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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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All modern rodents possess a pair of hypselodont, chisellike 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



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 rodentlike 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.

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 $(3,872 \times 2,592 \text{ pixel})$ JPEGs, taken with a PENTAX K10D SLR digital camera and 50-mm macro lens; PENTAX Imaging Company, Golden,



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.

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

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 ($\sim 5\%$) 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 twothirds 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			

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.

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.

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LITERATURE CITED

- BADGLEY, C., W. S. BARTELS, M. E. MORGAN, A. K. BEHRENSMEYER, AND S. M. RAZA. 1995. Taphonomy of vertebrate assemblages from the Paleogene of northwestern Wyoming and the Neogene of northern Pakistan. Palaeogeography, Palaeoclimatology, Palaeoecology 115:157–180.
- BEN-MOSHE, A., T. DAYAN, AND D. SIMBERLOFF. 2001. Convergence in morphological patterns and community organization between Old and New World rodent guilds. American Naturalist 158:484–495.
- BIKNEVICIUS, A. R. 1993. Biomechanical scaling of limb bones and differential limb use in caviomorph rodents. Journal of Mammalogy 74:95–107.
- BLOIS, J. L., J. L. MCGUIRE, AND E. A. HADLY. 2010. Small mammal diversity loss in response to late-Pleistocene climatic change. Nature 465:771–774.
- CANDELA, A. M., AND M. G. VUCETICH. 2002. *Hypsosteiromys* (Rodentia, Hystricognathi) from the early Miocene of Patagonia (Argentina), the only Erethizontidae with a tendency to hypsodonty. Geobios 35:153–160.
- CIFELLI, R. L. 1985. South American ungulate evolution and extinction. Pp. 249–266 in The Great American Biotic Interchange (F. G. Stehli and S. D. Webb, eds.). Plenum Press, New York.
- CROFT, D. A. 1999. Placentals: South American ungulates. Pp. 890– 906 in Encyclopedia of paleontology (R. Singer, ed.). Fitzroy-Dearborn Publishers, Chicago, Illinois.
- CROFT, D. A. 2007. The middle Miocene (Laventan) Quebrada Honda fauna, southern Bolivia, and a description of its notoungulates. Palaeontology 50:277–303.
- CROFT, D. A., J. J. FLYNN, AND A. R. WYSS. 2007. A new basal glyptodontid and other Xenarthra of the early Miocene Chucal fauna, northern Chile. Journal of Vertebrate Paleontology 27:781–797.
- DAYAN, T., AND D. SIMBERLOFF. 1994. Morphological relationships among coexisting heteromyids: an incisive dental character. American Naturalist 143:462–477.
- DUBOST, G. 1988. Ecology and social life of the red acouchy, *Myoprocta exilis*; comparison with the orange-rumped agouti, *Dasyprocta leporina*. Journal of Zoology (London) 214:107–123.
- DUBOST, G., O. HENRY, AND P. COMIZZOLI. 2005. Seasonality of reproduction in the three largest terrestrial rodents of French Guiana forest. Mammalian Biology 70:93–109.
- EISENBERG, J. F. 1978. The evolution of arboreal herbivores in the class Mammalia. Pp. 135–152 in The ecology of arboreal folivores (G. G. Montgomery, ed.). Smithsonian Institution Press, Washington, D.C.
- ELISSAMBURU, A., AND S. F. VIZCAINO. 2004. Limb proportions and adaptations in caviomorph rodents (Rodentia: Caviomorpha). Journal of Zoology (London) 262:145–159.
- ERONEN, J. T. 2006. Eurasian Neogene large herbivorous mammals and climate. Acta Zoologica Fennica 216:1–72.
- Evans, A. R., G. P. WILSON, M. FORTELIUS, AND J. JERNVALL. 2007. High-level similarity of dentitions in carnivorans and rodents. Nature 445:78–81.

