javanicus*, which is a browser–frugivore species that also ingests some grass, was assigned values of 10% grass, 45% browse and 45% fruit. *Boselaphus tragocamelus*, a mixed feeder, was assigned values of 50% grass and 50% browse.

(b) Phylogenetic information

In this study, we used two phylogenetic trees for the same group of species; this was a compromise to: (i) have reliable phylogenetic information for all our species; and (ii) meet the requisites of the different statistical analyses applied. For the REML (residual maximum-likelihood) model (see § 2c) we used a phylogeny based on Pérez-Barbería & Gordon (1999a,b, 2000) and Pérez-Barbería *et al.* (2001b, 2002). This phylogeny allowed us to include, in the REML model, all species for which we had information on fibre digestibility.

To investigate the rates of evolution of fibre digestibility (see § 2d) we used a statistical model (CONTINUOUS directional model; see § 2d) that can be applied only to non-ultrametric trees (i.e. trees where the path lengths from the root of the tree to each tip vary). To meet this requirement we created a new tree based exclusively on genetic information at the cost of not including all species. Detailed information on the methods and information used to create the phylogenies is given in electronic Appendix B.

(c) Statistical analysis

One of the main problems that researchers face when using comparative techniques is the lack of flexibility of some of the methods available (Harvey & Pagel 1991; Myserud *et al.* 2001). One of the techniques commonly used is that of independent contrasts (Felsenstein 1985) through application of user-friendly software, phenotypic diversity analysis programs (PDAP) (Garland *et al.* 1992, 1993, 1999; Diaz-Uriarte & Garland 1996;

Garland & Ives 2000). Independent contrasts struggle with complex analyses (Garland & Ives 2000) and cannot cope with linear mixed models. A more flexible approach is the use of generalized least-squares models (Martins & Hansen 1997; Rohlf 2001). However, this method has not been extensively used in the literature owing to its statistical complexity.

To solve these problems for the relationship between NDFD and LLigNDF we applied linear mixed models using the REML method (Patterson & Thompson 1971). Various models were fitted to explore different aspects of the data. The fixed term in the final model included $\log_e(\text{body mass})$ as a covariate, to standardize for animal size, along with the main effects of feed quality, measured by LLigNDF, and the diet of the species in the wild, measured by the percentages of grass and browse. Percentage of fruit was excluded as the three percentages sum to 100%. The interactions between LLigNDF and both grass and browse were also excluded, as preliminary tests found no evidence to support their inclusion. The random term in the final model allowed for differences among literature sources (ref), the batch of food offered to the animals in the experiment (food) and a species effect (sp). The species effect was incorporated either ignoring the correlation induced by phylogenetic relatedness or taking phylogenetic relatedness into account, in which case the variance of observation y_i was modelled as:

$$\text{var}(y_i) = \sigma_{\text{ref}}^2 + \sigma_{\text{food}}^2 + \sigma_{\text{sp}}^2 + \sigma^2$$

and the covariance, $\text{cov}(y_i, y_j)$, between different trials y_i and y_j was modelled as:

$$\text{cov}(y_i, y_j) = R(i, j) \times \sigma_{\text{ref}}^2 + F(i, j) \times \sigma_{\text{food}}^2 + G(i, j)^q \times \sigma_{\text{sp}}^2,$$

where $R(i, j)$ and $F(i, j)$ take the values of 1 or 0 depending on whether or not feeding trials i and j share the same value of 'ref' and 'food', respectively, and $G(i, j)$ indicates the degree of phylogenetic relatedness ranging from 1 (same species) to 0 (least related) based on a rescaled-branch-lengths matrix of the phylogenetic tree. The parameters estimated in the random-effects model were the variance components σ_{ref}^2 and σ_{food}^2 for 'ref' and 'food', respectively, along with σ_{sp}^2 and q , which define the relationship between relatedness and covariance, and the residual variance σ^2 . Conditional on the value of q , this is a standard REML model and the optimal values of all five covariance parameters were determined by a grid search on values of q using the final model. The covariance matrix of all parameters in the random-effects model was obtained by numerically estimating, then inverting, the matrix of second derivatives of the residual likelihood. Degrees of freedom for individual covariates were obtained, following the approach of Giesbrecht & Burns (1985), by expanding the corresponding variance as a linear sum of the covariance parameters and using Satterthwaite's approximation (Satterthwaite 1946). Statistical analyses were performed using the GENSTAT 6 statistical package (GenStat 2002).

