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Using left-right asymmetry to estimate non-genetic variation in vole teeth (Arvicolinae, Muridae, Rodentia)

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ABSTRACT

Arvicoline rodents, which are important index fossils for late Cenozoic terrestrial deposits, are often said to have the greatest amount of dental variation of any mammal. If true, if that variation is environmental (ecophenotypic) in nature, and if variation within species is greater than between species, then the scientific basis of taxonomic identifications of these common fossils is questionable. We used left-right asymmetry in the shape of the lower first molar of four arvicoline species as a measure of the environmental (non-genetic) component of variance within vole species. Using both Eigenshape and semilandmark (Procrustes) analysis, we found that environmental variance accounted for about 10%-30% of within-species variance, suggesting heritabilities (h^2) of 0.71 to 0.89 for molar tooth shape. However, the magnitude of this non-genetic variance was considerably smaller than that found between individuals belonging to the same species and nearly an order of magnitude smaller than differences between species. It is unlikely that environmental variance or within-species variation regularly confound species-level taxonomic identifications of vole teeth.

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INTRODUCTION

Voles and lemmings (Arvicolinae, Muridae, Rodentia) are sometimes said to have more dental variation than any other mammal (e.g., Yablokov 1974; Carleton 1985). Variation can manifest itself at different hierarchical levels, notably between species (or clades) and within species (or populations). High levels of variation between species are an advantage for the study of fossil taxa because it makes species easily distinguishable from one

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another. Such inter-specific variation, which is sometimes called disparity, is known to be an important phenomenon in arvicoline rodents. The distinctive, rapidly evolving dental morphology of voles and lemmings make them important index fossils for late Cenozoic terrestrial biostratigraphy (e.g., Fejfar 1976; Repenning 1987; Maul et al. 1998; Bell et al. 2004). Conversely, variation within species is generally a disadvantage for the study of fossil taxa because it makes species difficult to diagnose. Such intra-specific variation is also known to be common in arvicolines, especially in the anterior cap of the lower molars (e.g., Hinton 1926; Van der Muelen 1973; Carleton 1985; Jaarola et al. 2004). High intra-specific variation can be an especial problem if it is coupled with low inter-specific variation because that combination leads to morphological overlap between species, hindering accurate identification of fossils and potentially leading to erroneous biostratigraphic or biogeographic interpretations.

Variation within species can be divided into genetic and environmental components of variance (e.g., Lynch and Walsh 1998). Quantitative geneticists describe this division using the equation

$$P = G + E, \text{ (Equation 1)}$$

where *P* is the phenotypic variance, or the variation we see in morphological structures such as teeth, *G* is the genetic variance, or the variation in a species that is passed from parent to offspring, and *E* is the environmental variance, or the variation that is directly determined by local environment regardless of parentage. *G* represents heritable variation, regardless of whether the heritability has a direct one-to-one correspondence to genes coded on the DNA or a less direct but equally heritable developmental system whose morphogenetic outcomes are determined by the effects directly heritable regulator genes. *E* represents variation from all non-genetic sources, regardless of whether the sources are internal or external developmental noise, norms of reaction, or epigenetic variation. *E* is a quantitative genetics formulation of what is often known as morphological or ecophenotypic plasticity in the palaeontological literature (e.g., Newell 1948; Hughes 1991).

Generally speaking, the palaeontological study of taxonomy, species relationships, rates of evolution, and evolutionary patterns depends on variation being primarily genetic in nature because non-genetic variation may obscure underlying genetic and, therefore, evolutionary patterns. Conclusions about taxonomy or evolution could be misguided if environmental variance is great enough to cause undetected similarity among distantly related species or difference among conspecific populations. These potentially pernicious environmental effects, which are also called ecophenotypic or plastic variation, manifest themselves over the lifetime of an individual and should not be confused with evolutionary adaptation to environment, which is a consequence of genetic variance and natural selection over tens, hundreds, thousands, or millions of generations (e.g., Kratochvíl 1983). For these reasons, palaeontologists have often distinguished between the genetic and environmental components of variance in skeletal traits as a tool for better understanding evolutionary and environmental change (e.g., Schopf 1976; Pachut 1987; Hadly 1997; Polly 2004; Kavanagh et al. 2007).

Because the teeth of voles and lemmings are noted for both their inter- and intra-specific variation and because their teeth are so important for biostratigraphic interpretation, it is of interest to know the extent to which this variation is genetic. The proportion of genetic and environmental components of phenotypic variance is usually determined by large breeding experiments that allow the similarity between parents and their offspring to be measured directly or indirectly through 'common garden' experiments that bring genetically diverse individuals into the same environmental conditions in order to measure directly the resulting similarities (e.g., Lynch and Walsh 1998). Such experiments are expensive and time consuming even for living species, and in any case they cannot be applied to fossil animals.

