CRANIAL DIMENSIONS AS ESTIMATORS OF BODY MASS AND LOCOMOTOR HABITS IN EXTANT AND FOSSIL RODENTS

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ABSTRACT—Estimating body mass and locomotor habits of fossil rodents is challenging for taxa without available postcranial material. Although equations exist to estimate body mass from dental dimensions based on extant rodents, the applicability of such equations is doubtful given that modern rodents have evolved highly specialized teeth, whereas fossil taxa often exhibit a much less derived condition. For the present study, 11 cranial variables from a sample of 203 extant rodents of known body mass representing a range of taxonomic groups were assessed using reduced major axis (RMA) regression. The results show a strong correlation between body mass and each of the 11 cranial variables. The best estimators for body mass are skull length and cheek-tooth area, whereas the least reliable measures are palate length, and foramen magnum, as well as braincase and occipital condyle dimensions. We estimated body mass for specimens of five fossil Ischyromyidae rodents for which body mass had never been estimated (Paramys copei, P. delicatissimus, Reithroparamys delicatissimus, Rapamys atramontis, and Ischyromys typus). Principal components and canonical variates analyses based on 10 cranial dimensions for 103 members of Sciuromorpha demonstrate that a relationship exists between locomotor habits and cranial variables in this suborder. In these analyses, early ischyromyids are all placed in the terrestrial group with Aplodontia, Marmota, Cynomys, and Spermophilus. This contradicts previous hypotheses regarding early rodent locomotion, which suggested that they were arboreal or more generalized in their habits.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

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INTRODUCTION

Body mass is a fundamental aspect of an animal’s biology, and as such its reconstruction has been a significant research focus in vertebrate paleontology (e.g., Damuth and MacFadden, 1990; Dagosto and Terranova, 1992; Morgan et al., 1995). For rodents, dental data have been employed to reconstruct body mass (e.g., Gagnon, 1996; Martin, 1996; Antoine et al., 2012). In particular, Legendre (1986) provided an equation that allows the estimation of body mass in rodents using first lower molar area. However, because modern rodent teeth are highly derived and extremely variable, it is questionable whether an equation based on a modern dental sample would provide reliable estimates for all fossil members of the order. Indeed, Legendre’s (1986) equation has been found to overestimate the body mass of extant muroid rodents (Lindsay, 1988; Morgan et al., 1995; Hopkins, 2008).

Early fossil rodents generally have simpler, more nearly tribosphenic molars than is typical of modern rodents, including muroids. It would seem problematic, therefore, to apply a formula based on modern forms to Eocene members of the order. On the other hand, because even the earliest rodents already have enlarged incisors (McKenna and Meng, 2001; Meng, 2004), and because the enlargement of these teeth is of such profound importance to the form of the skull, it may make more sense to use cranial variables to estimate body mass. Cranial dimensions have been used previously to estimate body mass in ungulates (Janis, 1990), carnivores (Van Valkenburgh, 1990), pinnipeds

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this reason, in the current paper, we follow the systematic framework proposed by Korth (1994), which places *Paramys* in the Ischyromyidae, *Reithroparamys* and *Rapamys* in Reithroparamyidae, and *Ischyromys* in Ischyromyidae, and clusters all of these subfamilies in the Ischyromyidae without positing specific relationships among the various subfamilies. According to many authors (e.g., Hartenberger, 1980; Dawson et al., 1984; Korth, 1984, 1994; Flynn et al., 1986), Ischyromyidae is closely related to modern Sciuromorpha. Concerning the body mass of those early rodents, only broad comparisons with extant rodents (Wood, 1962) or other ischyromyids (Wahlert et al., 2006) are available.

Also rarely considered is the value of cranial data for determining patterns of locomotor behavior in fossil rodents. Links have been found between cranial shape and locomotor habits in fossorial rodents (cf. Agrawal, 1967; Lessa and Patton, 1989) and to different types of environments in hystricomorphs (e.g., woody vs. open areas; Haultier et al., 2012). Other authors have found connections between locomotor behavior and brain size in rodents (Pilleri et al., 1984; Budeau and Verts, 1986). Despite documentation of these relationships, cranial data are not often used for estimating locomotor patterns (but see Spoor et al., 2007; Samuels and Van Valkenburgh, 2009). Instead, postcranial data are more typically used for estimating locomotor behavior (e.g., Wood, 1962; Rose and Chinnery, 2004; Dunn and Rasmussen, 2007). However, when postcrania are not available for a particular taxon, or if postcranial data do not allow for a clear reconstruction of locomotor habits, cranial data may become useful.

