

Article

Geometric morphometrics of mandibles for dietary differentiation of Bovidae (Mammalia: Artiodactyla)

Bian WANG^{a,b,*}, Miriam ZELDITCH^b, and Catherine BADGLEY^{b,c}

^aDepartment of Earth and Environmental Sciences, University of Michigan, Ann Arbor, MI, 48109-1005, USA,

^bMuseum of Paleontology, University of Michigan, Ann Arbor, MI, 48109-1085, USA, and ^cDepartment of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI, 48109-1085, USA

*Address correspondence to Bian Wang. E-mail: bianwang@umich.edu.

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Abstract

The mammalian family Bovidae has been widely studied in ecomorphological research, with important applications to paleoecological and paleohabitat reconstructions. Most studies of bovid craniomandibular features in relation to diet have used linear measurements. In this study, we conduct landmark-based geometric-morphometric analyses to evaluate whether different dietary groups can be distinguished by mandibular morphology. Our analysis includes data for 100 species of extant bovids, covering all bovid tribes and 2 dietary classifications. For the first classification with 3 feeding categories, we found that browsers (including frugivores), mixed feeders, and grazers are moderately well separated using mandibular shape. A finer dietary classification (frugivore, browser, browser–grazer intermediate, generalist, variable grazer, and obligate grazer) proved to be more useful for differentiating dietary extremes (frugivores and obligate grazers) but performed equally or less well for other groups. Notably, frugivorous bovids, which belong in tribe Cephalophini, have a distinct mandibular shape that is readily distinguished from all other dietary groups, yielding a 100% correct classification rate from jackknife cross-validation. The main differences in mandibular shape found among dietary groups are related to the functional needs of species during forage prehension and mastication. Compared with browsers, both frugivores and grazers have mandibles that are adapted for higher biomechanical demand of chewing. Additionally, frugivore mandibles are adapted for selective cropping. Our results call for more work on the feeding ecology and functional morphology of frugivores and offer an approach for reconstructing the diet of extinct bovids.

Key words: ecomorphology, frugivory, geometric morphometrics, herbivory, paleoecology

The Ruminantia is the largest suborder in the Cetartiodactyla today and consists of a diverse group of small, medium, and large herbivorous mammals with a rich fossil record. The dietary ecology of fossil ruminants has been widely studied and provides useful information about paleoenvironment (e.g., Ungar et al. 2007; DeMiguel et al. 2011). A large body of literature on ruminant ecomorphology focuses on the Bovidae, with important applications

to reconstructing the paleohabitat of hominin sites in East Africa (e.g., Kappelman et al. 1997; Kovarovic and Andrews 2007; Plummer et al. 2008). The Bovidae is 1 of 6 families of the Ruminantia, comprising 66% of extant species richness of the suborder (Burgin et al. 2018). Bovids encompass a wide range of body sizes, morphologies, and dietary behaviors; they are widely distributed across Africa, Eurasia, and North America, and occur in

numerous habitats that differ in vegetation, climate, and topography (Groves and Leslie 2011; Castelló 2016). The ecological and morphological diversity of this group makes the bovinds useful analogs for various extinct ungulates.

In the literature on ruminant feeding ecology, 3 dietary categories have been widely used. (1) Browsers, in a broad sense, primarily feed on leafy dicotyledonous material or fruits; (2) grass and roughage eaters (the grazers) primarily feed on monocotyledonous material which is generally more abrasive; and (3) intermediate (mixed) feeders feed on a mixture of dicotyledonous and monocotyledonous materials across space and seasons (Hofmann and Stewart 1972). Each category may be further divided into 2–3 subcategories based on detailed forage selectivity and preference. These categories and subcategories, with slight modifications in terminology and definition, have been widely used to classify the feeding habits of living as well as fossil ruminants (e.g., Gordon and Illius 1988; Janis and Ehrhardt 1988; Langer 1988; Solounias and Dawson-Saunders 1988; Bodmer 1990; Solounias and Moelleken 1993b; Spencer 1995; Dompierre and Churcher 1996; Sponheimer et al. 1999; Pérez-Barbería and Gordon 2001; Clauss et al. 2008; Fraser and Theodor 2011a; Forrest et al. 2018; Supplementary Table S1). A number of studies have alternatively used the percentage of grass in species' diets to quantitatively (as opposed to categorically) place species along the browser–grazer spectrum (e.g., Clauss et al. 2003; Pérez-Barbería et al. 2004; Kaiser et al. 2011; Codron et al. 2019).

Comparative anatomical studies have shown that grazing and browsing ruminants differ in masticatory muscles, craniomandibular morphology, and dental features (Table 1), which can be attributed to differences in feeding habits and forage selection. Adaptations for browsing typically alter the anterior jaw and are primarily associated with the prehension of plant material. Because edible leaves tend to occur as spatially variable clusters (Demment and van Soest 1985; Sanson 2006), browsers have muzzle characteristics adapted for selective cropping whereas foraging, such as a tall, narrow premaxilla on the cranium (Solounias and Moelleken 1993a, 1993b; Spencer 1995; MacFadden and Shockey 1997; Mendoza and Palmqvist 2006). In the anterior mandible, browsing adaptations include a relatively narrow symphysis, a relatively round incisor arcade, and central incisors that are large relative to

lateral incisors (Owen-Smith 1985; Gordon and Illius 1988; Janis and Ehrhardt 1988; Solounias and Moelleken 1993a; Janis 1995; Fraser and Theodor 2011a).

In contrast, the craniomandibular adaptations of grazers are primarily associated with processing food. Grasses occur in greater density than leaves and fruits and can be taken in larger amounts per bite (Solounias and Dawson-Saunders 1988). Grazers generally have wider and flatter muzzles, with wider and more protruding incisors, than browsers (Janis and Ehrhardt 1988; Pérez-Barbería and Gordon 2001). Other dental, as well as muscular adaptations to diet, are also commonly recognized. Grasses are more abrasive than broad-leaf vegetation and are generally consumed in large quantities. Chewing tougher food material requires higher wear resistance of the teeth and a greater amount of occlusal pressure applied to the plant material during mastication. Grazing taxa have significantly higher dental wear rates than browsing taxa (Solounias et al. 1994). As a result, grazers generally have hypsodont (high-crowned) cheek teeth, whereas browsers have brachyodont (low-crowned) cheek teeth (Janis 1988). Hypsodonty is particularly associated with the second and third molars, resulting in a deeper mandibular body under those teeth. Taller teeth also bring occlusal surfaces closer to the condyle, which serves as the fulcrum of the chewing muscular apparatus (Solounias and Dawson-Saunders 1988; Pérez-Barbería and Gordon 1999). Hypsodonty, however, does not always signify increased grass consumption; high wear resistance is also an adaptation for consuming more dust and grit in the diet (Janis 1988; MacFadden et al. 1999; Solounias and Semperebon 2002; Strömberg 2002; Damuth and Janis 2011). Grazing ruminants generally have reduced pre-molar lengths compared with molar lengths and a more elongated diastema than browsing species (Solounias and Dawson-Saunders 1988; Janis 1990; Spencer 1995; Lazagabaster et al. 2016). Grazers also have larger masseter muscles than browsers (Clauss et al. 2008). The larger area of attachment for the masseter profundus creates a fuller (less concave) outline on the posterior margin of the mandibular ramus, whereas the large masseter superficialis attachment fills out the ventral margin of the angular (Solounias and Dawson-Saunders 1988).

