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Source: Journal of Mammalogy, 92(4) : 871-879

Published By: American Society of Mammalogists

URL: https://doi.org/10.1644/10-MAMM-A-226.1

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Journal of Mammalogy, 92(4):871–879, 2011

Incisor morphology reflects diet in caviomorph rodents

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Rodents are important components of most modern ecosystems. Understanding their roles in paleocommunities requires robust methods for inferring diet and other autecological characteristics. This pilot study tests whether a relationship between incisor morphology and diet exists among extant rodents that might be used to infer diets of extinct species. We focused on 11 genera of caviomorph rodents classified in 3 dietary categories: fruit–leaf, fruit–seed, and grass–leaf. For each genus 6 variables describing morphology of the upper incisor were measured on 5 specimens. Data were analyzed using a series of stepwise discriminant analyses. Discriminant analyses correctly predicted diets of nearly all training cases (~95%) using 4 incisor characteristics. Five additional species (1 caviomorph and 4 noncaviomorph), treated as unknowns, also were classified correctly. Jackknife analyses correctly predicted diets of approximately two-thirds of training cases. Our study indicates that incisor morphology is related to diet in extant caviomorph rodents. Incisor data therefore might be useful for inferring diets of extinct species.

Key words: dentition, discriminant analysis, ecomorphology, herbivory, hystricognath, paleoecology, South America

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DOI: 10.1644/10-MAMM-A-226.1

All modern rodents possess a pair of hypselodont, chisel-like incisors in the upper and lower jaws (Landry 1999; Meng and Wyss 2005; Van Valen 2004). These enlarged teeth arguably are the most easily recognized characteristic of rodents, and it is for these gnawing teeth that rodents are named (from the Latin *rodere*, meaning to gnaw). In addition to their obvious role in food acquisition and processing, these gnawing incisors are used by some species for digging, defense, or cutting tough materials such as wood (Nowak 1999). Relative to their morphological prominence and functional importance in rodents, rodent incisors have been the focus of surprisingly little ecomorphological investigation. Most recent studies that have examined rodent incisors in an ecological context have attempted to correlate their morphology with digging behavior rather than diet (e.g., Fernández et al. 2000; Hopkins and Davis 2009; Millien and Jaeger 2001; Millien-Parra 2000; Mora et al. 2003; Rybczynski 1999). Other studies have focused on size evolution and guild partitioning among a small number of sympatric species using incisor data and have demonstrated character displacement indicative of dietary resource partitioning (Ben-Moshe et al. 2001; Dayan and Simberloff 1994; Parra et al. 1999). Although a recent study by Samuels (2009) explored how cranial morphology differs among major dietary categories of rodents (e.g., carnivores, generalist herbivores, and omnivores), no study yet has focused solely on the relationship between incisor morphology and diet in rodents nor attempted to discriminate among herbivore diets at a finer scale.

The aim of our pilot study is to test whether a relationship between incisor morphology and diet exists among primarily herbivorous rodents. We do so by focusing on a morphologically diverse yet taxonomically limited group of rodents, the South American caviomorphs. In addition to exploring relationships that might provide insights into modern rodent ecomorphology, our ultimate goal is to determine features that can be used to infer diets of extinct species, especially those of the Tertiary of South America.

Caviomorphs are a monophyletic group of hystricognathous rodents that include 231 extant species in 11 families (Huchon and Douzery 2001; Woods and Kilpatrick 2005). They originated in South America prior to the earliest Oligocene, potentially as early as 50 million years ago (Flynn and Wyss 1998; Flynn et al. 2003; Rowe et al. 2010; Wyss et al. 1993, 1994), and quickly became prominent components of South American mammalian paleocommunities (Marshall and Cifelli 1990; Pascual and Ortiz Jaureguizar 1990; Patterson and

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Pascual 1968; Vucetich et al. 1999). Modern caviomorphs span a wide range of body sizes (Sánchez-Villagra et al. 2003) and are ecologically diverse in their dietary and locomotor adaptations, at least within the general dietary category of herbivory (Biknevicius 1993; Elissamburu and Vizcaíno 2004; Townsend and Croft 2008). They have been hypothesized to fill niches occupied by lagomorphs, artiodactyls, and hyracoids on other continents (Dubost 1988; Dubost et al. 2005; Mares and Ojeda 1982) and might have competed with rodent-like native South American ungulates in Tertiary mammal communities (Cifelli 1985; Simpson 1980). The ecological and morphological diversities of caviomorph rodents make them particularly amenable to a study of the relationship between incisor morphology and diet.