Locomotor patterns for ischyromyid rodents are not well known because postcranial material is often fragmentary (Rose and Chinnery, 2004), and debates persist concerning the ecological adaptations of members of this group. Korth (1994) considered ischyromyids to be terrestrial, whereas Szalay (1985) interpreted *Paramys* as being arboreal. Rose and Chinnery (2004) concluded that early rodents (Paramyinae) were generalists, with more terrestrial than arboreal adaptations based on postcranial material. The current paper considers whether or not cranial dimensions exhibit a relationship with locomotor categories in living rodents and therefore might have some bearing on the debate regarding the behavior of these fossil species.

**MATERIALS AND METHODS**

**Materials**

A total of 203 crania from living species of Rodentia with associated individual body masses from the Royal Ontario Museum (ROM) and the American Museum of Natural History (AMNH) were measured, with the following taxonomic distribution: Anomaluroidea (n = 1), Castoridae (n = 12, 1 species), Geomyidea (n = 9, 7 species), Hystricognathia (n = 26, 21 species), Myodonta (n = 49, 41 species), Aplodontiidae (n = 2), Gliridae (n = 1), and Sciuridae (n = 103, 19 species). Only adults were selected (see Supplementary Data, Tables S1 and S2 for the complete list).

The suborder Sciuromorpha was selected to evaluate locomotor patterns in rodents because of its wide taxonomic and ecological diversity. One hundred and three sciuromorph rodents were used for this analysis, and grouped by locomotor habits based on their postcranial anatomy (Krubitzer et al., 2011; Rose and Chinnery, 2004) and positional behavior (Youlatos et al., 1999, 2008; Parker et al., 2014; see Table S2). The terrestrial group is composed of *Marmota* (n = 28), *Spermophilus* (n = 5), *Aplodontia* (n = 2), and *Cynomys* (n = 6). Arboreal genera are *Sciurus* (n = 22), *Tamiasciurus* (n = 14), *Funisciurus* (n = 3) and, finally, the only included gliding genus is *Glaucousmys* (n = 23; see discussion below).

The fossil rodents selected for these analyses are all here included in the Ischyromyidae: *Paramys copei*, *Paramys delicatus*, *Reithroparamys delicatissimus*, *Rapamys atramontis*, and *Ischyromys typus* (Fig. 1). They are all from the Eocene of North America except *Ischyromys typus*, which is Oligocene in age (Table 1).

**Methods**

The cranial dimensions assessed in this study include skull length (SL), cheek-tooth length (CTL), cheek-tooth width (CTW), cheek-tooth area (CTL × CTW), occipital condyle length (COL), occipital condyle width (COW), foramen magnum height (FMH), foramen magnum width (FMW), braincase height (CH), braincase width (CW), and palate length without incisor (PAL-I; see Fig. 2). Tables S1 and S2 include body mass, sex, and cranial dimensions for all of the extant specimens used in the analysis, whereas the cranial dimensions of the fossil taxa are given in Table S3.

Reduced major axis (RMA) regression was used to obtain 11 different regression formulas based on 11 craniodental dimensions (Table 2). This method was used rather than least squares (LS) regression because there is likely to be error in the measurement of both cranial dimensions and body mass (Aiello, 1992). Martin and Barbour (1989) specify that RMA is the preferred method when interspecific data are used to estimate body mass, as in the current analysis.

Principal components analysis (PCA) and canonical variates analysis (CVA) of 10 cranial measurement variables were used to assess the morphological variation of the extant sciuromorph taxa comprising three locomotor groupings (Arboreal, Terrestrial, Gliding), and to assess possible membership in those groups for the five fossil rodents. Both PCA and CVA were conducted on log10-transformed data. A covariance matrix was used to calculate the principal components, which were then interpreted based on their corresponding eigenvectors. Prior to conducting CVA, we assigned each extant taxon to an a priori grouping based on locomotor habits. The fossil specimens were left unclassified. A test of the assumption of normality revealed that the data were not multivariate normally distributed (Doornik and Hansen test, P < 0.001). Similarly, the formal test of equality of covariance matrices among a priori groupings revealed that this assumption also was violated (Box’s M = 222.2, P < 0.001). Therefore, CVA was used solely for ordination (see Schillaci and Gunz, 2013), and to evaluate the position of the fossil specimens relative to the ecological groupings of extant species in multivariate space. Proximity of a given fossil specimen to the centroids of these ecological groupings is considered to be proportional to the probability of group inclusion. Because neither PCA nor CVA allows for missing data, we estimated missing dimensions for the fossil taxa using LS regression. We chose to estimate missing values using regression rather than using the mean of existing values for a given variable because it takes into consideration that variable’s linear relationship with the variable it is most correlated with. Perhaps more importantly, using regression in this way to estimate a missing value does not affect the variance of that variable. Using the mean as the estimate for a missing value would reduce the variance (see Pietrusewsky, 2008). We imputed values for skull length (SL) and palate length without incisor (PAL-I) for *P. copei*, and PAL-I for *R. delicatissimus*. The equation to estimate SL for *Paramys copei* is based on the log-transformed foramen magnum width (FMW): (log(SL) = 0.684 + 1.1634 × log(FMW), r² = 0.962). Foramen magnum width was used because it had the highest correlation with SL among the extant rodents used in the current study after PAL-I, which was missing in the *P. copei* specimen. The regression equation used to estimate PAL-I in both specimens was based on log10-transformed SL (PAL-I = −0.7614 + 1.2323 × log(SL), r² = 0.983). Reduced major axis regression analyses were conducted using the program PAST 2.5 (Hammer et al., 2001).
RESULTS