- FERNÁNDEZ, M. E., I. VASSALLO, AND M. ZÁRATE. 2000. Functional morphology and palaeobiology of the Pliocene rodent Actenomys (Caviomorpha: Ocotodontidae): the evolution to a subterranean mode of life. Biological Journal of the Linnean Society 71:71–90.
- FLYNN, J. J., AND A. R. WYSS. 1998. Recent advances in South American mammalian paleontology. Trends in Ecology & Evolution 13:449–454.
- FLYNN, J. J., A. R. WYSS, D. A. CROFT, AND R. CHARRIER. 2003. The Tinguiririca fauna, Chile: biochronology, paleoecology, biogeography, and a new earliest Oligocene South American Land Mammal "Age." Palaeogeography, Palaeoclimatology, Palaeoecology 195:229–259.
- FLYNN, J. J., ET AL. 2002. A new fossil mammal assemblage from the southern Chilean Andes: implications for geology, geochronology, and tectonics. Journal of South American Earth Sciences 15:285–302.
- FLYNN, J. J., ET AL. 2008. Chronologic implications of new Miocene mammals from the Cura-Mallín and Trapa Trapa formations, Laguna del Laja area, south central Chile. Journal of South American Earth Sciences 26:412–423.
- HOPKINS, S. S. B., AND E. B. DAVIS. 2009. Quantitative morphological proxies for fossoriality in small mammals. Journal of Mammalogy 90:1449–1460.
- HUCHON, D., AND E. J. P. DOUZERY. 2001. From the Old World to the New World: a molecular chronicle of the phylogeny and biogeography of hystricognath rodents. Molecular Phylogenetics and Evolution 20:238–251.
- JANIS, C. M. 1976. The evolutionary strategy of the Equidae and the origins of rumen and cecal digestion. Evolution 30:757–774.
- JANIS, C. M. 1995. Correlations between craniodental morphology and feeding behavior in ungulates: reciprocal illumination between living and fossil taxa. Pp. 76–98 in Functional morphology in vertebrate paleontology (J. J. Thomason, ed.). Cambridge University Press, New York.
- JANIS, C. M., AND D. EHRHARDT. 1988. Correlation of relative muzzle width and relative incisor width with dietary preference in ungulates. Zoological Journal of the Linnean Society 92:267–284.
- KAY, R. F., AND W. L. HYLANDER. 1978. The dental structure of mammalian folivores with special reference to Primates and Phalangeroidea. Pp. 173–191 in The ecology of arboreal folivores (G. G. Montgomery, ed.). Smithsonian Institution Press, Washington, D.C.
- KAY, R. F., AND R. MADDEN. 1997. Paleogeography and paleoecology. Pp. 520–550 in Vertebrate paleontology in the Neotropics: the Miocene fauna of La Venta, Colombia (R. F. Kay, R. H. Madden, R. L. Cifelli, and J. J. Flynn, eds.). Smithsonian Institution Press, Washington, D.C.
- KRAMARZ, A., AND E. S. BELLOSI. 2005. Hystricognath rodents from the Pinturas Formation, early–middle Miocene of Patagonia, biostratigraphic and paleoenvironmental implications. Journal of South American Earth Sciences 18:199–212.
- LANDRY, S. O., JR. 1999. A proposal for a new classification and nomenclature for the Glires (Lagomorpha and Rodentia). Zoosystematics and Evolution 75:283–316.
- LESSA, E. P., AND J. L. PATTON. 1989. Structural constraints, recurrent shapes, and allometry in pocket gophers (genus *Thomomys*). Biological Journal of the Linnean Society 36:349–363.
- Lucas, P. W. 2004. Dental functional morphology: how teeth work. Cambridge University Press, Cambridge, United Kingdom.
- MACFADDEN, B. J., AND B. J. SHOCKEY. 1997. Ancient feeding ecology and niche differentiation of Pleistocene mammalian herbivores from Tarija, Bolivia: morphological and isotopic evidence. Paleobiology 23:77–100.