It has been argued that the browser–grazer spectrum of ungulate diet should be, strictly speaking, a frugivore–browser–grazer

Table 1. Differences in craniodental characteristics between browsing and grazing ruminants

	Browser	Grazer
Morphological features		
Shape of the incisor arcade	Curved	Straight
Size of incisors	I_1 and I_3 of similar size	I_1 larger than I_3
Muzzle width	Narrow	Broad
Premaxilla width	Narrow	Broad
Depth of mandibular corpus	Shallow	Deep
Hypsodonty index (M_3 height/width)	Low	High
Mandible size	Small	Large
Mandible diastema	Long	Short
Relative length of premolar row to molar row	High	Low
Masseter size	Small	Large
Posterior and ventral borders of angular	Concave	Full
Tooth-wear patterns		
Mesowear score (sharpness of cusps)	Low (sharp)	High (flat)
Microwear (microscopic abrasion)	More complex	Less complex
Stable isotope composition		
Stable carbon isotope value of tooth enamel	Depleted	Enriched

Sources: Solounias and Dawson-Saunders (1988), Mendoza et al. (2002), and references therein, Sponheimer et al. (2003); Scott (2012).

spectrum, as intermediate forms, can be found between fruit-eaters and leaf-eaters and between leaf-eaters and grass-eaters, but not between fruit-eaters and grass-eaters (Bodmer 1990). Dietary data from Gagnon and Chew (2000) confirm this general pattern in African bovids. Enamel morphology and tooth-wear also distinguish patterns in frugivorous ruminants that differ from those in other feeding categories (Heywood 2010; Louys et al. 2011; Scott 2012; Gailer and Kaiser 2014; DeSantis 2016), suggesting that frugivores should be considered as a distinct dietary group in ecomorphological analyses. Indeed, fruits likely differ from leafy vegetation and grasses in terms of physical, chemical, and biological properties. Lumping frugivore and other browsers into 1 broad feeding category in ecomorphological studies may obscure patterns that are potentially important.

Much of the ecomorphological literature about bovid diets have used linear measurements of craniomandibular features (e.g., Solounias et al. 1995; Spencer 1995; Mendoza and Palmqvist 2006). More recently, several studies have utilized landmark-based, geometric-morphometric analyses to study ungulate jaw shape in relation to diet and function (Raia et al. 2010; Cassini 2013; Cassini et al. 2017; Forrest et al. 2018; Cassini and Toledo 2020). Results of these analyses show that mandibular shape is useful for reconstructing the ecology of extinct taxa. However, these studies cover limited taxonomic diversity of modern bovids.

The goal of this study is to identify mandibular morphological characteristics that are correlated with diets across the full spectrum of bovid taxonomic and functional diversity to increase the utility of bovid ecomorphology for reconstructing dietary habits and interpreting paleoenvironments in the fossil record. Using landmark-based geometric morphometrics, we address 2 questions: (1) Can browsers, mixed feeders, and grazers be distinguished in the morphospace of their mandibles? (2) Does a finer dietary classification scheme provide greater accuracy in differentiating diets? Our expectations are that browsers and grazers will be more readily differentiated from each other than from mixed feeders and that a finer classification will allow for certain groups, such as frugivores, to be better differentiated. We discuss the implications of our results for future ecological and paleoecological studies.

Data and Methods

We obtained data on lower jaw morphology, dietary consumption, and phylogeny for 100 species of extant bovids, with representatives from all bovid tribes. Nearly two-thirds of these species have not been examined previously in ecomorphological studies of bovid diet. No domesticated species (e.g., *Bos frontalis*, *Bos grunniens*, *Bos taurus*, *Bubalus bubalis*, and *Ovis aries*) were included. We analyzed the relationship between lower jaw shape and diet using multivariate analyses, taking phylogeny into account in most analyses.

Morphological data

We gathered geometric-morphometric data from standardized photographs of bovid mandibles in lateral view. Our sample includes 377 specimens from 3 museums: the Field Museum of Natural History (Chicago, IL), the University of Michigan Museum of Zoology (Ann Arbor, MI), and the Michigan State University Museum (East Lansing, MI). All mandibles have fully erupted dentition and no obvious deformation from dental pathology or preparation. Each mandible represents a unique individual animal. The sample size ranges from 1 to 13 specimens per species, and the average sample size per species is comparable among dietary groups

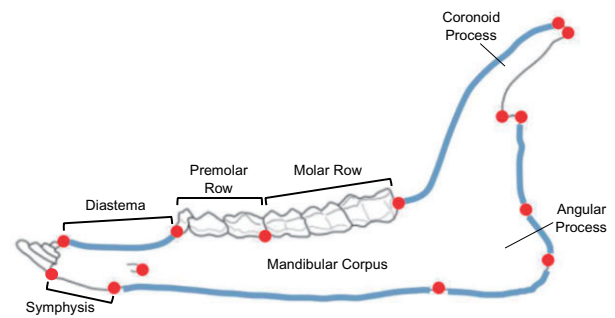


Figure 1. Landmarks (red circles) and semilandmarks (along blue curves) on a representative mandible of *Madoqua kirkii*.

(Supplementary Table S2). Whenever possible, we sampled an even number of males and females, although for many specimens this information was not available.

Fourteen landmarks and 53 semi-landmarks on the mandible were digitized with the program tpsDig (Rohlf 2006; Figure 1 and Supplementary Table S3). Landmarks represent analogous and morphologically distinct features; semi-landmarks are used to outline the curvature of the mandible between landmarks. Landmarks were superimposed by Generalized Procrustes Analysis using the R package for geometric morphometrics, geomorph (Adams et al. 2020), sliding semi-landmarks using the minimum bending-energy criterion (Green 1996; Bookstein 1997). Mandible size was measured as the centroid size of the jaw, which is the square root of the sum of squares of distances of all the landmarks and semi-landmarks from the specimen's centroid (Bookstein 1989). Following Procrustes superimposition, the mean shape and mean size were computed for each species and used in subsequent analyses.