Body Mass Estimation

The results for the reduced major axis regressions of body mass against each anatomical dimension are listed in Table 2. All variables were strongly correlated with body mass, with 10 out of 11 variables exhibiting an $r^2 > 0.90$. Skull length and palate length without incisor were the most strongly correlated with body mass, each with $r^2 > 0.95$. The cheek-tooth area (CTL $\times$ CTW) is slightly more highly correlated ($r^2 = 0.94$) with body mass than CTL and CTW are individually ($r^2 = 0.93$). The remaining dimensions relating to the foramen magnum, braincase, and occipital condyles have $r^2$ values between 0.84 and 0.93.

whereas PCA and CVA were both conducted using the software NCSS (Hintze, 1998).

FIGURE 1. Lateral, dorsal, and ventral views of surface renderings based on high-resolution X-ray computed tomography scans of the different fossils used in the analyses. A, Paramys copei (AMNH 4756); B, Paramys delicatus (AMNH 12506); C, Reithroparamys delicatissimus (AMNH 12561); D, Rapamys atramontis (AMNH 128706); E, Ischyromys typus (ROMV 1007). All scale bars equal 10 mm.
Details about the different variables will be presented in Discussion below.

Body mass estimates for the different fossils based on all 11 RMA regression equations are given in Table 3. Even though all 11 variables are highly correlated with body mass in the modern sample, the range of estimates for the fossils is quite wide. Skull length and cheek-tooth area give similar body mass estimates for each specimen in which both can be estimated. The oldest specimen in the sample, identified as *Paramys copei*, has two missing dimensions (SL and PAL-I) because the rostrum is broken (Fig. 1A). Consequently, body mass estimates based on those dimensions are not available.

Principal Components Analysis

The results of the principal components analysis are presented in Table 4 and Figure 3. The first two principal components explain >96% of the total variation. The loadings for PC1 are all negative, indicating that this component primarily describes size variation, with larger crania having more negative values on this axis. The loadings for PC2 are a mixture of positive and negative values. In light of this pattern, and given that PC2 is orthogonal to PC1, we can interpret this component as describing size-independent shape variation (Fig. 3). For PC2, the variables CTL and CTW have strong positive loadings, and FMH has a strong negative loading (~0.41), whereas the rest of the variables have loadings very close to zero. This suggests that PC2 can be interpreted as partly describing variation attributable to the size of the cheek teeth and height of the foramen magnum relative to the size of the rest of the skull.

In the plot of PC1 vs. PC2 (Fig. 3), the arboreal and terrestrial groups do not overlap in multivariate space, and the genus *Glaucomys*, the only gliding taxon, is isolated from the two other groups. Even though PC2 explains only a limited amount of variation (1.78%), the fact that it separates terrestrial from arboreal sciuromorphs, and the glider from the arboreal species, suggests that it contains some biological information and does not simply represent noise. All fossils are within or very near the terrestrial group. *Ischyromys typus* and *Rapamys atramontis* are close to the modern genus *Cynomys* (prairie dogs; numbered ‘2’ in Fig. 3), whereas both *Paramys* species are close to *Marmota* (marmots or groundhogs; numbered ‘1’ in Fig. 3). Finally, *Reithroparamys delicatissimus* does not plot particularly near any specific modern genus, but still falls within the polygon defined by the modern terrestrial taxa.

Canonical Variates Analysis

The results of the CVA are very similar to the results of the PCA, with three nonoverlapping locomotor groupings apparent...
(Fig. 4). The groups are clearly differentiated on CV1 but not on CV2, with arboreal and gliding species overlapping with terrestrial Sciuromorpha in this dimension. *Paramys delicatus* is located at some distance from the other fossils, but all of them are closer to the centroid of the terrestrial group than to the centroid of the arboreal or gliding groups. *Paramys delicatus* is close to the genus *Marmota* (labeled ‘1’ in Fig. 4). *Rapamys atramontis* and *Ischyromys typus* are equally close to *Spermophilus richardsonii* (Richardson’s ground squirrel; labeled ‘2’ in Fig. 4) and the genus *Cynomys* (labeled ‘3’ in Fig. 4). The fossil *Reithroparamys delicatissimus* is also near *Cynomys*. Finally, *Paramys copei* is isolated and not positioned close to any of the extant specimens, but is still much closer to the centroid of the terrestrial grouping than to the centroids of either the arboreal or gliding groups.