Non-genetic variance can be estimated less laboriously by measuring asymmetry between right and left teeth. The right and left sides of an animal have the same genetic underpinnings, so the difference between the sides must logically be due to non-genetic factors (Grüneberg 1935; Van Valen 1962; Palmer and Strobeck 1986). Exceptions to this logic include directional asymmetry, consistent asymmetry in organs like the heart, and antisymmetry, consistent differences between right and left parts like the disproportionate size of the claws of some crabs (Morgan 1923; Rosenberg 2002). These exceptions do not, however, pertain to differences between right and left teeth, except insofar as the two sides are normally mirror images of one another. Difference in shape between left and right teeth (apart from mirroring) is an example of fluctuating asymmetry, or inconsistent, randomly distributed difference that results from the inability of the underlying genetics to determine identical structures. Leamy and Klingenberg (2005) reviewed the

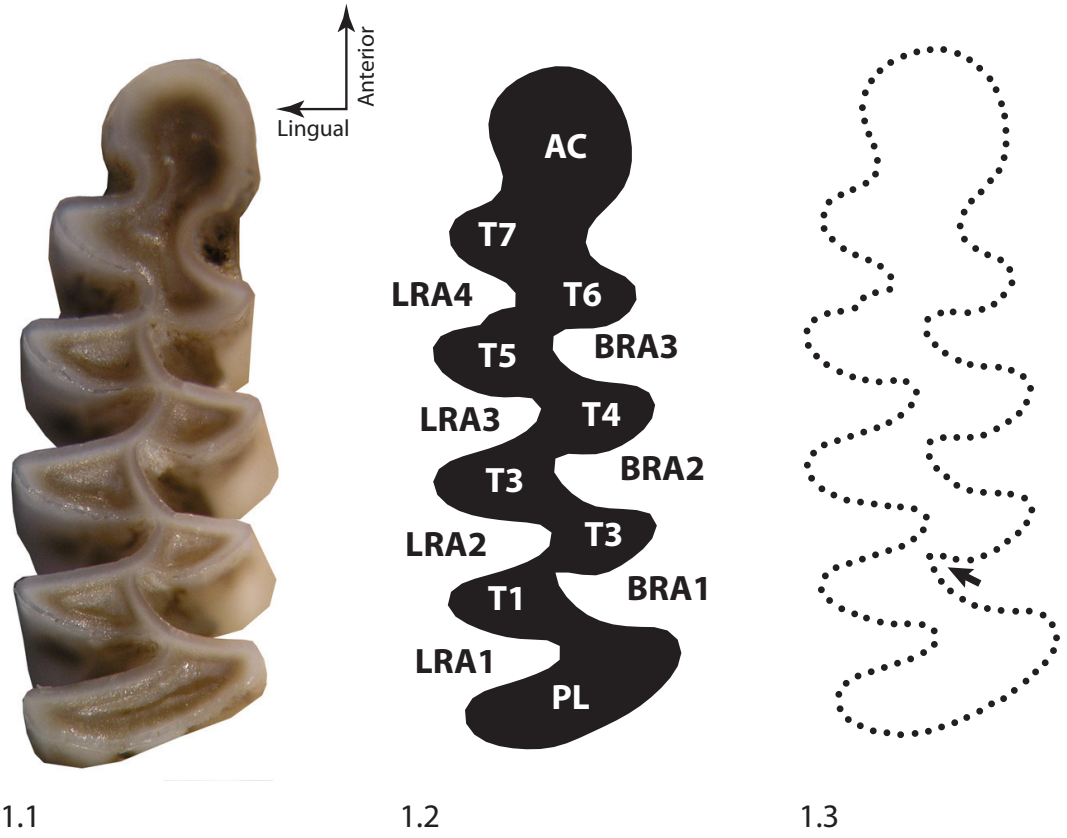

FIGURE 1. Morphology and outlines of the first lower molar. 1.1, photograph of the occlusal surface of *Microtus arvalis*. 1.2, outline of the same molar. 1.3, two hundred fifty outline coordinates running anticlockwise from the starting point marked by the arrow. AC, anterior cap. BRA, buccal reentrant angle. LRA, lingual reentrant angle. PL, posterior lobe. T, triangle.

genetics of fluctuating asymmetry. An estimate of the variance between right and left teeth relative to the variance between the teeth of different individuals can be thought of as a minimum estimate of *E*, the environmental component of variance within that species, because the right-left asymmetry is non-genetic. Analysis of variance (ANOVA) can be used to mathematically partition the within-species variance in tooth shape into between-individual and between-sides components, the latter being an estimate of *E*. This estimate of environmental variance is a minimum one, however, because some environmental effects, like quality of diet or ambient temperature, will affect both sides equally to the extent that they have an effect at all. But despite its shortcomings, an estimate of *E* based on asymmetry can be made on fossil specimens as easily as extant ones, presuming that the left and right teeth can be associated with the same individual.