Dietary data

We used 2 feeding classification schemes in this study. The first scheme includes 3 feeding categories that are commonly used in the literature: browsers, mixed feeders, and grazers. The second includes 6 feeding categories identified by Gagnon and Chew (2000) based on proportional consumption of fruits, dicots, and monocots: frugivores, browsers, browser-grazer intermediates, generalists, variable grazers, and obligate grazers (Table 2). Browsers in the first classification correspond to browsers and frugivores in the second classification; mixed feeders correspond to browser-grazer intermediates and generalists; and grazers correspond to variable grazers and obligate grazers. Although other detailed dietary classifications have been useful in previous studies (e.g., Janis and Ehrhardt 1988; Sponheimer et al. 1999; Supplementary Table S1), we chose this classification because its quantitative criteria make it readily applicable to a wide range of species. Gagnon and Chew (2000) studied 78 African bovid species, 63 of which are included in our sample. Based on more recent dietary data in the literature, we reclassified 8 of these species to a different feeding category. We also collated dietary information for 37 additional species and assigned each to a feeding category following the criteria derived from Gagnon and Chew's (2000) analysis (Table 2). These assignments were based on a combination of quantitative data from primary dietary studies, review papers that summarized primary data from various locations, and estimates of percent consumptions used in previous ecological or ecomorphological (Supplementary Table S2). When quantitative information was lacking for a species and estimates were also difficult from existing qualitative descriptions of dietary habits, we

Table 2. Two dietary classification schemes of 100 species of extant bovids used in this study

Dietary classification 1	Dietary classification 2 (after Gagnon and Chew 2000)	Dietary composition (after Gagnon and Chew 2000)	No. sampled species
Browser	Frugivore	>70% fruits, little or no monocots	11
	Browser	>70% dicots	22
Mixed feeder	Browser–grazer intermediate	<70% dicots, <60% monocots, <20% fruits ^a	19
	Generalist	>20% of all food types	5
Grazer	Variable grazer	60–90% monocots, variable	28
	Obligate grazer	>90% monocots, not variable	15

^a Classification criterion for browser–grazer intermediates in the original paper has been modified for a more accurate description.

assigned species into feeding groups based on qualitative descriptions. Because most species exhibit seasonal and geographic dietary variation, tracking the availability of plant material in their environment, we calculated the average percentages of each food type consumed by each species. Therefore, we note that the spatiotemporally averaged data reflect the general position of species on the dietary spectrum but do not fully capture the breadth of their dietary niche or plasticity in their dietary habits.

Phylogenetic data

We obtained 1,000 source trees of Artiodactyla from Upham et al. (2019). Then we used *TreeAnnotator* (Drummond et al. 2012) to generate a maximum clade credibility tree, which was pruned to the extant species in our sample for use in subsequent analyses. As evident from Figure 2, molecular studies show that some of the traditionally recognized tribes are polyphyletic (e.g., Bibi 2013; Bärmann and Schikora 2014). For the purpose of this study (i.e., to differentiate among dietary groups), we employed the conventional taxonomic assignments of *Ammotragus clarkei* to tribe Antilopini and *Neotragus pygmaeus* to tribe Neotragini, following Groves and Leslie (2011).

Multivariate analyses

We conducted a principal component analysis (PCA) to summarize the main dimensions of shape variation and projected phylogenetic branches and estimated ancestral states onto the resulting morphospace, using the *gm.prcomp* function in *geomorph* (Adams et al. 2020). This analysis allows for visualization of shape variation in phylogenetic context.

To determine whether the shape is predicted by diet, we conducted a Phylogenetic Generalized Least Square (Procrustes PGLS) analyses using the *procD.pgls* function in *geomorph*. Because our goal is to test the applicability of our results to paleontological studies of bovids, in which the exact phylogenetic placements of species are often not known a priori (and are often dependent, at least in part, on craniodental morphology, which would result in circular reasoning), we also conducted a Procrustes Analysis of Variance (Procrustes ANOVA), which does not account for phylogeny, using the *procD.lm* function in *geomorph*. We then conducted pairwise comparisons among the means of each feeding category to determine which categories can be distinguished statistically, using the *pairwise* function in the R package RRPP (Collyer and Adams 2019). Because of the large number of pairwise comparisons, we used Holm's (1979) method to maintain a table-wide error rate of 5%. The magnitude of morphological differences was quantified by the Procrustes distance between group-mean shapes, also using the *pairwise* function in RRPP. All statistical analyses were performed using both dietary classifications. The shape variations between

dietary groups are visualized as deformations. Because body size affects how morphology performs ecological functions, and ruminant body size correlates with digestive physiology and diet (e.g., Jarman, 1974), we tested for the effect of allometry using a PGLS analysis and generated box plots to compare ln-transformed centroid sizes (LCSs) values among dietary groups.

In addition to comparison of the mean shapes, we used a between-group PCA (bgPCA) to determine whether dietary groups can be effectively discriminated by shape. This involves conducting a PCA of the mean shapes of dietary groups, then projecting the data from all species onto those principal components. Unlike a canonical variates analysis, this method does not assume a homogeneous covariance matrix or require inverting it, so a bgPCA can be computed even when the data are not full rank (Mitteroecker and Bookstein 2011). Even bgPCA can result in spurious separation between groups when the sample size is small relative to the number of variables (Bookstein 2019; Cardini et al. 2019), although covariances among the variables reduces that effect, and semilandmarks are highly correlated with each other (Cardini et al. 2019). However, cross-validation largely solves the issue of spurious separation, and the results will be largely consistent with distance-based permutation tests of statistical significance of the difference between means in the full data space (Cardini and Polly 2020). To evaluate the performance of this classification function, we performed a jackknife (leave-one-out) cross-validation of the shape data, using the *groupPCA* function in the R package Morpho (Schlager 2017), which provided estimates of classification accuracies and misclassification rates.

Results

Results are presented in 3 parts. First, the PCA presents a visual assessment of how well dietary groups are separated in 2D morphospace, as well as the directions in which mandibular morphologies vary. We use PGLS Analysis to test the hypothesis that evolutionary changes in shape are related to diet. Differences in mean mandibular shapes among dietary groups are also visualized as deformation plots. Lastly, we present results from Procrustes ANOVA and jackknife cross-validation to test the statistical significance of the between-group differentiation. We use these non-phylogenetic approaches to determine how well shapes could be classified to dietary groups in the absence of phylogenetic information, as would be the case for most fossil specimens.