**DISCUSSION**

**Body Mass Estimation**

Researchers have typically used individual dental measurements for estimating body mass in rodents (e.g., Legendre, 1986; Gagnon, 1996; Martin, 1996; Antoine et al., 2012), and when available postcranial material is used preferentially (e.g., Sánchez-Villagra et al., 2003; Geiger et al., 2013). When postcranial material is not available, there are currently few options for estimating body mass in extinct rodents because individual dental dimensions have proven problematic (e.g., Lindsay, 1988; Morgan et al., 1995; Hopkins, 2008). The current analysis shows that cranial as well as composite upper cheek-tooth dimensions can be used to estimate body mass, because they are highly correlated with that variable in living rodents. Nevertheless, the various dimensions gave a wide range of body mass estimates for each fossil specimen. This prompts some consideration of the likely reasons behind this very broad range of estimates, and how we might determine which variables are expected to be the most useful in generating estimates for fossil specimens.

Skull length (SL) is the cranial measurement that is the most highly correlated with body mass in living rodents. This dimension has been used in previous studies to estimate body mass in primates when postcranial material was not available (e.g., Martin, 1990; Begun and Kordos, 2004). Martin (1990) found skull length to be highly correlated ($r^2 = 0.98$) with body mass in a non-human primate sample; Sears et al. (2008) also found that skull length was one of the best predictors of body mass in their study of the fossil New World monkey *Chilecebus*. Van Valkenburgh (1990) showed that skull length was also the best predictor for determining body mass in carnivores ($r^2 = 0.95$). More specifically, Churchill et al. (2014) showed that skull length ($r^2 = 0.80$) was one of the best predictors for the body mass of Phocidae (earless seals). Rinderknecht and Blanco (2008) used skull length to estimate the body mass of the largest fossil rodent known to date (*Josephoartigasia monesi*), whereas Millien and Bovy (2010) revised the body mass estimated for the second largest rodent known (*Phoberomys pattersoni*; originally published by Sánchez-Villagra et al., 2003) and found a high correlation between skull length and body mass ($r^2 = 0.94$). These various studies would seem to imply that skull length generally scales closely with body mass in mammals, suggesting that when it is available it should be given priority as an estimator of body mass.

Martin (1990) also used cheek-tooth dimensions to estimate body mass and found cheek-tooth area ($CTL \times CTW$) to be highly correlated with body mass in non-human primates ($r^2 = 0.95$). Millien and Bovy (2010) and later Freudenthal and Martin-Suárez (2013) found that upper tooth row length was highly correlated with body mass in rodents, with $r^2 = 0.89$ and $r^2 = 0.85$, respectively. Churchill et al. (2014) also found cheek-tooth length to be one of the best predictors of body mass in

**TABLE 2.** Slopes and intercepts of the different regressions, coefficients of determination, and 95% confidence intervals ($\pm SE \times 1.96$) for the 11 cranial variables used to estimate body mass with reduced major axis (RMA) regression. SE is the standard error of the slope.

| Dimension                 | Abbreviation | Slope a | Intercept b | $r^2$ | 95% CI       |
|---------------------------|--------------|---------|-------------|-------|--------------|
| Skull length              | SL           | 3.9519  | -4.2316     | 0.9648| 0.10296076  |
| Check-tooth length        | CTL          | 3.1047  | -0.5796     | 0.9276| 0.11542832  |
| Check-tooth width          | CTW          | 3.3134  | 0.98322     | 0.9342| 0.1174432   |
| Occipital condyle length  | COL          | 4.1781  | -0.77376    | 0.9173| 0.16604336  |
| Occipital condyle width   | COW          | 3.6294  | 0.92033     | 0.9205| 0.1414552   |
| Foramen magnum height     | FMH          | 5.1475  | -1.6249     | 0.8446| 0.2804564   |
| Foramen magnum width       | FMW          | 4.6018  | -1.5143     | 0.9271| 0.1717352   |
| Braincase height           | CH           | 4.2295  | -2.5441     | 0.9215| 0.16375604  |
| Braincase width            | CW           | 4.5235  | -3.4908     | 0.9314| 0.1637482   |
| Palate length without incisor | PAL-I     | 3.3273  | -2.0254     | 0.9557| 0.09675148  |
| Cheek-tooth area           | CTL $\times$ CTW | 1.6137  | 0.1606      | 0.9435| 0.05301221  |