(i) Testing the phylogenetic independence

Following Harvey & Pagel (1991) there has been a general tendency to introduce phylogenetically controlled analyses in most studies that involve interspecific comparisons. However, after a series of recent reappraisals (Cunningham *et al.* 1998; Abouheif 1999; Harvey & Rambaut 2000; Martins 2000) there has been some concern about the necessity of testing for the phylogenetic independence of each particular dataset. To provide evidence that overcomes the criticisms of indiscriminate use of phylogenetic correction we have applied two methods. First, a graphical assessment was made by fitting species as a random

effect but ignoring phylogenetic relatedness in the REML analysis. The estimated species effects were then saved and used to construct a semivariogram in which one-half of the squared differences in each pair of effects was plotted against the corresponding relatedness value $G(i, j)$. The effect of phylogeny is relevant if the plot indicates a positive association between phylogenetic relatedness and NDFD similarity between pairs of species. Second, an analytical assessment was made by comparing the REML log-likelihood associated with the best-fitting parameter values and those associated with the constraint $q = 10^6$, which corresponds to treating species as a standard random effect ignoring any effect of relatedness. Under the null hypothesis that species effects are independent of the relatedness between species, the difference in deviances should follow a χ^2 distribution on 1 d.f.

(d) Inferring rates of evolution and ancestral states

We used the CONTINUOUS program (Pagel 1997, 1999) to estimate the direction and rates of evolution of NDFD along the tree branches. CONTINUOUS implements a generalized least-squares model for the analysis of comparative data across species. We used the estimated effects for each species, having included species as a random effect in the REML model (see § 2c), but, in this case, the model did not account for phylogenetic relationships between species, since we were interested in retaining the phylogenetic relatedness to study its evolution. Two models of NDFD evolution were then fitted using CONTINUOUS. The first model (non-directional) corresponded to the standard constant-variance random-walk model (Pagel 1997). This model has a single parameter, the instantaneous variance of evolution. The model represents a pattern of evolution in which the efficiency of digesting fibre has been subjected to changes in both directions (i.e. the efficiency of digesting fibre can increase or decrease) across different paths in the phylogenetic tree.

A second model (directional) was a directed random walk, assuming that NDFD has followed a dominant direction of evolutionary change across the tree. The directional model accounts for the same variance of evolution as the non-directional model but in addition has a parameter describing the tendency for directional change. Whether or not the directional model fitted the data better than the simpler non-directional model was tested by using the likelihood-ratio test.

Once the model that best fitted the dataset was defined, we used different scaling parameters on the branch lengths to reveal further models of evolution rate. These parameters are described in CONTINUOUS as κ and δ . The parameter κ is used to test for a punctuated versus a gradual mode of trait evolution: $\kappa = 0.0$ suggests a punctuated mode of evolution in which changes in the efficiency of digesting fibre occurred rapidly. The parameter δ is useful in detecting whether the rate of evolution of the trait has accelerated (i.e. species-specific adaptation) or slowed (adaptive radiation) over time. Adaptive radiation (i.e. a greater rate of evolution in the earlier states followed by slower rates of evolution among related species) is defined by $\delta < 1.0$. By contrast, $\delta > 1.0$ suggests species-specific adaptation—that is, longer paths (i.e. paths from the root to the tips that contain greater numbers of nodes) contribute more than shorter ones to trait evolution. Maximum-likelihood estimates of these parameters (κ_{ML} , δ_{ML}) were compared with their corresponding values for the null hypotheses being tested (H_0 : $\kappa = 1$; H_0 : $\delta = 1$). Results from CONTINUOUS should be treated with caution