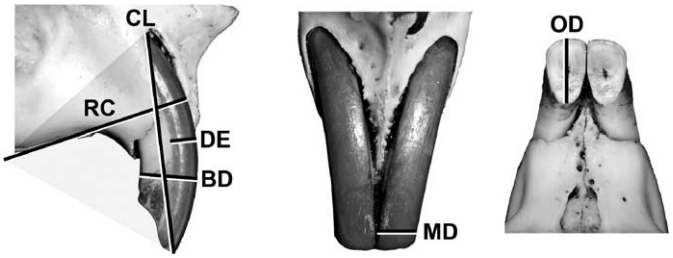


FIG. 1.—Upper incisor variable measured for this study, illustrated using the rostrum of an agouti (*Dasyprocta punctata*; CM 5259) in right lateral (left), anterior (middle), and occlusal (right) views. Abbreviations: BD, buccolingual diameter; CL, chord length; DE, distal enamel extent; MD, mesiodistal diameter; OD, buccolingual occlusal diameter; and RC (plus shading), outer radius of curvature.

MATERIALS AND METHODS

Our data set included an ecologically and taxonomically broad subsample of caviomorph rodents from the mammalogy collections of Carnegie Museum of Natural History (Pittsburgh) and the Field Museum (Chicago), representing 8 families and 11 genera (Appendix I). We limited our data set to species for which good dietary data are available (Townsend and Croft 2008). Only adult individuals (i.e., those in which M3 had erupted) with undamaged upper incisors were used. Data were collected from 5 specimens of each genus, 55 specimens in total. Data were recorded from a single species of each genus, except for *Coendou*, for which sufficient specimens of a single species were not available. Additionally, 5 rodents (from 1 caviomorph and 3 noncaviomorph families) from the teaching collection of the lead author (DAC)—*Aplodontia rufa* (mountain beaver), *Castor canadensis* (American beaver), *Erethizon dorsatum* (North American porcupine), *Marmota monax* (woodchuck), and *Sciurus carolinensis* (eastern gray squirrel)—were measured and treated as unknowns to test the fidelity of a discriminant analysis used to predict diet from incisor morphology.

Six upper incisor variables were measured for each specimen (Fig. 1): BD, buccolingual diameter, measured perpendicular to the buccal enamel surface at the midpoint of the lingual face; CL, chord length, the straight-line distance from the alveolar border to tooth tip, measured at the distal limit of the buccal surface; DE, distal enamel extent, measured perpendicular to buccal face at the midpoint of the tooth; MD, mesiodistal diameter, one-half of the combined mesiodistal diameters of the pair where they meet at their tips; OD, buccolingual occlusal diameter, measured along the occlusal surface at its mesiodistal midpoint; and RC, outer radius of curvature, calculated along the buccal face of the tooth using points at its base, midpoint, and tip. MD was measured manually with Mitutoyo CD-6″CX digital calipers (Mitutoyo America, Aurora, Illinois) to the nearest 0.1 mm, whereas BD, CL, DE, OD, and RC were measured digitally using ImageJ (Rasband 2005) and digital photos (3,872 × 2,592 pixel JPEGs, taken with a PENTAX K10D SLR digital camera and 50-mm macro lens; PENTAX Imaging Company, Golden, Colorado). RC was calculated using a function in Matlab Release 2009a (Mathworks 2009) called calc_circle (Appendix II). All variables were log-transformed prior to analysis to facilitate comparisons among species of highly disparate body mass. These particular variables were chosen because they encompass most of the functionally important aspects of incisor morphology, and because they are relatively straightforward to measure, thereby facilitating their use by other researchers should they prove useful for interpreting diet in extinct species.

We categorized species by feeding behavior into 3 broad dietary categories following Townsend and Croft (2008; Table 1): fruit–leaf, a varied diet including fruit, leafy, or woody vegetation, animal matter, and some seeds; fruit–seed, a diet primarily of seeds, supplemented with other materials; and grass–leaf, a diet mainly of leafy vegetation. In contrast to the goals of Samuels (2009), we were interested primarily in discriminating among different types of herbivores; most caviomorph rodents are primarily herbivorous, and our dietary categories reflect this distinction. All 5 genera and 3 species common to both of our analyses were included in the specialist herbivore category of Samuels (2009).

Stepwise discriminant analyses were performed using IBM SPSS Statistics 19 (SPSS, Inc. 2010) to test whether species could be classified into their correct dietary category based on the shape of their incisors. For each analysis the program determined the variables to be included based on the degree to which each lowered Wilks' lambda (λ). The diets of the 5 additional species were treated as unknowns in both analyses and were not used to generate the models (i.e., as training specimens). To further test the fidelity of the models we conducted a series of jackknife analyses in which the diets of all individuals of a single training genus also were treated as unknown.