**TABLE 3.** Body mass estimates using the 10 cranial dimensions and the standard deviation associated with the body mass estimates for each fossil rodent.

| Dimension      | *Paramys copei* | *Paramys delicatus* | *Reithroparamys delicatissimus* | *Rapamys atramontis* | *Ischyromys typus* |
|----------------|------------------|---------------------|---------------------------------|----------------------|-------------------|
| SL             | NA               | 2913.82             | 856.23                          | 1307.61              | 1342.23           |
| CTL            | 1192.06          | 2651.52             | 844.79                          | 1124.54              | 1800.40           |
| CTW            | 866.88           | 2682.05             | 830.51                          | 974.63               | 1015.27           |
| COL            | 2341.71          | 4682.96             | 972.89                          | 750.00               | 1344.49           |
| COW            | 1846.66          | 3078.83             | 382.09                          | 852.30               | 753.10            |
| FMH            | 1111.73          | 2254.98             | 1118.83                         | 423.96               | 401.64            |
| FMW            | 1880.81          | 2918.47             | 1228.85                         | 942.85               | 1315.90           |
| CH             | 556.65           | 1687.60             | 368.98                          | 584.94               | 492.28            |
| CW             | 519.28           | 1130.61             | 444.13                          | 475.88               | 870.61            |
| PAL-I          | NA               | 1841.13             | 959.69                          | 893.69               | 1317.01           |
| CTL $\times$ CTW | 1029.89         | 2704.83             | 843.33                          | 1057.82              | 1401.80           |
| Standard deviation | 630.19         | 956.12              | 317.08                          | 242.39               | 453.97            |
Otariidae. In the current study, CTL × CTW provided body mass estimates that were generally comparable to those provided by skull length, suggesting that it may also be a useful variable for estimating body mass in fossil rodents. Importantly, maxillae are commonly recovered fossils, making this measurement particularly useful. The individual dimensions cheek-tooth length (CTL) and cheek-tooth width (CTW) provided fairly consistent estimates for three of the five fossil taxa, but quite different estimates for the body mass of *Paramys copei* and *Ischyromys typus.*

In the case of *I. typus,* neither is very congruent with the estimate from skull length (SL), whereas the estimate calculated from cheek-tooth area is closer to the SL estimate. This may reflect a difference in the scaling of the length and width dimensions of the teeth in *I. typus* relative to the modern sample. Using cheek-tooth area instead of the individual dimensions CTL or CTW might help to account for some of these types of differences in proportion and therefore may make it a better estimator of body mass than the individual dimensions.

Radinsky (1967, 1970) used the area of the foramen magnum (FMH × FMW) to estimate body mass; however, for several reasons these dimensions might be problematic (Martin, 1990). In the current study, foramen magnum height (FMH) is the least highly correlated variable with body mass in the modern sample ($r^2 = 0.84$). Furthermore, the relationship between foramen magnum area and body mass is known to vary among different mammalian groups—it scales differently, for example, between Old World and New World monkeys (Martin, 1990). Also, several authors have noted that the area of the foramen magnum is correlated with brain size (Jerison, 1973; Martin, 1973, 1990; Gould, 1975). This is particularly a problem when body mass is being estimated in order to allow for calculation of the encephalization quotient.

Measurements of the braincase stand out as providing some of the lowest body mass estimates for the fossil taxa (Table 3). Braincase width (CW) gives the lowest estimate of body mass for *Paramys copei* and *P. delicatus,* whereas braincase height (CH) gives the lowest body mass estimate for *Reithroparamys delicatissimus.* The lower estimates of body mass obtained using measurements of the braincase might be due to a temporal effect in brain size (e.g., Jerison, 1973, Martin, 1990). This phenomenon has been observed in a range of other mammalian groups, and preliminary indications (Bertrand et al., 2014) suggest that rodents also followed this trend. If rodents demonstrate such a temporal effect, fossil taxa may be expected to have smaller brains than would be seen in modern species of equivalent body mass and therefore exhibit lower values for variables related to the size of the braincase (CH and CW). If this is the case, it makes sense that measurements associated with the braincase

| Variable | PC1     | PC2     |
|----------|---------|---------|
| SL       | -0.328516 | -0.236293 |
| CTL      | -0.437028 | 0.470075  |
| CTW      | -0.399324 | 0.482752  |
| COL      | -0.251266 | -0.118353 |
| COW      | -0.32025  | 0.00699   |
| FMH      | -0.15516  | -0.419786 |
| FMW      | -0.271983 | -0.342699 |
| CH       | -0.226547 | -0.326272 |
| CW       | -0.224857 | -0.27562  |
| PAL-I    | -0.410242 | 0.002598  |
| Eigenvalue | 0.195886 | 0.003672  |
| Percentage | 94.87    | 1.78      |

**TABLE 4.** Loadings from the principal component analysis, and eigenvalue and percentage of the variation explained by each principal component (PC) for PC1 and PC2.