Principal component analysis

PCA reveals moderate separation among dietary groups in a 2D morphospace (Figure 3a,b and Supplementary Table S4). PC1 and PC2 explain 45.59% and 14.70% of the shape variance, respectively. Browsers generally plot at the higher ends of PC1 and PC2

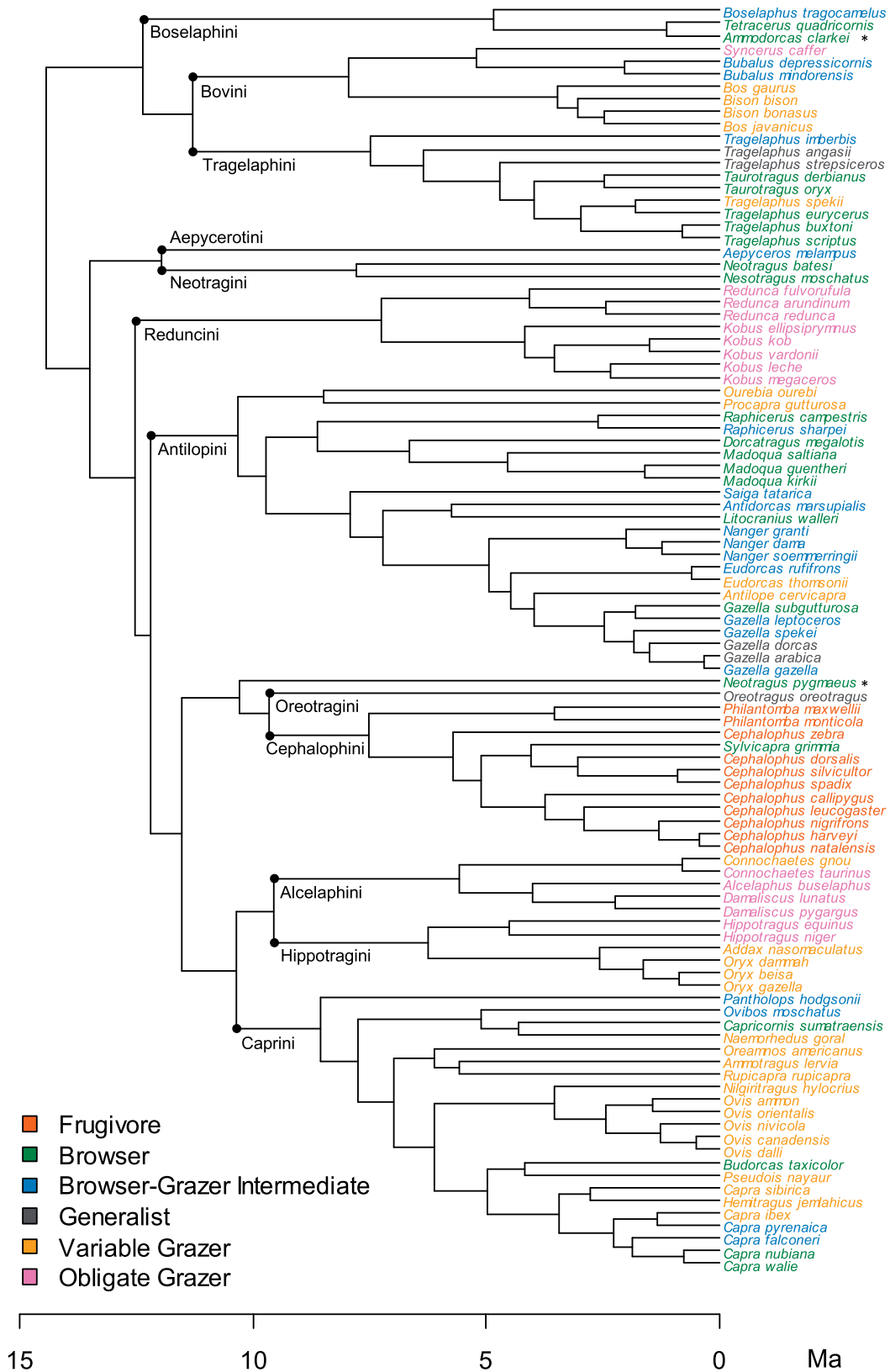


Figure 2. Distribution of 6 feeding categories in the bovid phylogenetic tree. Phylogeny from Upham et al. (2019). Species with polyphyletic tribe assignments are noted with an asterisk (see Data and Methods).

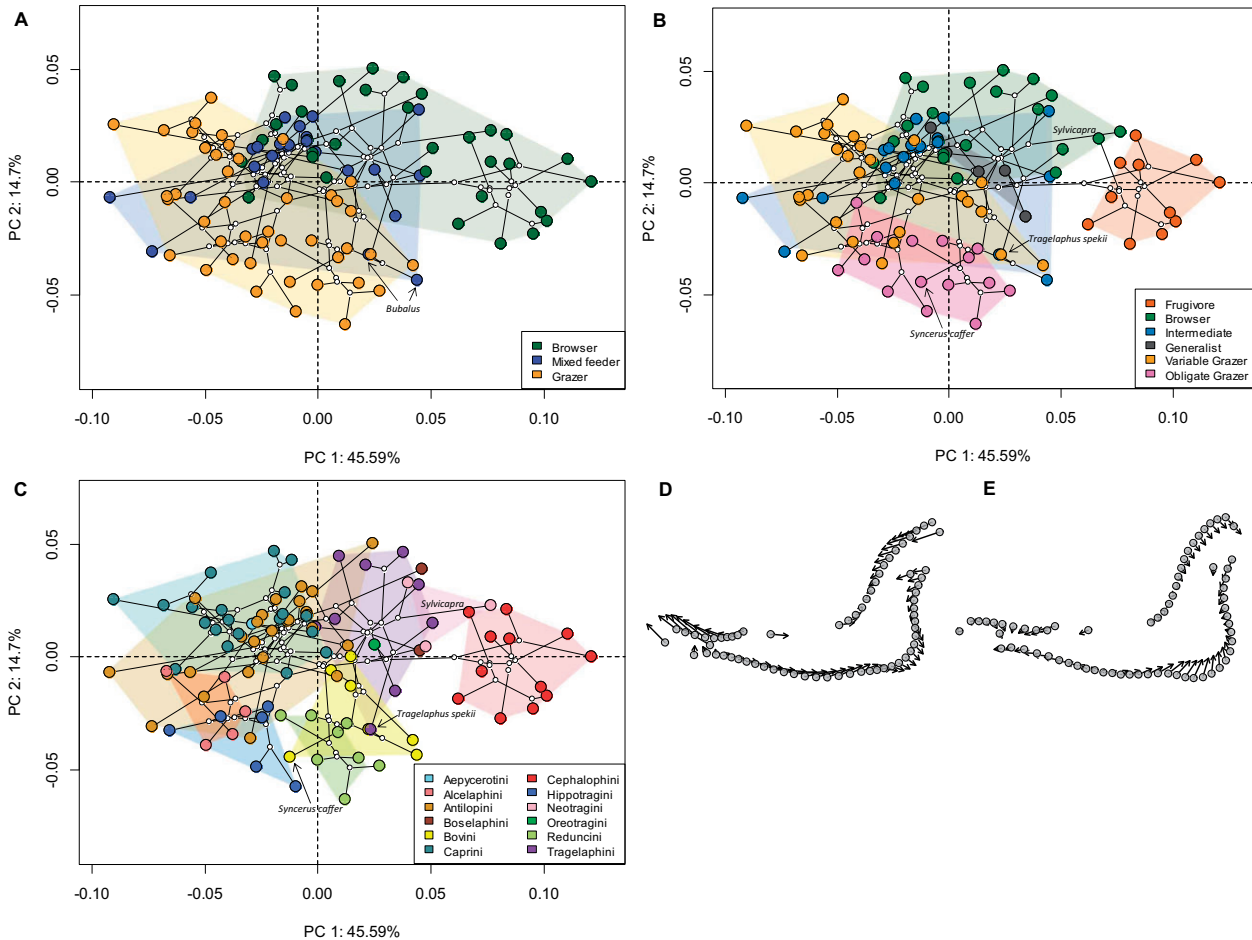


Figure 3. Phylomorphospace of bovid mandibles, color coded by (A) dietary classification 1, (B) dietary classification 2, (C) tribe, and deformation plots showing changes along (D) PC1 and (E) PC2. Data points in the phylomorphospace represent mean shapes each species ($N = 100$). Circles in the deformation plots outline the shape at the low end of the PC axis and vectors point to corresponding positions at the high end of the axis.

compared with grazers, with a relatively small overlap (Figure 3A). Mixed feeders overlap extensively with both browsers and grazers in this plane, with little range of distinct morphospace. The total range of mixed feeders is stretched out considerably by *Bubalus depressicornis* and *Bubalus mindorensis*, leaving much space unoccupied by mixed feeders in between. These 2 bovines are the only insular species in our dataset, occurring on islands of Southeast Asia.