RESULTS

The stepwise discriminant model of all 55 training specimens included 4 of 6 variables and showed significant separation of dietary categories (Wilks' $\lambda = 0.151$, $P < 0.0001$). The analysis yielded 2 significant discriminant

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Table 1.—Means and *SD*s for log-transformed variables used in discriminant analyses for each training genus, grouped by diet. BD, buccolingual diameter; CL, chord length; MD, mesiodistal diameter; OD, buccolingual occlusal diameter.

	BD	CL	MD	OD
Fruit–leaf	0.73 ± 0.11	1.29 ± 0.11	0.59 ± 0.13	0.86 ± 0.11
Coendou	0.59 ± 0.04	1.16 ± 0.03	0.47 ± 0.06	0.77 ± 0.05
Dasyprocta	0.69 ± 0.03	1.24 ± 0.09	0.51 ± 0.02	0.76 ± 0.09
Cuniculus	0.77 ± 0.03	1.34 ± 0.06	0.62 ± 0.06	0.98 ± 0.09
Myocastor	0.86 ± 0.06	1.42 ± 0.08	0.77 ± 0.04	0.94 ± 0.06
Grass–leaf	0.51 ± 0.20	1.13 ± 0.24	0.46 ± 0.32	0.55 ± 0.19
Cavia	0.35 ± 0.06	0.94 ± 0.05	0.14 ± 0.02	0.34 ± 0.04
Dolichotis	0.49 ± 0.05	1.08 ± 0.09	0.32 ± 0.03	0.51 ± 0.10
Hydrochoerus	0.84 ± 0.07	1.54 ± 0.08	0.99 ± 0.06	0.84 ± 0.07
Ctenomys	0.38 ± 0.04	1.00 ± 0.04	0.37 ± 0.02	0.59 ± 0.07
Lagidium	0.47 ± 0.07	1.09 ± 0.08	0.46 ± 0.06	0.46 ± 0.10
Fruit–seed	0.43 ± 0.05	0.92 ± 0.05	0.22 ± 0.01	0.47 ± 0.03
Proechimys	0.40 ± 0.03	0.89 ± 0.03	0.22 ± 0.04	0.45 ± 0.06
Thrichomys	0.47 ± 0.03	0.95 ± 0.05	0.23 ± 0.03	0.48 ± 0.05

functions that accounted for 100.0% of variance in the data set. The 1st discriminant function accounted for nearly 80% of the total variance. BD and OD positively influenced scores on this axis, whereas CL and MD negatively influenced scores. The 1st discriminant function primarily separated fruit–leaf feeders, with buccolingually deep incisors, from grass–leaf eaters, with longer, broader incisors (Fig. 2; Table 1). Fruit–seed feeders had intermediate values on the 1st discriminant function but were separated from other groups by the 2nd discriminant function, primarily based on their short, deep incisors. Three (~5%) of the 55 training specimens were misclassified, 1 each of *Cavia*, *Dasyprocta*, and *Dolichotis*. Diets of all 5 species included as unknowns were predicted correctly.

In stepwise discriminant analyses in which the diets of all individuals of a single training genus were considered unknown, most (9 of 11) relied on the same 4 variables for discrimination (BD, CL, MD, and OD; Table 2). About two-thirds of cases (36 of 55 specimens) were classified correctly overall. All individuals of 4 genera were classified correctly (*Cuniculus*, *Lagidium*, *Proechimys*, and *Myocastor*), whereas none of 2 genera were (*Hydrochoerus* and *Ctenomys*). Of the remaining 5 genera, the majority of individuals were classified correctly in 4.

Discussion

The goal of this pilot study was to test whether a relationship between incisor morphology and diet exists among rodents. The ability of the discriminant analysis to group rodents correctly by diet using incisor measurements indicates that such a relationship does exist. We plan to test these patterns further by expanding the number of species and specimens included in our data set, but the results of this initial analysis are promising. Our analysis suggests that grass–leaf eaters have long, mesiodistally broad incisors; fruit–seed eaters have short, buccolingually deep incisors; and fruit–leaf