**FIGURE 3.** Plot of the first two principal components (PC1 vs. PC2). Squares, fossils; Circles, terrestrial taxa; Triangles, gliding taxon; Diamonds, arboreal taxa. The numbered points represent 1, *Marmota monax,* 2, *Cynomys ludovicianus.*

**FIGURE 4.** Plot of the first two canonical variates (CV1 and CV2). Squares, fossils; Circles, terrestrial taxa; Triangles, gliding taxon; Diamonds, arboreal taxa. The numbered points represent 1, *Marmota monax,* 2, *Cynomys ludovicianus,* 3, *Spermophilus richardsonii.*
would systematically give a lower estimate of body mass for fossils and should probably be avoided when possible. In their study, Sears et al. (2008) also found that CH (vault height; Sears et al., 2008) was not a good predictor of body mass in platyrhines.

In the current analysis, the occipital condyles provide a mixture of higher and lower estimates of body mass for the fossil rodents compared with estimates obtained from skull length. It is worth noting that the same pattern is also observable for body mass estimates derived from measurements of the occipital condyles in a non-human primate sample (Martin, 1990:table 8.8). Churchill et al. (2014) found the size of the occipital condyles to be a poor predictor of body mass for otariids, although there was a stronger relationship between these variables for phocids. Occipital condyles play a biomechanical role in balancing of the head (Adams and Moore, 1975) and therefore would be expected to vary in size based on positional behavior and other ecological considerations, rather than simply scaling to body mass. Consequently, the size of the occipital condyles might not be the most reliable predictor of body mass in rodents.

When palate length without incisor was available, this variable gives a lower estimate of body mass compared with estimates derived from skull length. In non-human primates, this variable provides reasonable estimates in some cases, but for taxa with very long faces (e.g., baboons), palate length provides a higher estimate of body mass (Martin, 1990:table 8.8). In pinnipeds, this dimension was found to provide good estimates for otariids but not to work well for phocids (Churchill et al., 2014). One element affecting the utility of this measure may be diet, because phocids are more diverse in their food choices than otariids (Goswami, 2010). Among living rodents, Samuels (2009:fig. 10) found that insectivores tend to have a very elongate rostrum, whereas the rostrum was wider and shorter in carnivores and specialized herbivores, suggesting a dietary effect in Rodentia as well. There is also evidence that length of the diastema varies with ecology in rodents. For example, Beccera et al. (2013) showed that a shortening of the diastema is associated with an enlargement of the jaw adductor muscles in a subterranean caviomorph rodent Ctenomys tuconax, and Alvarez et al. (2011) suggested that variation in length of the diastema is related to ecological variables in caviomorph rodents with fossorial habits. Because this dimension will necessarily affect palate length, such ecological differences may cause variation in the scaling relationships between PAL-I and body mass amongst groups with different ecological habits. Therefore, it would seem that palate length is problematic for determining body mass in rodents because it can be expected to vary for reasons other than variation in the overall size of the body. Given that PAL-I consistently gives a lower estimate of body mass relative to estimates from skull length in the fossil sample, modern rodents must generally have longer palates relative to skull length compared with ischyromyids. The reasons for this are not immediately apparent, but could reflect ecological differences such as diet, or a general reorganization of the cranium through time.

In sum, with respect to choosing cranial dimensions to estimate body mass in rodents, skull length seems to provide the best estimator, and when that measurement is not available, cheek-tooth area should be used. The least preferred dimensions to estimate body mass are those related to palate length, or to the size of the braincase, occipital condyle, or foramen magnum.

**Body Mass in Fossil Ischyromyids**

Based on these considerations, the preferred body mass estimate based on SL for *Paramys delicatus* would be 2914 g, *Reithroparamys delicatissimus*: 856 g, *Rapamys atramontis*: 1308 g, and *Ischyromys typus*: 1342 g. Because SL cannot be measured for *Paramys copei*, the preferred estimate is 1030 g based on cheek-tooth area. Each body mass estimate is based on one specimen; consequently, no measures of species-level variation (e.g., dimorphism) could be calculated from the data presented in this study. Very little has been published regarding the body mass of ischyromyids. *Paramys delicatus* is the only specimen in our sample with associated postcrania. Although a quantitative estimate based on the postcranium has never been calculated, the species was described as being the size of a marmot by Wood (1962). The range of *Marmota monax* body mass from our sample (28 individuals) is 1138–6250 g, with a mean body mass of 2526 g. *Paramys delicatus* (2914 g) fits well within that range. Wood (1962) considered *Paramys copei* to be smaller than *P. delicatus*, which is consistent with our results (1030 vs. 2914 g). *Rapamys* was referred to as an “intermediate to large sized ischyromid” by Wahlert (2006:40), but without providing any basis for this assessment. In the context of our estimates, *Rapamys atramontis* (1308 g) is intermediate in size between the larger *P. delicatus* (2914 g) and the smaller *Reithroparamys delicatissimus* (856 g) and *P. copei* (1030 g). No previously published information on body mass is available for *Reithroparamys* or *Ischyromys*.