Grouping species with the 6-category classification reveals more about the relationship among dietary groups (Figure 3B). Frugivores are well separated from other feeding categories along PC1 and occupy a distinct region of morphospace unoccupied by any other category. Obligate grazers, representing the opposite end of the dietary spectrum, overlap considerably with variable grazers but are separated from browsers and generalists along PC2. Browsers, browser-grazer intermediates, and variable grazers occupy the largest area of morphospace, in part due to the larger number of species in these groups (Table 2), with overlapping relationships similar to those in the first classification (Figure 3A). Generalists are represented by only 5 species in our dataset and cluster near the center of the plot (Figure 3B).

Comparing morphospace occupation across bovid tribes, the most distinctive pattern is the separation of Cephalophini (duikers) from other tribes along PC1 (Figure 3C). This result is unsurprising because all frugivores sampled in our study belong to this tribe

(Figure 2). However, it is notable that the only browsing duiker, *Sylvicapra grimmia*, diverges markedly from its closest extant relatives and converges with other browsers. Other than frugivores, all dietary groups have common ancestors tracing back to the root of the tree (Figure 2). Most obligate grazers belong in tribes Reduncini, Alcelaphini, and Hippotragini. *Syncerus caffer* is the only obligate grazer in tribe Bovini and, interestingly, its morphological convergence with other obligate grazers notably stretches the tribe's range of morphospace, which would otherwise not overlap with that of Reduncini (Figure 3C). Variable grazers are common in the Caprini. The only grazer in Tragelaphini *Tragelaphus spekii* diverges markedly from its browsing sister taxa and converges with Bovini and Reduncini, which are grazers. These examples suggest that, although dietary habits exhibit a certain amount of phylogenetic clustering (Figure 2), mandibular morphology reflects dietary adaptations.

Variation along the first principal component primarily concerns the length and height of the mandible (Figure 3D). From the left to the right sides of the PC1 axis: (1) the mandible becomes more elongated, largely due to elongation of the diastema and the premaxillary row, (2) the coronoid process shortens and bends anteriorly, forming a right angle with the mandibular corpus, (3) the mandibular corpus becomes shallower, and (4) the curvature around the angular process increases. Variation along the PC2 axis primarily concerns the shape of the angular and coronoid processes (Figure 3E). From

Table 3. Effects of size on shape, diet on shape, and diet on size analyzed by PGLS for 100 species of extant bovids

Effect	df	SS	MS	R^2	F	Z	P
Size on shape	1	0.0011	0.0011	0.018	1.800	1.375	0.091
Residuals	98	0.0613	0.0006				
Total	99	0.0625					
3 diets on shape	2	0.0050	0.0025	0.080	4.214	3.660	0.001
Residuals	97	0.0575	0.0006	—	—	—	—
Total	99	0.0625		—	—	—	—
3 diets on size	2	0.0083	0.0041	0.008	0.375	-0.426	0.663
Residuals	97	1.0699	0.0110	—	—	—	—
Total	99	1.0782		—	—	—	—
6 diets on shape	5	0.0105	0.0021	0.168	3.805	4.952	0.001
Residuals	94	0.0520	0.0006	—	—	—	—
Total	99	0.0625		—	—	—	—
6 diets on size	5	0.0852	0.0170	0.079	1.613	1.006	0.167
Residuals	94	0.9930	0.0106	—	—	—	—
Total	99	1.0782		—	—	—	—

Notes: A 3-part classification (browser, mixed feeder, and grazer) and a 6-part classification (frugivore, browser, browser-grazer intermediate, generalist, variable grazer, and obligate grazer) of diet are used. Note that the 6-category classification yields a greater effect size of diet on shape.

lower to higher values along PC2: (1) the angular process becomes prominently reduced in size, (2) the coronoid process bends posteriorly and ventrally, accommodated by a more ventrally positioned mandibular condyle, and (3) the cheek-tooth row lengthens despite no elongation of the mandible in general, accommodated by slight shortening of the diastema and the symphysis. Differences in the shape of the coronoid and angular process, as well as in relative tooth lengths, are captured in both principal components. Changes in the relative length of the anterior mandible, however, occur primarily on PC1 (Figure 3D), which separates frugivores from other feeding categories (Figure 3B).

Relationship among diet, shape, and size

PGLS analysis shows that changes in dietary habits have a significant impact on evolutionary changes in shape ($P < 0.001$) (Table 3). The effect of the 6-category classification of diet on shape has a greater standardized effect-size ($Z = 4.3$) than the 3-category classification ($Z = 3.5$), which measures the strength of the relationship between variables. Deformation plots illustrate the differences in mean shapes among the feeding categories (Figure 4). Using the first classification, grazers have a shorter cheek-tooth row, a deeper mandibular corpus, a shorter diastema and symphysis, a taller coronoid process, and a more dorsally and posteriorly positioned condyle than browsers (Figure 4A). Comparing species using the second classification scheme reveals more details about shape variation among dietary groups. Differences found between browsers and grazers in the first classification, are magnified in the second classification when comparing the mean shape of frugivores with that of variable grazers (Figure 4B) and, to a lesser extent, with that of obligate grazers (Figure 4C). Notable variations exist between frugivores and other browsers, which are often grouped as 1 category, with frugivores having a longer anterior mandible, a deeper mandibular corpus, a larger angular process, and a shorter coronoid process (Figure 4D). Comparing the 2 grazers in the second classification scheme, obligate grazers have shorter a molar row, a longer diastema, a slightly larger angular, and a slightly anteriorly and dorsally oriented coronoid process than variable grazers (Figure 4E). In addition to differences in tooth-crown height and coronoid process, obligate grazers also have a larger angular process than non-frugivorous browsers (Figure 4F). No significant allometric effect