Table 1. Estimated values of parameters in the model for random variation $\text{var}(y_i) = \sigma_{\text{ref}}^2 + \sigma_{\text{food}}^2 + \sigma_{\text{sp}}^2 + \sigma^2$, $\text{cov}(y_i, y_j) = R(i, j) \times \sigma_{\text{ref}}^2 + F(i, j) \times \sigma_{\text{food}}^2 + G(i, j)^q \times \sigma_{\text{sp}}^2$.

parameter	estimate	standard errors	
		conditional on q	unconditional
σ_{ref}^2	15.74	15.71	17.50
σ_{food}^2	84.48	16.46	16.92
σ_{sp}^2	54.18	32.42	80.8
q	0.605	—	0.93
σ^2	13.16	2.63	2.62

Table 2. Slopes of the best-fitting regressions of NDFD against body mass (in kg), LLigNDF, 'grass' and 'browse' in the full REML model (see § 2c). (Standard errors in parentheses. Intercept estimated at LLigNDF = 0, grass = 0, browse = 0 and body mass = 150 kg.)

estimate of regression parameters	
intercept	74.97 (11.4)
log(body mass)	0.12 (1.09)
LLigNDF	-17.0 (1.8)
grass	-0.16 (0.11)
browse	-0.26 (0.12)

because the phylogeny used was based on only one gene (cytochrome *b*; electronic Appendix A).

3. RESULTS

(a) Testing for the phylogenetic effect

When species was fitted as a random effect, ignoring phylogenetic relatedness, then estimated species effects tended to be more similar for closely related species (electronic Appendix C). The optimal value of the phylogenetic parameter, q , was 0.605, suggesting that the covariance between species depends approximately on the square root of the measure of genetic similarity. The deviance test against the null hypothesis of independent species (nominally represented by $q = 10^6$) gave $\chi_1^2 = 3.51$ and $p = 0.06$, suggesting that the evidence for a phylogenetic effect is sufficiently strong that it should be allowed for in the analysis.

Comparison of the parameters in the model for covariance (table 1) suggests that the largest sources of random variation in NDFD were 'species' and 'food'; the latter even after using the covariate LLigNDF to allow for differences in food quality.

(b) The effect of body mass and feeding style

No significant effect of body mass on NDFD was detected (slope = 0.12, s.e. = 1.09; table 2). This was owing to the high values of NDFD of the two smallest species in our dataset, *T. javanicus* and *Cephalophus monticola*. The addition of LLigNDF to log(body mass) in the model made a great contribution in explaining the variances among levels of 'ref' and 'food' (reductions of 42% and 52%, respectively), but owing to a repartitioning of the residual variation led to an increase of 18% in the

variance among levels of 'species' (table 3). Subsequent addition of the covariates 'grass' and 'browse' to describe the natural diet of the species led to a substantial reduction in the variance between levels of 'species' (25%). The slope of the regression on LLigNDF was strongly negative, indicating that NDFD tended to decrease with increasing lignin to NDF ratios. There was no evidence for an interaction between LLigNDF and the covariates describing the natural diet ($p > 0.1$).

The effect of species' diets on their ability to digest fibre can best be seen by fitting a REML model, without the dietary covariates but having transferred 'species' from the random to the fixed part of the model, and plotting predicted mean NDFD for each species against diet composition (figure 1). This suggests that increasing the percentage of grass and fruit in the diet is associated with increasing digestibility, while increasing the percentage of browse in the diet is associated with decreasing digestibility. The compositional nature of the dietary covariates leads to estimated negative slopes for both 'grass' and 'browse' in the final model (table 2) because of the strong positive relationship between the percentage of fruit in the diet and digestibility. Of greater interest is the difference between these slopes: this is estimated for grass – browse as 0.097 (s.e. = 0.040) with d.f. = 15, giving $t_{15} = 2.39$ and $p = 0.03$.