**Locomotor Habits in Rodents**

Previous studies have demonstrated relationships between ecological variables and cranial dimensions in rodents. For example, there is good evidence for skull adaptations for fossoriality in digging rodents (e.g., Agrawal, 1967; Lessa and Patton, 1989; Lessa and Thaeler, 1989). In particular, Agrawal (1967) found specific adaptations for fossorial habits and managed to differentiate two modes of digging based on cranial measurements and comparative anatomy. Samuels (2009) also used geometric morphometrics to demonstrate a relationship between the shape of the skull and diet. A recent study by Hautier et al. (2012) examined skull shape variation in Ctenohystrica using a geometric morphometric approach. That study assessed shape variation in relation to a range of different ecological parameters, including diet, activity patterns, and habitat. They showed that both habitat and diet influenced the shape of the skull. Indeed, they found that some rodents from different superfamilies (Octodontoidea and Cavioida) converged in skull shape when living in the same environment.

Our results from the PCA and CVA analyses show that cranial data can discriminate between locomotor patterns in Sciuromorpha. Given that PC1 explains nearly 95% of the total variation, overall size is clearly one element that is driving this discrimination among groups. In particular, the glider *Glaucomys volans* tends to be small, with an offset distribution of PC1 scores. The same effect can be seen in a plot of the body masses of the included extant taxa (Fig. 5), in which the one gliding genus included (*Glaucomys*) falls below the range of variation of both the arboreal and terrestrial groups. Interestingly, however, *Glaucomys* does not overlap with arboreal species on PC2 but instead with terrestrial taxa, suggesting that there are also some shape-related differences between that gliding taxon and arboreal non-gliding forms. However, it’s worth noting that no larger-bodied gliding species were included, because noting that no larger-bodied gliding species were included, because of a lack of availability of specimens with individual body mass data in the collections studied. Large gliding species would be interesting to incorporate because some have a body mass similar to terrestrial taxa. For example, *Petaurista petaurista* has a body mass range between 1.0 and 3.19 kg (Lee, 1999), which is in the range of the body mass of *Marmota monax*. Adding such taxa to this analysis could test the hypothesis of shape-related differences between gliders and non-gliding arborealists. The terrestrial and arboreal groups overlap on PC1, with the former showing a much wider range of variation, so that the taxa with the lowest scores on this axis (representing the largest body masses) are all terrestrial. This effect can also be seen in the boxplot of body mass data, in which
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the range of variation for arboreal forms overlaps with that of the terrestrial taxa, but is limited to the small end of that range.

However, it is not only size but also shape of the cranium that differentiate terrestrial from arboreal forms. For example, the arboreal Sciurus, Funisciusurus, and Tamasciurus have similar values as the terrestrial Spermophilus for PC1 but differ on PC2. Variables related to size of the cheek-teeth and foramen magnum have extreme eigenvector loadings for PC2, suggesting that they are key to discriminating various cranial shapes. Interestingly, a study by Satoh and Iwaku (2008) showed that a relationship exists between locomotor habits and the angle formed by the foramen magnum and the rest of the skull, which could provide an explanation for the separation between locomotor groups on this axis. Consequently, the size and position of the foramen magnum might have a role in ecologically relevant variation in the cranial shape of rodents, even though it cannot be considered a good proxy for body mass.

Lu et al. (2014) used geometric morphometrics and demonstrated that variation in skull shape in sciurids is correlated with different lifestyles (e.g., arboreal, gliding, terrestrial). They show that arboreal squirrels have convergently evolved (Ratufa and Sciurus) an inflated and rounded vault. According to Lu et al. (2014), terrestrial Sciuridae taxa tend to have flattened crania and gliding species can be seen as intermediate between those two extreme shapes. Those results are consistent with our observations and suggest that the form of the braincase has a stronger correlation with locomotor habits than with body mass.