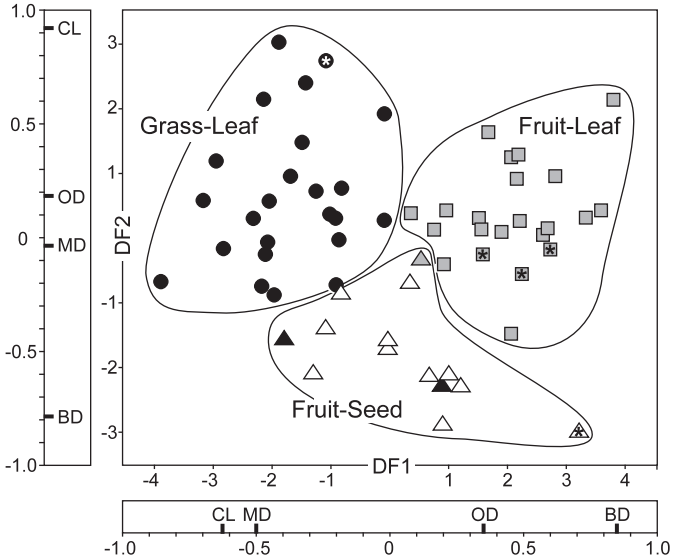


Fig. 2.—Scatterplot of a stepwise discriminant analysis of caviomorph rodent specimens based on 4 variables. Training specimens are plotted by predicted diet (shape) and actual diet (fill). Specimens treated as unknowns are indicated by an asterisk (*). Relative loadings of variables on each discriminant function are represented next to each axis: BD, buccolingual diameter; CL, chord length; MD, mesiodistal diameter; and OD, buccolingual occlusal diameter. Predicted diet: circles, grass–leaf; triangles, fruit–seed; and squares, fruit–leaf. Actual diet: black, grass–leaf; white, fruit–seed; and gray, fruit–leaf.

eaters have long, buccolingually deep incisors. These general patterns are logical from a functional standpoint (Lucas 2004; Popowics and Fortelius 1997). Broad incisors should be useful for cropping compliant but tough foods such as grasses and might be analogous to the wide muzzles and incisor arcades present in grazing bovid artiodactyls (Janis and Ehrhardt 1988). In contrast, short, buccolingually deep incisors would better resist the higher forces necessary to penetrate hard food items such as seeds. The longer incisors (as indicated by chord

Table 2.—Predicted diets (FL, fruit–leaf; GL, grass–leaf; FS, fruit–seed) when all members of a single training genus were treated as unknown in a stepwise discriminant analysis. Variables included in each analysis also are listed (BD, buccolingual diameter; CL, chord length; MD, mesiodistal diameter; OD, buccolingual occlusal diameter; DE, distal enamel extent; RC, outer radius of curvature). Incorrect classifications are italicized. For actual diets see Appendix I.

Genus	Predicted diet	Variables included
Coendou	4 FL, *1 GL*	BD, CL, MD, OD
Dasyprocta	*3 FS*, 2 FL	BD, CL, MD, OD
Cavia	3 GL, *2 FS*	BD, CL, MD, OD
Dolichotis	3 GL, *1 FL, 1 FS*	BD, CL, MD, OD
Hydrochoerus	*5 FL*	BD, CL, DE, MD, OD, RC
Cuniculus	5 FL	BD, CL, MD, OD
Lagidium	5 GL	BD, CL, MD, OD
Ctenomys	*3 FL, 2 FS*	OD, RC
Proechimys	5 FS	BD, CL, MD, OD
Thrichomys	4 FS, 1 *GL*	BD, CL, MD, OD
Myocastor	5 FL	BD, CL, MD, OD

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length) evident in fruit-eating rodents might relate to the consumption of larger food items.

The 3 misclassified training cases pertain to distinct species, all of which were predicted to be fruit–seed eaters. Their misclassifications appear to be due to individual variation rather than any systematic bias in the analysis and stem from atypical values for 1 or more variables. The misclassified *Dolichotis* (CM 44059), which plots deep within fruit–seed eater territory, has a low value for CL relative to its other measurements (Appendix I). The other 2 cases plot at the edge of the fruit–seed eaters, near to their correct dietary group; *Cavia* (CM 5292) also has a relatively low value for CL, and *Dasyprocta* (CM 5266) has slightly lower values for BD and OD.

The ability of the discriminant analysis to determine the diets of all 5 test species treated as unknowns further suggests that a relationship between incisor morphology and diet is common to all rodents (or at least relatively large-bodied ones) and is not exclusive to caviomorphs. This parallels the results obtained by Samuels (2009) for a broader taxonomic range of rodents. Incisor morphology therefore should be useful for inferring diet in extinct species.