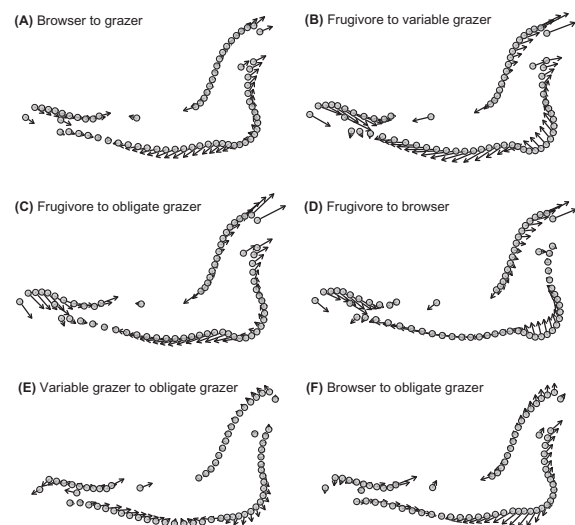


Figure 4. Deformation plots showing differences between feeding categories. Circles in the deformation plot outline the mean shape of the reference dietary group and vectors point to corresponding positions in the mean shape of the target dietary group.

was detected ($P = 0.091$) (Table 3). Although diet does not have a significant impact on size ($P > 0.16$), LCS of mandibles do show differences among the dietary groups, with the smallest mean LCS value found in frugivores and the largest in obligate grazers (Figure 5).

Differentiation of dietary groups

Most feeding categories can be statistically distinguished ($P < 0.05$) from each other in their mandibular shape using either classification scheme (Table 4 and Supplementary Table S5). Only 3 pairwise comparisons were statistically non-significant: generalists versus browsers ($P = 0.50$), generalists versus browser-grazer intermediates ($P = 0.47$), and variable grazers versus browser-grazer intermediates ($P = 0.07$). After adjusting for P -values using Holm's (1979) method, all comparisons in the first classification are still significant

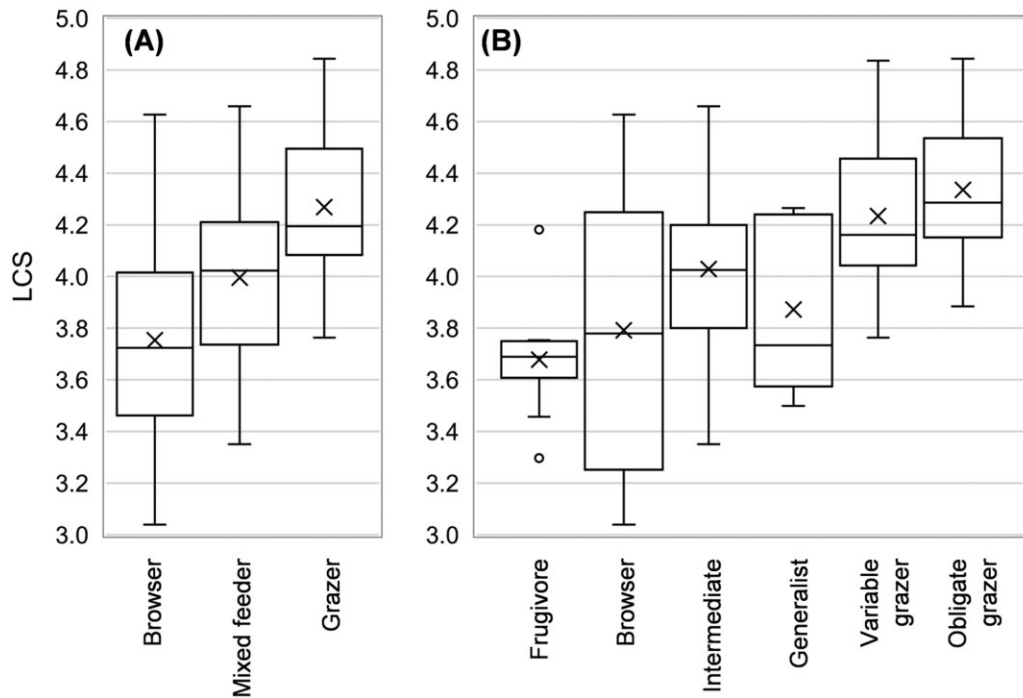


Figure 5. Box plots of LCSs of dietary groups for the first (A) and second (B) classification schemes. Crosses (×) are mean values. Horizontal lines of boxes mark the first quartile, mean, and third quartile values. Whiskers represent the range of values (excluding outliers). Circles are outliers.

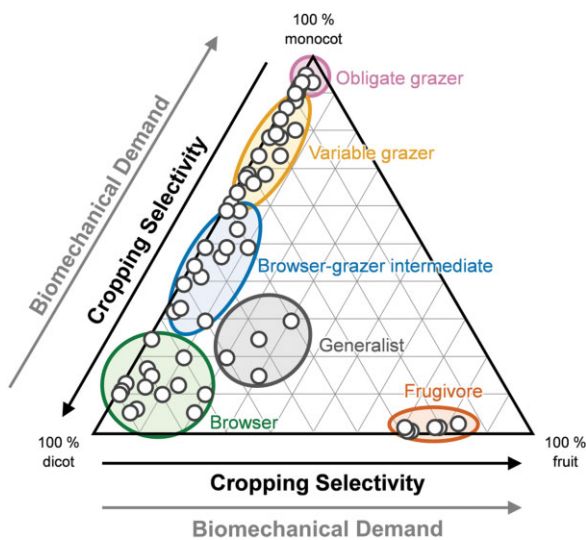


Figure 6. Proposed conceptual ruminant dietary spectrum and its properties. Ternary diagram shows the average diets of 100 species of bovids. Black arrows point to higher cropping selectivity during foraging. Gray arrows point to higher mechanical demand of processing food.

($P < 0.05$); in the second classification, significant comparisons include frugivores versus each of the other feeding categories, obligate grazers versus each of the other feeding categories except generalists, and browsers versus variable grazers.

Using the first classification scheme, jackknife cross-validation of shape data yielded an average classification accuracy of 69.0%, which the highest accuracy in grazers (76.7%; Table 5). Browsers

and grazers are both more frequently misclassified as mixed feeders (30.3% and 16.7% of the time, respectively) than with each other (<7%). Mixed feeders are misclassified as browsers and grazers at equal rates (16.7%). For the more detailed classification scheme, the classification accuracy averaged across all 6 feeding categories is 67.4%, similar to that of the first classification scheme. However, the 2 dietary extremes, frugivores and obligate grazers, have higher classification accuracies than any feeding category does in the first classification scheme (100.0% and 93.3% classification accuracy, respectively) (Table 5). Notably, frugivores are never misclassified as another dietary group, and species in other groups were rarely misclassified as frugivores. Variable grazers have the next highest classification accuracy (67.9%) but can be misclassified as browser-grazer intermediates and generalists and, less frequently, as obligate grazers. Browsers, browser-grazer intermediates, and generalists are not as well differentiated from each other. It is worth noting that the sample size for generalists is relatively small (5 species). Browsers have the lowest classification accuracy among all groups (40.9%).