(c) Directions and rates of evolution

There was no statistical evidence that the efficiency of digesting fibre has followed an increasing or decreasing trend across the phylogenetic tree (directional versus non-directional model: $p = 0.858$; table 4). The analysis failed to detect any relationship between the length of a branch of the tree and its contribution to the evolution of the NDFD. This was based on the fact that the maximum-likelihood estimate of κ , 0.166, could not be differentiated from $\kappa = 1$ ($p = 0.171$; gradual model) or $\kappa = 0$ ($p = 0.776$; punctuated model). There was strong evidence to support the premise that the rate of evolution of NDFD had accelerated with time ($\delta > 1$, species-specific adaptation model: maximum-likelihood estimate of $\delta = 4.538$ differed significantly from 1, $p = 0.003$).

4. DISCUSSION

(a) Phylogeny and body-mass contributions

The graphical and analytical assessments indicate that there is only weak evidence for closely related species having more similar digestive efficiencies than those that are less phylogenetically related. This contrasts with previous studies that investigated the effect of phylogeny on morphological features related to feeding styles (Pérez-Barbería & Gordon 1999a, 2001; Pérez-Barbería *et al.* 2001a). In these studies, phylogeny explained a large proportion of the total variance of the model.

There was no significant effect of body mass on NDFD, which is surprising since particle retention in the digestive tract increases with body mass allowing more extensive digestion (Illius & Gordon 1990; Gordon & Illius 1994). Other authors have detected a positive significant effect of body mass on fibre digestibility (Robbins 1993; Iason & van Wieren 1999), although van Wieren (1996) also found no significant effect of body mass on fibre digestibility for

Table 3. Estimated variance components with different fixed-effect models.

(‘Body mass’ constitutes the base fixed model; additional effects are sequentially added to the base model. The sequential percentage of explained variance is given in brackets.)

random terms	fixed-effect models		
	+ body mass	+ log(body mass) + LLigNDF	+log(body mass) + LLigNDF + grass + browse
references	30.89	18.06 (41.55)	15.74 (12.84)
food	173.28	84.10 (51.47)	84.48 (−0.45)
species	61.15	72.05 (−17.82)	54.18 (24.81)
σ^2	15.92	13.69 (13.97)	13.16 (3.86)

Figure 1. NDFD from the REML model of 24 species of ruminant that differ in their dietary habits (i.e. different contributions of (a) grass, (b) browse and (c) fruit in their natural diets). The REML model accounted for ‘body mass’, LLigNDF and ‘species’ as fixed effects and ‘ref’ and ‘food’ as random effects. For numbers 1–24, see electronic Appendix A for species identification.

a variety of diets. However, van Wieren (1996) found a significant positive effect when only diets of medium quality were used in the analysis.

In our analysis the regression of fibre digestibility on log(body mass) was negligible, after controlling for random variability imposed by the different sources of information and types of food. The main reason for the effect of body mass on NDFD not being significant seems to be the high values of NDFD of the two smallest species in our dataset, *T. javanicus* and *C. monticola* (body masses of 1.5 and 4.2 kg; NDFDs of 72.1% and 50.6–68.7%, respectively). These values are higher than expected for the body masses of these species (Illius & Gordon 1992) but they cannot be discarded from the analysis because the available information about these species consistently points to their high digestive efficiency, relative to body mass (Nordin 1978; Nolan *et al.* 1995; Conklin-Brittain & Dierenfeld 1996; Shipley & Felicetti 2002). Richardson *et al.* (1988) found a mean passage time of the digesta of 44 h in *T. javanicus* and Conklin-Brittain & Dierenfeld (1996) found a mean retention time of 42 h in *Cephalophus maxwellii*, which are higher than those values predicted by allometric regression (Illius & Gordon 1992). How these small species achieve such long retention times of the food in their digestive tracts is unknown and apparently counterintuitive (Robbins 1993), although Van Soest *et al.* (1995) have suggested that avoidance of consumption of the more lignified structures of the vegetation by small herbivores allows higher digestibility and longer retention times. However, this cannot explain our results since we controlled for lignin content in the food and the original data sources point out that no food selection occurred during the digestibility trials. In our view, further, more controlled experiments, using ruminants of a range of body sizes consuming diets of a range of qualities, are required before body mass can be ruled out as a contributor to variation in NDFD.