- MARES, M. A., AND R. A. OJEDA. 1982. Patterns of diversity and adaptations in South American hystricognath rodents. Pp. 393–431 in Mammalian biology in South America (M. A. Mares and H. H. Genoways, eds.). Special Publication Series, Pymatuning Laboratory of Ecology, University of Pittsburgh, Pittsburgh, Pennsylvania. Vol. 6.
- MARSHALL, L. G., AND R. L. CIFELLI. 1990. Analysis of changing diversity patters in Cenozoic land mammal age faunas, South America. Palaeovertebrata 19:169–210.
- MATHWORKS. 2009. Release 2009a. MATLAB. Mathworks, Inc., Natick, Massachusetts.
- MENDOZA, M., C. JANIS, AND P. PALMQVIST. 2005. Ecological patterns in the trophic-size structure of large mammal communities: a 'taxon-free' characterization. Evolutionary Ecology Research 7:505–530.
- MENG, J., AND A. WYSS. 2005. Glires (Lagomorpha, Rodentia). Pp. 145–158 in The rise of placental mammals (K. D. Rose and J. D. Archibald, eds.). Johns Hopkins University Press, Baltimore, Maryland.
- MILLIEN, V. 2008. The largest among the smallest: the body mass of the giant rodent *Josephoartigasia monesi*. Proceedings of the Royal Society of London, B. Biological Sciences 275:1953–1955.
- MILLIEN, V., AND J. DAMUTH. 2004. Climate change and size evolution in an island rodent species: new perspectives on the island rule. Evolution 58:1353–1360.
- MILLIEN, V., AND J.-J. JAEGER. 2001. Size evolution of the lower incisor of *Microtia*, a genus of endemic murine rodents from the late Neogene of Gargano, southern Italy. Paleobiology 27:379–391.
- MILLIEN-PARRA, V. 2000. Species differentiation among muroid rodents on the basis of their lower incisor size and shape: ecological and taxonomical implications. Mammalia 64:221–239.
- MORA, M., A. I. OLIVARES, AND A. I. VASSALLO. 2003. Size, shape and structural versatility of the skull of the subterranean rodent *Ctenomys* (Rodentia, Caviomorpha): functional and morphological analysis. Biological Journal of the Linnean Society 78:85–96.
- NowAK, R. M. (ed.) 1999. Walker's mammals of the world. 6th ed. Johns Hopkins University Press, Baltimore, Maryland.
- PALMQVIST, P., D. R. GRÖCKE, A. ARRIBAS, AND R. A. FARIÑA. 2003. Paleoecological reconstruction of a lower Pleistocene large mammal community using biogeochemical (δ^{13} C, δ^{15} N, δ^{18} O, Sr:Zn) and ecomorphological approaches. Paleobiology 29:205–229.
- PARRA, V., M. LOREAU, AND J.-J. JAEGER. 1999. Incisor size and community structure in rodents: two tests of the role of competition. Acta Oecologica 20:93–101.
- PASCUAL, R., AND E. ORTIZ JAUREGUIZAR. 1990. Evolving climates and mammal faunas in Cenozoic South America. Journal of Human Evolution 19:23–60.
- PASCUAL, R., E. ORTIZ JAUREGUIZAR, AND J. L. PRADO. 1996. Land mammals: paradigm for Cenozoic South American geobiotic evolution. Münchner Geowissenschaftliche Abhandlungen A 30:265–319.
- PATTERSON, B., AND R. PASCUAL. 1968. The fossil mammal fauna of South America. Quarterly Review of Biology 43:409–451.
- POPOWICS, T. E., AND M. FORTELIUS. 1997. On the cutting edge: tooth blade sharpness in herbivorous and faunivorous mammals. Annales Zoologici Fennici 34:73–88.
- RASBAND, W. S. 2005. ImageJ. United States National Institutes of Health, Bethesda, Maryland.
- REED, K. E. 1997. Early hominid evolution and ecological change through the African Plio–Pleistocene. Journal of Human Evolution 32:289–322.