Discussion

Mandibular morphology of bovids is moderately useful for differentiating the 3 feeding categories widely used in the ruminant literature: browsers, mixed feeders, and grazers (Figure 3A and Tables 4A and 5A). Using a 6-category dietary classification, our results show that frugivores and obligate grazers, which represent end members of the frugivore–browser–grazer spectrum proposed by Bodmer (1990), can be identified accurately with mandibular morphology alone (Figure 3B and Tables 3–5). The finer classification also reveals subtle differences within browsing species (i.e., frugivore versus browser; Figure 4D) and within grazing species (i.e., variable

Table 4. Procrustes distances (above diagonal line) and *P*-values (below diagonal line) of pairwise comparisons between feeding categories of 100 bovid species

(A) The 3-category classification scheme						
	Browser		Mixed feeder			Grazer
Browser			0.052			0.071
Mixed feeder	0.001*		—			0.037
Grazer	0.001*		0.003*			
(B) The 6-category classification scheme						
	Frugivore	Browser	Browser–grazer intermediate	Generalist	Variable grazer	Obligate grazer
Frugivore		0.086	0.107	0.085	0.124	0.108
Browser	0.001*		0.039	0.031	0.057	0.071
Browser–grazer intermediate	0.001*	0.016	—	0.032	0.030	0.059
Generalist	0.003*	0.501	0.467	—	0.055	0.067
Variable grazer	0.001*	0.001*	0.067	0.029		0.052
Obligate grazer	0.001*	0.001*	0.001*	0.009	0.001*	—

Note: Asterisks (*) denote adjusted *P*-values <0.05.

Table 5. Cross-validated classification rate (%) of feeding categories of 100 bovid species

(A) The 3-category classification scheme (average classification accuracy = 69.0%)							
		Inferred diet					
		Browser	Mixed feeder	Grazer			
Observed diet	Browser	63.6	30.3	6.1			
	Mixed feeder	16.7	66.7	16.7			
	Grazer	4.7	16.7	76.7			
(B) The 6-category classification scheme (average classification accuracy = 67.4%)							
		Inferred diet					
		Frugivore	Browser	Browser–grazer intermediate	Generalist	Variable grazer	Obligate grazer
Observed diet	Frugivore	100.0	0	0	0	0	0
	Browser	9.1	40.9	27.3	13.6	9.1	0
	Browser–grazer intermediate	0	10.5	42.1	21.1	26.3	0
	Generalist	0	20.0	20.0	60.0	0	0
	Variable grazer	0	0	14.3	14.3	67.9	3.6
	Obligate grazer	0	0	0	0	6.7	93.3

grazer versus obligate grazer; Figure 4E). Distinguishing mixed feeders from browsers and grazers has traditionally been difficult (Janis 1995). Browser–grazer intermediates and generalists in our data are not well differentiated from each other or from most other dietary groups (Figure 3B and Tables 4B and 5B). These groups by definition have broad, unspecialized dietary habits, and this is unsurprisingly reflected by their mandibular morphology. Although dietary extremes are more clustered in the bovid phylogeny than other feeding categories are (Figure 2), which could have contributed to their distinctive shapes, the association of shape with dietary differentiation renders mandibular shape a potentially useful paleodietary proxy, regardless of the mechanism that creates the association. Our geometric morphometrics analysis identified variations in mandibular shape among dietary groups, including relative diastema length, relative cheek-tooth length and height, and relative

size of muscle insertion areas (Figures 3 and 4). In the context of existing knowledge about ungulate ecology and functional morphology, our findings have implications for bovid ecology and raise questions that invite further research, discussed below.

Implications for frugivore ecology

Comparison between group-mean shapes shows that frugivorous bovines have a deeper mandibular corpus and a larger angular process than browsing bovines (Figure 4D) and some grazing bovines (Figure 4B) relative to mandible size. These differences suggest that consumption of fruits requires greater bite forces than of leafy material. Certain fruit tissues (e.g., large seed shells) have been considered as the most common hard-food objects eaten by mammals (Lucas et al. 2008). For example, tayassuid species that feed on palm fruits, which are tougher than other food materials they

consume, have more biomechanically powerful skulls (Hendges et al. 2019). For bovids, studies have shown that frugivores are more similar to grazers than to browsers in the inter-tooth variation of enamel indentation, and they possess thickened enamel and large occlusal surface areas relative to body size (Heywood 2010; Gailer and Kaiser 2014). Higher biomechanical demands for hard-object feeding are considered to be a primary driver of occlusal dental morphology in bovids. Extant frugivorous bovids consume fruits from dozens of plant species but preferentially feed on those with small seeds (Gautier-Hion et al. 1985; Hofmann and Roth 2003). However, little is known about the material properties of the specific fruits consumed by bovids or the biomechanical demand of frugivory in relation to body size. Our results call for more research on these topics.

Previous work on ruminant muzzle shape revealed that browsers have a longer diastema and a narrower symphysis than grazers, which is related to selectivity of feeding, the ability to discriminate and procure high-quality food from surrounding foliage (e.g., Fraser and Theodor 2011a). Our shape data show that 1 notable difference between frugivores and other feeding groups (including browsers) is the elongation of the mandible anterior to the cheek teeth, including elongation of the symphysis, in frugivores. This difference implies even higher selectivity in the frugivore diet (i.e., fruits) than in the browser diet (i.e., leaves and stems).

In modern ecosystems, frugivorous bovids live in tropical forests of Africa, where temperature and precipitation conditions allow a year-round supply of fruits. Identifying frugivorous species in fossil faunas would be crucial for reconstructing paleo-ecosystems with dense vegetation. Although microwear and mesowear analyses of bovids have found distinctive tooth-wear patterns in frugivores (Solounias and Semprebon 2002; Louys et al. 2011; Scott 2012; DeSantis 2016), existing ecomorphological studies of bovids (and ungulates in general) have given little attention to frugivores as a feeding group separate from browsers (Supplementary Table S1). Our results show that frugivorous bovids show the most distinctive mandibular morphology which is readily distinguished from any other groups using geometric morphometrics (Figure 3B and Table 4B).

Implications for browser ecology

Non-frugivorous browsers in our data exhibit greater shape variation than we expected, and this is likely related to the nature of our classification criterion for this dietary group (>70% dicots, Table 2). Browsing is the most common dietary guild among ungulate species, occurring in open grassland, arid habitats, and tropical rainforests. The wide distribution of browsers reflects the presence of dicotyledonous plants in a vast array of habitats. Resource partitioning among co-occurring species can occur in at least 3 ways: choice of primary food, habitat preference, and feeding-height preference (Jarman and Sinclair 1979; Janis 1995; Spencer 1995; Mendoza et al. 2002). Our dietary classification reflects the first way, and further division of this dietary group may be possible. Our results highlight the high disparity and diversity within browsing bovids (and ungulates in general), which have likely been understudied in ecomorphological and ecometric analyses using broad-brush dietary classifications.