The type of food offered (i.e. grass, forbs, browse) retained a significant amount of variance even after fitting LLigNDF as a covariate. This fact suggests that there are compositional or morphological features of plants, other than lignin content, linked to grass, forbs and browse that affect the efficiency of digesting fibre (Robbins 1993).

(b) Feeding styles: a continuum rather than a classification

Interspecific studies have dealt with differences in morphology, physiology and behaviour between species with different feeding styles by assessing differences in

Table 4. Comparison of different models of the rate of evolution of NDFD in ruminants.

(Maximum-likelihood (ML) estimates of different scaling parameters and hypotheses tests are shown (see § 2d for definition of the parameters). Tests failed to detect either gradual or punctuated models of evolution because the ML estimate for $\kappa = 1$ (gradual model) or $\kappa = 0$ (punctuated model) did not differ from $\kappa = 1$ (gradual model) or $\kappa = 0$ (punctuated model). The ML estimate of δ is compared against $\delta = 1$, which represents a gradualism model, that is, NDFD is evolving as expected given the tree topology and a random walk model.)							
model and hypothesis test	ML estimate	H_0 log-likelihood	H_1 log-likelihood	likelihood-ratio test	d.f.	p	most likely model
non-directional (H_0 : one parameter) versus directional (H_1 : two parameters)	—	−73.29	−73.31	0.038	1	0.858	non-directional
gradual (H_1 : $\kappa = 1$) versus ML estimate (H_0 : $\kappa = 0.166$)	$\kappa = 0.166$	−73.29	−72.36	0.935	1	0.171	inconclusive
punctuated (H_1 : $\kappa = 0$) versus ML estimate (H_0 : $\kappa = 0.166$)	$\kappa = 0.166$	−73.29	−72.36	0.040	1	0.776	inconclusive
gradualism (H_0 : $\delta = 1$)	$\delta = 4.538$	−73.29	−68.95	8.792	1	0.003	species-specific adaptation

intercepts and slopes of regression lines between grazers, mixed feeders and browsers (Axmacher & Hofmann 1988; Gordon & Illius 1988, 1996; Janis & Ehrhardt 1988; van Wieren 1996; Iason & van Wieren 1999; Myrsterud 1998; Pérez-Barbería & Gordon 1999*b*, 2000, 2001; Brashares *et al.* 2000; Myrsterud *et al.* 2001; Mendoza *et al.* 2002). The main problem with previous analyses lies in the arbitrary definition of the boundaries chosen to separate each feeding style. By modifying the boundaries, the number of species in each feeding style varies, and this can have a significant effect on the intercepts and slopes for each group. Sensitivity analysis has been applied to assess the effect of uncertain classification of a few species within the total number of species in the analysis (Pérez-Barbería *et al.* 2001*a*), but this is not an efficient approach.

The new approach, proposed in this study, is simple and straightforward, to use a covariate or group of covariates containing information on the diet of each species as a continuous variable rather than a categorical variable. In this paper, the three main dietary components (i.e. grass, browse, fruit) were defined by two covariates, percentage of grass and percentage of browse, since the percentages of the three components total 100%. Datasets containing n dietary components can be defined by $n - 1$ independent covariates (Elston *et al.* 1996). A similar approach could be used when the classification of the species is based on their stomach morphology or any other morphological, behavioural or physiological trait.