The discriminatory ability of the jackknife analyses of specimens—in which all members of a training genus were treated as unknowns—varied considerably; all specimens of 4 genera were classified correctly, all specimens of 2 genera were classified incorrectly, and classifications of specimens of the remaining 5 genera were mixed. In the 5 genera that had mixed (correct and incorrect) classifications the majority of specimens were classified correctly in 4. In only 2 instances were specimens assigned incorrectly to 2 different groups as opposed to all being assigned to the same incorrect group. For extinct species this suggests that using a majority rule criterion would be effective at predicting diet nearly 75% of the time. Furthermore, at least 1 dietary category (the one to which no cases are assigned) can be ruled out $>80\%$ of the time. Integrating other types of dietary evidence (e.g., hypsodonty and enamel microwear) might help clarify the correct category in the event that more than 1 is suggested by incisor morphology alone. We plan to explore this in future investigations of diet in extinct rodents.

The 2 genera in which all specimens were misclassified were *Hydrochoerus*, the capybara, and *Ctenomys*, the tawny tuco-tuco. These results are unsurprising considering that *Hydrochoerus* is the largest rodent in the data set and *Ctenomys* is the only chisel-tooth digger. Treating the former as an unknown requires extrapolating far outside the size range of the remaining training set. When the diet of *Hydrochoerus* was treated as unknown, it was classified with fruit–leaf feeders, the group with the largest average body mass. The hazards of extrapolation in paleoecological studies are well known (Millien 2008), and they also apply here. *Ctenomys* would be expected to have conflicting demands on its incisors that might result in an atypical morphology relative to nondiggers. Specimens of *Ctenomys* were split incorrectly between the other 2 dietary groups; the genus as a whole was predicted to be a fruit–seed consumer because of its blunter teeth and smaller radius of curvature.

The misclassification of *Hydrochoerus* raises a more general question about the role of body mass in an analysis such as this. Because incisor morphology can change allometrically (Lessa and Patton 1989; Samuels 2009), such effects could confound dietary interpretations, especially in groups such as caviomorphs in which species vary by several orders of magnitude. Conversely, body mass is related broadly to diet in primates, hoofed herbivores, and marsupials (Eisenberg 1978; Janis 1976; Kay and Hylander 1978; Tyndale-Biscoe 2005) and therefore might provide important information about diets of extinct species. Given that the primary goal of this study is paleodietary inference, we did not attempt to exclude size effects in the present analysis.

Compared to mammals such as ungulates, primates, and carnivorans, surprisingly few investigations of diet in Tertiary rodents have been conducted. This could be attributable in part to their generally small size, although many caviomorph rodents are obvious exceptions. Adequate sampling of smaller-bodied mammals in the fossil record usually requires different collecting techniques such as screen washing (Badgley et al. 1995). Such techniques were used less frequently by early fossil collectors and even currently are not useful for highly indurated sediments. Small mammals therefore are more likely to be underrepresented in paleontological collections. Compounding this issue is the belief that rodents generally are less useful for climate and habitat inference than are megafauna. Accordingly, they mostly have been excluded from community paleoecological analyses (Eronen 2006; Mendoza et al. 2005; Palmqvist et al. 2003; Reed 1997, 1998). Given that climate change can result in rapid body mass changes in rodents (Millien and Damuth 2004; Smith et al. 1998; Yom-Tov and Yom-Tov 2004) and in the structure of small mammal communities (Blois et al. 2010), such exclusions might not be warranted. Stable isotope studies of tooth enamel have neglected all but some of the largest rodents; until the relatively recent advent of microlaser sampling (Sharp and Cerling 1998), most rodent teeth were too small to provide sufficient material for bulk analysis of carbon isotopes. The incisors of large rodents are highly suitable for serial sampling (Stuart-Williams and Schwarcz 1997), and the new microsampling techniques promise to increase the pool of species that can be investigated in this manner.

Caviomorph rodents include a diversity of relatively large species. Accordingly, many of the aforementioned reasons for excluding them from paleoecological analyses do not apply. Caviomorphs are abundant in most Neogene South American faunas (Croft 2007; Flynn et al. 2002, 2008; Kramarz and Bellosi 2005; Walton 1997) and undoubtedly played key roles in ancient South American mammal communities. Understanding the historical development of Neotropical mammal communities therefore requires understanding the biology of extinct caviomorph rodents. This, in turn, requires robust methods for inferring their diets and other aspects of their biology.