**Locomotor Habits in Fossil Ischyromyids**

Some authors (Matthew, 1910; Szalay, 1975) have hypothesized that Eocene rodents might have been arboreal based on postcranial elements, whereas others have viewed ischyromyids as terrestrial (Korth, 1994). Rose and Chinnery (2004) described Paramyinae as generalist taxa existing on both the ground and in the trees. The results of our PCA and CVA clearly show three nonoverlapping locomotor groupings, allowing for the use of cranial variables to test these hypotheses. All of the fossil taxa except P. copei fall within the terrestrial polygon in the plot of PC1 vs. PC2 (Fig. 3). Again, with the exception of P. copei, all fossils also fall within the 95% confidence ellipse of the terrestrial group in the CVA (Fig. 4). Even though P. copei falls outside the modern range of terrestrial forms in both analyses, it is much closer to the terrestrial centroids, suggesting that it too lived on the ground. Support for the view that these taxa were all terrestrial comes from the observation that only a minority of living sciuromorphs of comparable body mass are arboreal or gliders (e.g., Ratufa, giant squirrel; Petaurista, giant flying squirrel).

In terms of the particular habits of the various species, Paramys delicatus is clustered with Marmota in both analyses (Fig. 3, 4), so it had a similar cranial shape and might have had locomotor habits comparable to this extant genus. The fact that P. copei falls outside the modern range of variation in both PCA and CVA analyses suggests that it might have had a cranial shape somewhat different from those of all the extant terrestrial rodents in this sample, making it difficult to choose a relevant living analog. Ischyromys and Rapamys are clustered with Cynomys in the PCA and with both that genus and Spermophilus when looking at the CVA. This suggests that these fossil taxa might have displayed locomotor habits similar to those two modern genera, both of which are ground-living burrowers. In the PC1 vs. PC2 plot, Reithroparamys is isolated from all of living sciuromorph taxa but clusters near Cynomys in the CVA. Wood (1962) interpreted relatives of this genus as subricochetal to ricochetal partly based on elongated limbs (e.g., metatarsals, longer tibia than femur). Saltatorial rodents are terrestrial, so the current analyses are in general agreement with this inference. However, no saltatorial specimens were included because no living sciuromorph rodents exhibit this type of locomotion, so this hypothesis cannot be tested more precisely. Nevertheless, if Reithroparamys were saltatorial, that might explain why it is separated from the living forms in the PCA plot.

**CONCLUSIONS**

Researchers preferentially use postcrania (e.g., Sánchez-Vilraga et al., 2003) or individual dental dimensions (e.g., Gingerich et al., 1982) to estimate body mass, and postcranial data are frequently used to estimate locomotor habits (e.g., Rose and Chinnery, 2004). The current study shows that, in the absence of associated postcrania, body mass and locomotor behavior can be estimated using cranial and cheek-tooth dimensions. High correlations exist between those measurements and body mass in rodents, as has been previously shown for primates (Martin, 1990; Sears et al., 2008), carnivores (Van Valkenburgh, 1990),
ungulates (Janis, 1990), and rodents (Rinderknecht and Blanco, 2008; Millien and Bovy, 2010; Freudenthal and Martín-Suárez, 2013). Skull length and cheek-tooth area are herein considered the best predictors of body mass for fossil rodents. These variables have been demonstrated to be of value in rodents (Rinderknecht and Blanco, 2008; Millien and Bovy, 2010; Freudenthal and Martín-Suárez, 2013) and in other groups (Martin, 1990; Van Valkenburgh, 1990; Begun and Kordos, 2004; Sears et al., 2008; Churchill et al., 2014) and provide generally consistent estimates for ischyromyids. Other cranial variables provide widely varying estimates, likely as a result of the influence of brain size, biomechanics, and ecological variables, indicating that they are less reliable estimators of body mass.

This study is the first to provide body mass estimates for five ischyromyid fossil rodents (four Eocene and one Oligocene specimens), with *Paramys delicatus* being the largest (marmot-sized; Wood, 1962) and *Reithroparamys delicatissimus* the smallest extant in the sample. Conflicting views have been proffered about the locomotor mode of ischyromyid rodents (Matthew, 1910; Wood, 1962; Szalay, 1975; Korth, 1994; Rose and Chinnery, 2004). In this paper, we show that the ecological diversity of Sciuromorpha is reflected in the variation of cranial shape in this suborder, with terrestrial, arboreal, and gliding species forming three distinct groups in PCA and CVA analyses. The five ischyromyids under consideration cluster with the terrestrial group. *Reithroparamys* is isolated from the other fossils in the principal components analysis, and this result could be related to the presence of saltatorial adaptations, inferred based on postcranial data (Wood, 1982) and not represented in modern sciuromorphs.

In sum, this work demonstrates the utility of cranial measurements for reconstructing both body mass and locomotor mode in fossil rodents.

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