- REED, K. E. 1998. Using large mammal communities to examine ecological and taxonomic structure and predict vegetation in extant and extinct assemblages. Paleobiology 24:384–408.
- REGUERO, M. A., M. T. DOZO, AND E. CERDEÑO. 2007. A poorly known rodentlike mammal (Pachyrukhinae, Hegetotheriidae, Notoungulata) from the Deseadan (late Oligocene) of Argentina. Paleoecology, biogeography, and radiation of the rodentlike ungulates in South America. Journal of Paleontology 81:1301–1307.
- ROWE, D. L., K. A. DUNN, R. M. ADKINS, AND R. L. HONEYCUTT. 2010. Molecular clocks keep dispersal hypotheses afloat: evidence for trans-Atlantic rafting by rodents. Journal of Biogeography 37:305– 324.
- RYBCZYNSKI, N. 1999. Function morphology of rodent incisors. American Zoologist 39:115A.
- SAMUELS, J. X. 2009. Cranial morphology and dietary habits of rodents. Zoological Journal of the Linnean Society 156:864–888.
- SÁNCHEZ-VILLAGRA, M. R., O. AGUILERA, AND I. HOROVITZ. 2003. The anatomy of the world's largest extinct rodent. Science 301:1708– 1710.
- SEMPREBON, G. M., AND F. RIVALS. 2007. Was grass more prevalent in the pronghorn past? An assessment of the dietary adaptations of Miocene to Recent Antilocapridae (Mammalia: Artiodactyla). Palaeogeography, Palaeoclimatology, Palaeoecology 253:332–347.
- SHARP, Z. D., AND T. E. CERLING. 1998. Fossil isotope records of seasonal climate and ecology: straight from the horse's mouth. Geology 26:219–222.
- SIMPSON, G. G. 1980. Splendid isolation: the curious history of South American mammals. Yale University Press, New Haven, Connecticut.
- SMITH, F. A., H. BROWNING, AND U. L. SHEPHERD. 1998. The influence of climate change on the body mass of woodrats *Neotoma* in an arid region of New Mexico, USA. Ecography 21:140–148.
- SPSS, INC. 2010. IBM SPSS Statistics 19, release 19.0.0. SPSS, Inc., Chicago, Illinois.
- STIRTON, R. A. 1947. Observations on evolutionary rates in hypsodonty. Evolution 1:32–41.
- STUART-WILLIAMS, H. L., AND H. P. SCHWARCZ. 1997. Oxygen isotopic determination of climatic variation using phosphate from beaver bone, tooth enamel, and dentine. Geochimica et Cosmochimica Acta 61:2539–2550.
- TOWNSEND, K. E., AND D. A. CROFT. 2008. Enamel microwear in caviomorph rodents. Journal of Mammalogy 89:728–742.

- TYNDALE-BISCOE, H. 2005. Life of marsupials. CSIRO Publishing, Collingwood, Australia.
- VAN VALEN, L. 2004. Adaptation and the origin of rodents. Bulletin of the American Museum of Natural History 285:110–119.
- VUCETICH, M. G., AND D. H. VERZI. 1991. Un nuevo Echimyidae (Rodentia, Hystricognathi) de la edad Colhuehuapense de Patagonia y consideraciones sobre la sistematica de la familia. Ameghiniana 28:67–74.
- VUCETICH, M. G., D. H. VERZI, AND J. L. HARTENBERGER. 1999. Review and analysis of the radiation of the South American Hystricognathi (Mammalia, Rodentia). Comptes Rendus de la Académie Des Sciences, Paris, Serie II, Fascicule A—Sciences De La Terre et Des Planetes 329:763–769.
- WALTON, A. H. 1997. Rodents. Pp. 392–409 in Vertebrate paleontology in the Neotropics: the Miocene fauna of La Venta, Colombia (R. F. Kay, R. H. Madden, R. L. Cifelli, and J. J. Flynn, eds.). Smithsonian Institution Press, Washington, D.C.
- WILLIAMS, S. H., AND R. F. KAY. 2001. A comparative test of adaptive explanations for hypsodonty in ungulates and rodents. Journal of Mammalian Evolution 8:207–229.
- WILSON, D. E., AND D. M. REEDER (EDS.). 2005. Mammal species of the world: a taxonomic and geographic reference. 3rd ed. Johns Hopkins University Press, Baltimore, Maryland.
- WOODS, C. A., AND C. W. KILPATRICK. 2005. Infraorder Hystricognathi Brandt, 1855. Pp. 1538–1600 in Mammal species of the world: a taxonomic and geographic referenc (D. E. Wilson and D. M. Reeder, eds.). 3rd ed. Johns Hopkins University Press, Baltimore, Maryland.
- Wyss, A. R., ET AL. 1993. South America's earliest rodent and recognition of a new interval of mammalian evolution. Nature 365:434–437.
- Wyss, A. R., ET AL. 1994. Paleogene mammals from the Andes of central Chile: a preliminary taxonomic, biostratigraphic, and geochronologic assessment. American Museum Novitates 3098:1–31.
- YOM-TOV, Y., AND S. YOM-TOV. 2004. Climatic change and body size in two species of Japanese rodents. Biological Journal of the Linnean Society 82:263–267.