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Other than analogy with modern representatives (Vucetich and Verzi 1991), the only method that has been used thus far for paleodietary inference in caviomorph rodents is the hypsodonty index (i.e., relative tooth crown height). Even so, this mostly has been applied subjectively, with species with higher crowns assumed to be grazers or open-habitat feeders, or both, and those with low crowns assumed to be closed-habitat browsers (Candela and Vucetich 2002; Croft et al. 2007; Kay and Madden 1997; Pascual et al. 1996). The only systematic investigation of the relationship between hypsodonty and diet and habitat in modern South American rodents (including caviomorphs) was that of Williams and Kay (2001). This study demonstrated that grazing or open-habitat species, or both, have higher hypsodonty indexes than other species, but it was not successful in discriminating among their 3 dietary categories using hypsodonty alone. The study also did not establish ranges of hypsodonty indexes that could be used to infer diet in extinct species. Factors other than diet can affect hypsodonty levels in mammals, such as exogenous abrasives (Stirton 1947), and the relationship between hypsodonty and diet in rodents warrants further investigation.

The ultimate goal for paleodietary studies of caviomorph rodents should be to refine traditional, hypsodonty-based dietary interpretations by incorporating data from other independent lines of evidence. Enamel microwear represents 1 such line of evidence (Townsend and Croft 2008), and incisor morphology might be another. Combined with studies of carbon isotopes (MacFadden and Shockey 1997) and potentially cheek tooth morphology (Evans et al. 2007), the accuracy of dietary interpretations for caviomorph rodents might approach that currently available for ungulates (Janis 1995; Palmqvist et al. 2003; Semprebon and Rivals 2007). Dietary data from caviomorph rodents also might prove useful for inferring diet in superficially rodent-like members of extinct clades, such as typothere notoungulates (Croft 1999; Reguero et al. 2007). Accurate autecological analyses of both caviomorph rodents and endemic ungulates is necessary if we are to understand better the development of Neotropical mammal communities.

In summary, our study demonstrates that upper incisor morphology likely represents an additional method of inferring diet in extinct caviomorph rodents and probably in other groups of rodents as well. A larger data set should be analyzed to strengthen this inference and to clarify characters that consistently discriminate among dietary groups. This approach would be particularly appropriate for dietary inference in extinct species because of the relatively limited material necessary for analysis; well-preserved rodent incisors are far more common in the fossil record than are complete maxillae or crania. Like hypsodonty and enamel microwear, this approach holds promise for wide application with limited materials and resources.

Acknowledgments

J. Samuels provided very helpful feedback on an earlier version of this manuscript; a later version was improved thanks to careful feedback provided by 2 anonymous reviewers. Access to specimens was kindly facilitated by S. McLaren and J. Wible at Carnegie Museum of Natural History and W. Stanley at the Field Museum. Specimens at the Cleveland Museum of Natural History were studied during the initial stages of project development, a process aided by T. Matson and R. Muehlheim. This research was supported by the National Science Foundation (EAR 0819817 to DAC) and the Case Western Reserve University School of Medicine.

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Submitted 1 July 2010. Accepted 12 February 2011.

Associate Editor was Elizabeth R. Dumont.

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Appendix I

Raw data (mm) for specimens included in this study (see text for variable abbreviations). Specimens indicated with an asterisk (*) were used only as unknowns in the discriminant analysis and were not part of the training sample. Taxonomy follows Wilson and Reeder (2005), except for *Coendou*, which includes species placed by some in *Sphiggurus*. Specimens are from Carnegie Museum of Natural History, Pittsburgh (CM), the Field Museum, Chicago (FMNH), and the teaching collection of the lead author (DAC). Dietary categories follow Townsend and Croft (2008): FL, fruit–leaf; FS, fruit–seed; GL, grass–leaf.