Implications for grazer ecology

Some dental and mandibular adaptations in grazers have been well studied. Specifically, hypsodont molars provide grazers with more

materials for wear, and larger masseter muscles provide greater bite force for consuming monocotyledonous plants (e.g., Mendoza et al. 2002; Damuth and Janis 2011). We were able to detect these features in our data with the depth of the mandibular corpus and the size of the angular process, respectively. Two other morphological characteristics of grazer mandibles evident in our results deserve further attention. The first characteristic is a taller, more posteriorly oriented coronoid process compared with browsers and frugivores (Figures 3D and 4). The coronoid process serves as the effective moment arm of the temporalis muscle, and a longer coronoid process allows the muscle to generate greater bite force with the same torque (Kiltie 1982; Pérez-Barbería and Gordon 1999; Hendges et al. 2019). Omnivorous ungulates (pigs and peccaries) have a shorter coronoid process than herbivorous ungulates, reflecting their less tough diet (Pérez-Barbería and Gordon 1999). These authors, however, found no difference in coronoid height between browsing and grazing species. Our results suggest that grazing bovids have temporalis muscles that generate greater bite force to meet the needs of a tougher diet. The second characteristic is a relatively short premolar row in grazers. Some extinct and living species (e.g., *Teleoceras* spp., *Connochaetes* spp.) have lost the second premolar (p2) over evolutionary time, and these species are generally considered grazers. Many other grazing species, whereas having maintained 3 premolars, have reduced premolar row lengths relative to mandible size (Figure 3). Solounias and Dawson-Saunders (1988) speculated that reduced premolar lengths in grazing ruminants resulted from a more posterior chewing position, bringing the food closer to the fulcrum of the chewing musculature. Other authors have attributed reduced premolars to the facilitation of larger bite sizes (e.g., Codron et al. 2008). These explanations have not been rigorously tested or applied to inferring grazing adaptations in extinct species. A finite element analysis may be able to address this question (e.g., Fletcher et al. 2010; Zhou et al. 2019). It is worth noting that reduction of the premolar row is not always correlated with percent grass consumption in ungulate groups (Codron et al. 2019). In perissodactyls, there is in fact an opposite trend for a more pronounced premolar row (through molarization of the premolars) in grazing perissodactyls compared with browsing ones (Janis 1990; Mendoza et al. 2002). Consequently, the total occlusal surface area (and the total occlusal volume) in grazing perissodactyls (e.g., horses) is larger than that of ruminants of similar diet (Janis 1988).

Implications for paleontological studies

The study by Forrest et al. (2018) is the only 1 prior to ours that uses geometric morphometrics to study bovid mandibles in relation to diet. Based on 3D shape data of 35 extant species, their analyses yielded cross-validated accuracy rates of 80–97% (for individual specimens), higher than those in the present study (for species). Other than differences in sampled specimens and statistical methods, several factors may explain the difference in results. First, 3D data capture variation in the transverse plane and frontal plane, including width of the symphysis (narrower in browsers) and lateral position of the coronoid process (more distally positioned in browsers). Second, different feeding categories can yield different results. Their classification scheme included grazing, fresh-grass grazing, mixed feeding-preferring grass, mixed feeding-preferring browse, and browsing (Supplementary Table S1), which may be more useful for differentiating diet, although it may not be readily applicable to species beyond their study due to its qualitative nature. Third, different taxonomic coverages capture different amounts of evolutionary and ecological information, which affects shape analysis. As shown

by Solounias and Dawson-Saunders (1988), species classified in the same dietary group can have a mosaic of craniodental features. Asynchronous evolution of dietary habits and morphology, evolutionary reversal of feeding habits, independent evolution of morphology in the same environment could also result in similar but variable forms that perform the same ecological function (Solounias and Dawson-Saunders 1988). Therefore, the wider taxonomic range covered in our study inherits more confounding factors that can complicate the significance of the functional signal. All these factors and associated uncertainties are important to consider in paleoecological reconstructions.

All but 1 species analyzed by Forrest et al. (2018) are also included in our data. Therefore, we re-ran a PCA and between-group PCA to compare the effect of dietary classification scheme. Our classification scheme performed better at the browsing end of the dietary spectrum, again highlighting the necessity of differentiating frugivores from other browsers, whereas their classification performed better on the grazing end of the spectrum (Supplementary Figure S1). This difference suggests that qualitative and quantitative dietary data should be combined to better capture the variable vegetation that species consume, thereby improving the utility of the classification scheme used in ecomorphological research.

To fully evaluate the effectiveness of our morphometrics method for inferring the diet of extinct species, data from fossil bovid specimens and from more extant ruminant species should be incorporated into the model. Inferences made with mandibular morphology can be compared with those derived from other methods, such as hypsodonty index, microwear and mesowear analyses, and stable isotopes (e.g., Solounias and Moelleken 1993b; MacFadden and Shockey 1997; Sponheimer 1999; Codron et al. 2008; Louys et al. 2011; Fraser and Theodor 2011b; Lazagabaster et al. 2016; Table 1). Combining results from multiple proxies should improve the dietary reconstruction of fossil taxa.

Implications for future studies

Overall, our study shows that a finer dietary classification has improvements over the traditional 3 categories (Figure 3 and Tables 3–5). How exactly to categorize diet should be, of course, tailored to the specific research goals of each ecomorphological study. However, based on findings of our comparative analyses, we recommend at least 4 dietary groups for ruminants: frugivores, browsers, mixed feeders, and grazers. Further divisions in browsers and in grazers could also reveal interesting patterns.

Combining evidence from this and previous studies, we here propose a conceptual model of the relative dietary mechanical demand and cropping selectivity along the frugivore–browser–grazer spectrum (Figure 6). In general, ruminants with small body sizes feed on higher-quality fruit and browse diets, which are often surrounded by lower-quality plant materials, whereas larger-bodied ruminants feed on browse and grass diets (Jarman 1974; Langer 1986). Comparison of mandible sizes and morphologies among dietary groups is consistent with this pattern (Figures 4 and 5). In frugivores, dental and angular morphologies indicate capability of consuming tough plants or plant parts, and anterior mandible morphologies and small body sizes suggest more selective cropping. In grazers, inferred hypsodonty (from mandibular depth), angular and coronoid morphologies, and potentially premolar length indicate capability of consuming tough plants, and their incisor morphology and large body size suggest low selectivity of forage. Details of this model require verification and refinement through further investigation. We note that “mechanical demand” here broadly summarizes all

mechanical resistance that teeth and muscles experience during the acquisition and processing of forage, which can result from the hardness of the food material itself, shear from anterior–posterior movements of the jaw, and shear from lateral movements of the jaw. Specifically, we need better understanding of (1) the material property of the fruits that frugivorous bovids consume, especially in relation to body size, (2) the feeding behavior and evolutionary history regarding fallback foods in frugivores, (3) the mastication mechanisms of frugivores and grazers, and (4) the range of feeding habits of non-frugivorous browsers and mixed feeders.

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Supplementary Material

Supplementary material can be found at <https://academic.oup.com/cz>.

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