The covariates describing the natural diet of the species in field conditions were not recorded by the references giving information on digestibility. Instead, we averaged the information available about the natural diet of each species. This will lead to the well-known problem of attenuation of regression coefficients that occurs when covariates are measured without error (Whittemore & Keller 1988). Even in the presence of this difficulty, we were still able to detect an effect of natural diet, perhaps because this problem was alleviated by our inclusion of species with a wide range of natural diets.

(c) *Evolution of fibre digestibility in ungulates*

The main difference in fibre digestibility between feeding styles is that, across the wide range of lignin content of the forages contributing to our dataset, ruminants with a high proportion of grass in their natural diet tended to have a greater digestibility of NDF than those tending to select browse plants. While it would be expected that browsers would have evolved a greater capability for digesting fibre in diets with a high content of lignin than would grazers (Spalinger *et al.* 1986), we found no evidence for an interaction between dietary covariates and feed quality. Iason & van Wieren (1999) found a significant effect of the interaction between dietary lignin and feeding styles on digestive efficiency, which was opposite to what should be expected from the composition of the natural diets consumed. In their study, grazers were better able than browsers to digest the fibre in diets with a high content of lignin. Iason & van Wieren's (1999) results and our results both seem counterintuitive when compared with observations of feeding behaviour of wild ruminants, since grazers avoid diets with a potentially high lignin content (van Wieren 1996; Owen-Smith 1997). It may be that they can digest it when forced to eat it, as in experiments,

but choose to avoid it because of other chemical or morphological characteristics of the plants.

The non-directional model suggests that the efficiency of fibre digestion has followed a non-dominant direction of evolution across the branching path of the tree but that the rate of evolution of fibre digestibility has accelerated gradually over time. It seems reasonable to think that the efficiency of digesting fibre in ruminant species has coevolved with the fibre content of plants (Robbins 1993). The digestion of fibre by ruminants is constrained by two factors: (i) the efficiency of the ruminal flora in digesting fibre; and (ii) the time that the fibre is exposed to the chemical action of the ruminal flora (Van Soest *et al.* 1995). The first factor probably evolved at the same rate as the second factor, since microbes can easily adapt to changing conditions (Gordon *et al.* 2002). Regarding the second factor, increasing the time that the fibre is exposed to the chemical action of the ruminal flora depends on changes in the morphology of the digestive tract, via an increase in the volume of the gut or by increasing the compartmentalization of the stomach (Van Soest *et al.* 1995). The increase in the gut volume is mainly an indirect effect of body size (Demment & Van Soest 1985) and a multi-chambered gut seems to have evolved in parallel with the increase in body size of proto-ruminants since the Early Oligocene (Janis 1976). How to explain the acceleration of the rate of evolution of fibre digestibility within this scenario? We suggest that this could be the result of a combination of increasing competition among ruminant species and adaptation to diets rich in fibre, both related to climatically driven environmental changes in the past few million years (Heinrichs *et al.* 2002). For example, some rapid changes in the faunal composition of particular fossil sites have been detected in ungulates (Janis *et al.* 2000; Jernvall & Fortelius 2002) and they could be the consequence of adaptive species diversification to climate-induced habitat shifts (Heinrichs *et al.* 2002; Pérez-Barbería *et al.* 2002). The dramatic decrease in the number of browsing ungulate species between the Early Miocene and Late Miocene in the Great Plains region of North America has also been related to climate change over this period (Janis *et al.* 2000). Although this event involved an extinction process for many browsing species, it is possible that similar events on a more local scale caused some species to shift to new habitats and subsequently adaptations to digesting different diets occurred in the novel habitats. The interesting point is that fibre digestion, in relation to dietary lignin, seems to have evolved in the same way across different feeding styles.