Specimen	Species	Family	Diet	BD	CL	DE	MD	OD	RC
CM 6403	*Coendou bicolor*	Erethizontidae	FL	4.04	14.80	1.20	3.55	5.70	15.15
CM 92117	*Coendou mexicanus*	Erethizontidae	FL	3.94	13.90	1.50	3.04	6.70	16.61
CM 10188	*Coendou prehensilis*	Erethizontidae	FL	4.09	14.60	1.30	3.12	6.30	14.10
FMNH 14182	*Coendou rothschildi*	Erethizontidae	FL	4.22	15.35	0.87	2.63	5.77	14.31
CM 1747	*Coendou villosus*	Erethizontidae	FL	3.35	13.24	1.43	2.52	4.91	10.80
DAC*	*Erethizon dorsatum*	Erethizontidae	FL	4.15	12.98	1.60	3.65	7.28	13.86
CM 1358	*Dasyprocta punctata*	Dasyproctidae	FL	4.86	14.00	1.78	3.32	5.26	14.98
CM 1359	*Dasyprocta punctata*	Dasyproctidae	FL	4.57	15.95	2.32	3.21	4.89	13.95
CM 5266	*Dasyprocta punctata*	Dasyproctidae	FL	4.51	15.94	2.57	3.30	4.68	13.89
FMNH 69560	*Dasyprocta punctata*	Dasyproctidae	FL	5.49	21.30	0.85	3.45	7.39	20.44
FMNH 70791	*Dasyprocta punctata*	Dasyproctidae	FL	5.03	21.96	1.06	3.09	7.21	21.61
CM 5281	*Cavia tschudii*	Caviidae	GL	1.94	9.27	0.79	1.33	2.08	7.69
CM 5292	*Cavia tschudii*	Caviidae	GL	2.28	7.98	1.07	1.44	2.01	7.50
FMNH 78390	*Cavia tschudii*	Caviidae	GL	2.05	8.30	0.81	1.43	2.41	8.85
FMNH 79885	*Cavia tschudii*	Caviidae	GL	2.77	10.39	0.73	1.32	2.35	9.10
FMNH 79887	*Cavia tschudii*	Caviidae	GL	2.13	8.29	0.92	1.37	2.08	6.87
CM 44059	*Dolichotis salinicola*	Caviidae	GL	3.17	8.69	1.04	2.15	3.49	11.45
CM 44060	*Dolichotis salinicola*	Caviidae	GL	2.57	11.05	1.14	1.91	2.17	9.04
CM 4925	*Dolichotis salinicola*	Caviidae	GL	3.30	13.20	1.23	2.22	3.29	11.15
FMNH 43340	*Dolichotis salinicola*	Caviidae	GL	3.57	14.57	1.50	1.97	3.64	11.70
FMNH 54337	*Dolichotis salinicola*	Caviidae	GL	3.07	13.46	1.58	2.16	3.77	12.03
FMNH 21382	*Hydrochoerus hydrochaeris*	Caviidae	GL	8.50	38.55	4.03	10.91	8.54	36.27
FMNH 26879	*Hydrochoerus hydrochaeris*	Caviidae	GL	6.31	32.59	2.65	8.67	6.88	24.99
CM 3596	*Hydrochoerus hydrochaeris*	Caviidae	GL	6.41	33.41	3.66	9.40	5.85	28.58
CM 54098	*Hydrochoerus hydrochaeris*	Caviidae	GL	7.78	43.84	4.32	11.64	7.34	30.73
CM 61429	*Hydrochoerus hydrochaeris*	Caviidae	GL	5.96	27.47	2.99	8.51	5.96	27.97
CM 3946	*Cuniculus paca*	Cuniculidae	FL	6.11	20.88	1.67	4.04	9.09	19.52
CM 678	*Cuniculus paca*	Cuniculidae	FL	5.27	18.62	1.94	3.55	7.08	19.99
FMNH 87884	*Cuniculus paca*	Cuniculidae	FL	5.79	22.29	1.59	5.32	9.75	22.65
FMNH 90072	*Cuniculus paca*	Cuniculidae	FL	6.49	26.73	1.73	4.09	12.82	26.37
FMNH 92630	*Cuniculus paca*	Cuniculidae	FL	6.05	20.57	1.08	3.95	9.72	22.03
FMNH 46137	*Ctenomys fulvus*	Ctenomyidae	GL	2.52	10.35	0.29	2.19	2.91	8.74
FMNH 46138	*Ctenomys fulvus*	Ctenomyidae	GL	2.60	11.03	0.18	2.39	4.08	8.80
CM 44081	*Ctenomys fulvus*	Ctenomyidae	GL	2.59	10.33	0.73	2.48	4.20	7.61
CM 44082	*Ctenomys fulvus*	Ctenomyidae	GL	2.29	9.14	0.80	2.36	4.23	7.41
CM 44084	*Ctenomys fulvus*	Ctenomyidae	GL	2.10	9.22	0.81	2.41	4.25	6.92
CM 64613	*Proechimys cuvieri*	Echimyidae	FS	2.52	8.44	1.22	1.71	2.54	6.89
CM 77002	*Proechimys cuvieri*	Echimyidae	FS	2.40	7.33	1.02	1.87	2.34	6.57
CM 77008	*Proechimys cuvieri*	Echimyidae	FS	2.29	7.04	0.86	1.51	2.95	6.29
FMNH 95743	*Proechimys cuvieri*	Echimyidae	FS	2.68	7.49	0.42	1.56	3.32	8.06
FMNH 95744	*Proechimys cuvieri*	Echimyidae	FS	2.59	8.19	0.37	1.62	2.96	8.42
CM 101585	*Thrichomys apereoides*	Echimyidae	FS	2.99	8.61	1.21	1.79	3.10	7.22
CM 101588	*Thrichomys apereoides*	Echimyidae	FS	3.13	8.31	1.34	1.70	2.76	7.61
CM 101594	*Thrichomys apereoides*	Echimyidae	FS	2.60	9.39	1.01	1.56	2.70	7.27
FMNH 18202	*Thrichomys apereoides*	Echimyidae	FS	2.90	8.16	0.37	1.83	3.46	9.27
FMNH 18203	*Thrichomys apereoides*	Echimyidae	FS	3.02	10.73	0.51	1.57	3.30	8.63
FMNH 24344	*Myocastor coypus*	Myocastoridae	FL	8.87	34.25	1.61	5.77	9.09	30.49
FMNH 24345	*Myocastor coypus*	Myocastoridae	FL	6.88	27.35	2.76	5.31	9.05	21.91
FMNH 24346	*Myocastor coypus*	Myocastoridae	FL	6.80	22.64	1.92	5.99	9.26	19.16
CM 1739	*Myocastor coypus*	Myocastoridae	FL	7.91	26.23	2.08	6.93	9.11	23.81
CM 2372	*Myocastor coypus*	Myocastoridae	FL	6.03	22.33	2.08	5.77	6.86	18.33
CM 44065	*Lagidium viscacia*	Chinchillidae	GL	3.29	11.92	1.77	3.24	2.91	9.32
CM 86541	*Lagidium viscacia*	Chinchillidae	GL	2.22	9.04	1.30	2.26	1.92	7.22
FMNH 51866	*Lagidium viscacia*	Chinchillidae	GL	3.08	13.20	0.80	3.01	3.19	10.92
FMNH 53672	*Lagidium viscacia*	Chinchillidae	GL	3.42	14.64	0.71	3.25	3.47	12.17
FMNH 53673	*Lagidium viscacia*	Chinchillidae	GL	2.85	13.91	0.74	2.84	3.17	11.24
DAC*	*Castor canadensis*	Castoridae	FL	7.88	24.85	3.51	7.58	9.50	26.33
DAC*	*Aplodontia rufa*	Aplodontiidae	GL	4.45	24.29	1.87	4.07	5.85	17.96