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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	Dasvprocta 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	1.66	2.01	7.50
FMNH 78390	Cavia tschudii	Caviidae	GL	2.05	8 30	0.81	1 43	2.01	8 85
FMNH 79885	Cavia tschudii	Caviidae	GL	2.03	10.39	0.73	1.32	2 35	9.10
FMNH 79887	Cavia tschudii	Caviidae	GL	2.17	8 29	0.92	1.32	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	1.01	1.91	2.17	9.04
CM 4925	Dolichotis salinicola	Caviidae	GL	3 30	13.20	1.14	2 22	3 29	11.15
EMNH 43340	Dolichotis salinicola	Caviidae	GL	3.50	14.57	1.20	1.07	3.64	11.15
FMNH 5/337	Dolichotis salinicola	Caviidae	GL	3.07	13.46	1.50	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 26870	Hydrochoerus hydrochaeris	Caviidae	GL	6.31	32 50	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	13.84	4 32	11.64	7 34	30.73
CM 61429	Hydrochoerus hydrochaeris	Caviidae	GL	5.96	45.84 27.47	2 99	8 51	5.96	27.97
CM 39/6	Cuniculus paca	Cuniculidae	FI	6.11	20.88	1.67	4.04	9.00	10.52
CM 678	Cuniculus paca	Cuniculidae	FI	5.27	18.62	1.07	3 55	7.08	19.92
EMNH 87884	Cuniculus paca	Cuniculidae	FI	5.27	22.29	1.54	5 32	9.75	22.65
FMNH 90072	Cuniculus paca	Cuniculidae	FI	6.49	26.73	1.59	4.09	12.82	26.37
FMNH 92630	Cuniculus paca	Cuniculidae	FL.	6.05	20.75	1.75	3.95	9.72	22.03
FMNH 46137	Ctenomys fulyus	Ctenomyidae	GL	2.52	10.35	0.29	2 19	2.91	8 74
FMNH 46138	Ctenomys fulvus	Ctenomyidae	GL	2.52	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	Echimvidae	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	Echimvidae	FS	2.59	8.19	0.37	1.62	2.96	8.42
CM 101585	Thrichomys apereoides	Echimvidae	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

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; $ax_is_0 = abs(delta_a(1)) \le 0.000000001;$ $bx_{is_0} = abs(delta_b(1)) \le 0.000000001;$ % 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 $(abs(grad_a - grad_b) \le 0.00000001)$ center $= [0 \ 0];$ radius = -1; return end % swap grads and points if grad_a is 0 if $abs(grad_a) \le 0.000000001$ $tmp = grad_a;$ $grad_a = grad_b;$ $grad_b = tmp;$ tmp = pt1;pt1 = pt3;pt3 = tmp;end % calculate center: where the lines perpendicular to the % center of segments a and b intersect. $center(1) = (grad_a*grad_b*(pt1(2) - pt3(2)) + grad_b*(pt1(1))$ $+ pt2(1)) - grad_a*(pt2(1) + pt3(1)))/(2*(grad_b - grad_a));$ $center(2) = ((pt1(1) + pt2(1))/2 - center(1))/grad_a + (pt1(2) + pt2(1))/2 - center(1))/grad_a + (pt1(2) + pt2(1))/2 - center(1))/2 - cente$ pt2(2))/2;% calculate radius radius = norm(center - pt1);