The loss of history within a phylogeny (i.e. incomplete representation of all species of a taxon) could have affected our results. For example, deeper branches in the tree appear to be longer because shorter branches have been lost at this level (Ridley 1996). This could be a problem because of the small number of species represented in our study; however, the tree used in this study is well balanced in relation to the number of species and taxonomic groups represented. There is an important point that should be considered in the interpretation of the evolutionary model. Our non-ultrametric tree based on the cytochrome *b* gene provides us with different path lengths back to the common ancestor, thus making it possible to measure directionality in the process of evolution. However, these

different path lengths might be the result of noise in the process of phylogenetic inference, and this could be tested by applying the model to many different markers, were they available for our group of species. Alternatively, the different path lengths could be caused by the existence of real differences in the rates of evolution between lineages. Assuming the latter point applied to our case, then we should expect there to be evidence that the rates of evolution detected in our marker can be extended to the part of the genome that regulates fibre digestibility. Until we can demonstrate this, the interpretation of the results of the evolutionary model must be cautious.

(d) *Morphology versus function*

Relating morphology to function is a common exercise among ecologists and biologists, although in most cases the functional linkage is unknown (Peters 1983; Reiss 1989). The results of this paper are surprising when compared with those obtained by Pérez-Barbería *et al.* (2001a) who analysed all biometric variables of the stomach morphology of Hofmann (1973) and found no evidence for different stomach morphologies associated with the different ruminant feeding styles, after controlling for body size. We would have to conclude that, at present, there do not appear to be any known differences in morphology that can explain differences in digestive efficiency. Are other morphological traits, which Hofmann (1973) described but did not measure, responsible for the differences in digestion efficiency found in this study? Ditchkoff (2000) criticized Gordon & Illius (1994, 1996) and Robbins *et al.* (1995) for failing to measure digestion features directly related to the hypotheses of Hofmann (1989), for example the amount of energy absorbed in the small intestine and the salivary flow during feeding. Our contention is that, until further explicit, controlled, statistically validated tests are conducted, the analyses of the current datasets will not find a link between form and function. At the present time, differences in stomach morphology between feeding styles, other than differences in body size, related to digestive function are still to be demonstrated.

(e) *Ruminal adaptation as a response to different diets?*

Evidence indicates that a great deal of flexibility in digestion efficiency can be achieved via rumen adaptation and that this varies between ruminant species and probably between feeding styles. Gordon *et al.* (2002) found that sheep (*Ovis aries*) were able to maintain their digestion efficiency across a wide variety of diets that differed in fibre content, while in red deer (*Cervus elaphus*) digestion efficiency decreased when feeding on diets rich in fibre. It has been pointed out that ruminal microbial flora is affected not only by the amount and type of solids and liquids ingested but also by the rate of the passage of food through the digestive tract (Giesecke & Van Gylswyk 1975; Cooper *et al.* 1995; Baker & Dijkstra 1999). Is the ruminal microflora responsible for differences in digestion efficiency between feeding styles? There is no information to support or refute this hypothesis although grazers may be able to retain larger particles of forage in the rumen than can browsers (Clauss & Lechner-Doll 2001). This could be related to differences in retention time or a mechanistic process of selective particle retention. However, these authors did not control for differences in the types

of food offered to animals of different feeding styles and they did not present a statistical test of their hypothesis. This contrasts with the studies of Gordon & Illius (1994) and Robbins *et al.* (1995), which did not detect differences in digesta retention time or ruminal liquid-flow rates between feeding styles.

5. CONCLUSIONS

We have analysed data from feeding trials that offered ruminants a range of different lignin to NDF ratios. Our results demonstrate that the digestive efficiency of NDF depends on the composition of a species' natural diet, higher ratios of grass to browse in the diet being associated with higher digestive efficiencies. We advocate that inter-specific studies that investigate differences in morphology, physiology, ecology and/or behaviour between ruminants with different feeding styles employ a continuous classification of the species based on their dietary habits, rather than a discrete classification into browsers, grazers and intermediate feeders.

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