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APPENDIX I.—Continued.

Specimen	Species	Family	Diet	BD	CL	DE	MD	OD	RC
DAC*	*Marmota monax*	Sciuridae	FL	3.88	12.80	1.90	3.45	6.64	13.17
DAC*	*Sciurus carolinensis*	Sciuridae	FS	3.51	8.06	0.80	1.99	4.70	9.50

APPENDIX II

Matlab (Mathworks 2009) function used to calculate radius of curvature (RC).

```
function [center radius] = calc_circle(pt1, pt2, pt3)
% function calc_circle(point 1, point 2, point 3)
%
% calculates a circle given 3 points, outputs center and radius
%
% adapted from Peter Bone at http://www.mathworks.com/matlabcentral/fileexchange/19083
%
% KAN 2/23/09
delta_a = pt2 - pt1;
delta_b = pt3 - pt2;
ax_is_0 = abs(delta_a(1)) <= 0.000000001;
bx_is_0 = abs(delta_b(1)) <= 0.000000001;
% check whether both lines are vertical - collinear
if (ax_is_0 && bx_is_0)
center = [0 0];
radius = - 1;
return
end
% make sure delta gradients are not vertical
% rearrange points to change deltas
if (ax_is_0)
[center radius] = calc_circle(pt1, pt3, pt2);
return
end
if (bx_is_0)
[center radius] = calc_circle(pt2, pt1, pt3);
return
end
grad_a = delta_a(2) / delta_a(1);
grad_b = delta_b(2) / delta_b(1);
% check whether the given points are collinear
if (abs(grad_a - grad_b) <= 0.000000001)
center = [0 0];
radius = - 1;
return
end
% swap grads and points if grad_a is 0
if abs(grad_a) <= 0.000000001
tmp = grad_a;
grad_a = grad_b;
grad_b = tmp;
tmp = pt1;
pt1 = pt3;
pt3 = tmp;
end
% calculate center: where the lines perpendicular to the
% center of segments a and b intersect.
center(1) = (grad_a*grad_b*(pt1(2) - pt3(2)) + grad_b*(pt1(1) + pt2(1)) - grad_a*(pt2(1) + pt3(1)))/(2*(grad_b - grad_a));
center(2) = ((pt1(1) + pt2(1))/2 - center(1))/grad_a + (pt1(2) + pt2(2))/2;
% calculate radius
radius = norm(center - pt1);
```

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