We estimated the minimum environmental component of variance using asymmetry in the outline shape of lower first molars from four species of arvicoline rodents. We used those estimates to determine the likelihood that environmental effects will result in erroneous species determinations. We also used the data to explore whether right and left molars from the same individual can be associated based on their shape alone.

MATERIALS AND METHODS

We measured the outline shape of the first lower molars (Figure 1) in *Arvicola terrestris*, the water vole (*N* = 28), *Microtus agrestis*, the field vole (*N* =24), *M. arvalis*, the common vole (*N* = 38), and *M. oeconomus*, the root vole (*N* = 14). Specimens are housed in the National Museum of Scotland and the The Harrison Zoological Institute (Sevenoaks, England).

The right and left teeth of each individual were photographed with a Canon 350D digital SLR camera with macro lens arrangement giving x2 magnification. Care was taken to orient each tooth so that its occlusal surface was oriented horizontally, perpendicular to the line of sight. The left tooth of each

individual was flipped to remove the effects of mirroring. The outline of each tooth was traced using image processing software (Adobe Photoshop CS2 ©). Chips in the enamel were ignored in the tracing because we did not want to include differences due to breakage in our estimate of asymmetry. Two hundred fifty evenly spaced points were then fitted to the traced outline for quantitative analysis. The points ran counterclockwise around each outline starting at the apex of the first buccal reentrant angle (Figure 1.3).

We analyzed the coordinates using two different outline methods to ensure that choice of method did not substantially affect the results.

The first method was Standard 2D Eigenshape (Lohmann 1983; MacLeod and Rose 1993; MacLeod 1999). In Eigenshape, the outline coordinates are transformed to a Zahn and Roskies (1972) shape function (φ), which is a vector of net angular change the positions of neighbouring outline coordinates beginning at an arbitrary starting position that is the same on all objects. The function was standardized by subtracting the angles describing a circle of the same mean radius (φ*) as recommended by MacLeod (1999). The tooth outlines were ordinated in principal components (PC) space by singular value decomposition of the covariance matrix of the φ* functions. The PC scores of the tooth outlines are, by definition, uncorrelated with one another but preserve the shape distances among the original outlines and so can be used as shape variables for further statistical analysis. Eigenshape distances between tooth outlines can be calculated either as the Euclidian distance between the φ* functions or as the Euclidean distance between the full set of PC scores (the two distances are identical). These distances are analogous to Procrustes distances in landmark analysis.

The second method of shape analysis was a Procrustes-based semilandmark analysis (Bookstein 1991; Rohlf 1993; Dryden and Mardia 1998; Zelditch et al. 2004). The same 250 outline coordinates were treated as semilandmarks (Bookstein 1997). The shapes were superimposed using Generalized Procrustes Analysis (GPA, Rohlf 1990). The mean shape was subtracted from the superimposed coordinate points. The tooth shapes were ordinated in PC space by singular value decomposition of the covariance matrix of the resulting Procrustes residuals. Like with Eigenshape, the PC scores are uncorrelated and preserve the original shape distances and so can be used as shape variables for further statistical analysis. Procrustes distances between the tooth shapes can be calculated either as the Euclidean distances between their Procrustes superimposed coordinate points or as the Euclidean distance between the full set of PC scores for the two teeth.

Shape variance was partitioned into between-individual and between-side components using Multivariate Analysis of Variance (MANOVA) on the PC score shape variables with both data sets for each of the four species. The between-individual component of variance is the part that describes the average difference between the teeth of individual voles independent of asymmetry; the between-side component describes the variance between left and right sides. The former is an estimate of within-species variance unbiased by the non-genetic variance associated with fluctuating asymmetry; the latter is a minimum estimate of environmental variance, *E* (Palmer and Strobeck 1985; Klingenberg and McIntyre 1998).

The absolute values of the variance components are rather arbitrary since the scale differs between Eigenshape and Procrustes analysis. However, the proportions of between-individual and between-side variances to the total variance can be compared from one analysis to the other. A maximum estimate of heritability (h^2), which is the proportion of phenotypic variance that is passed from parent to offspring, can be calculated as

h^2 = 1 – (between-sides variance / total variance), (Equation 2)

which is the same as h^2 = G/P since the between-sides variance is a proxy for *E*. By Equation 1, G/P = 1 – (E/P). This estimate of h^2 must be considered a maximum because some environmental variance will be undetected by the analyses presented here, as mentioned above.

RESULTS AND DISCUSSION

Shape variation

Typical variation among individuals and between left and right teeth is illustrated in Figure 2. Variation in the shape of the anterior cap is easily seen between individuals, but the left and right teeth of the same individual have the similar cap shapes.

The similarity between left and right molars may also be seen in the PC scatterplots (Figures 3 and 4). More often than not, the left and right teeth of the same individual are nearest neighbours in the plots, both for Eigenshape and semilandmarks.

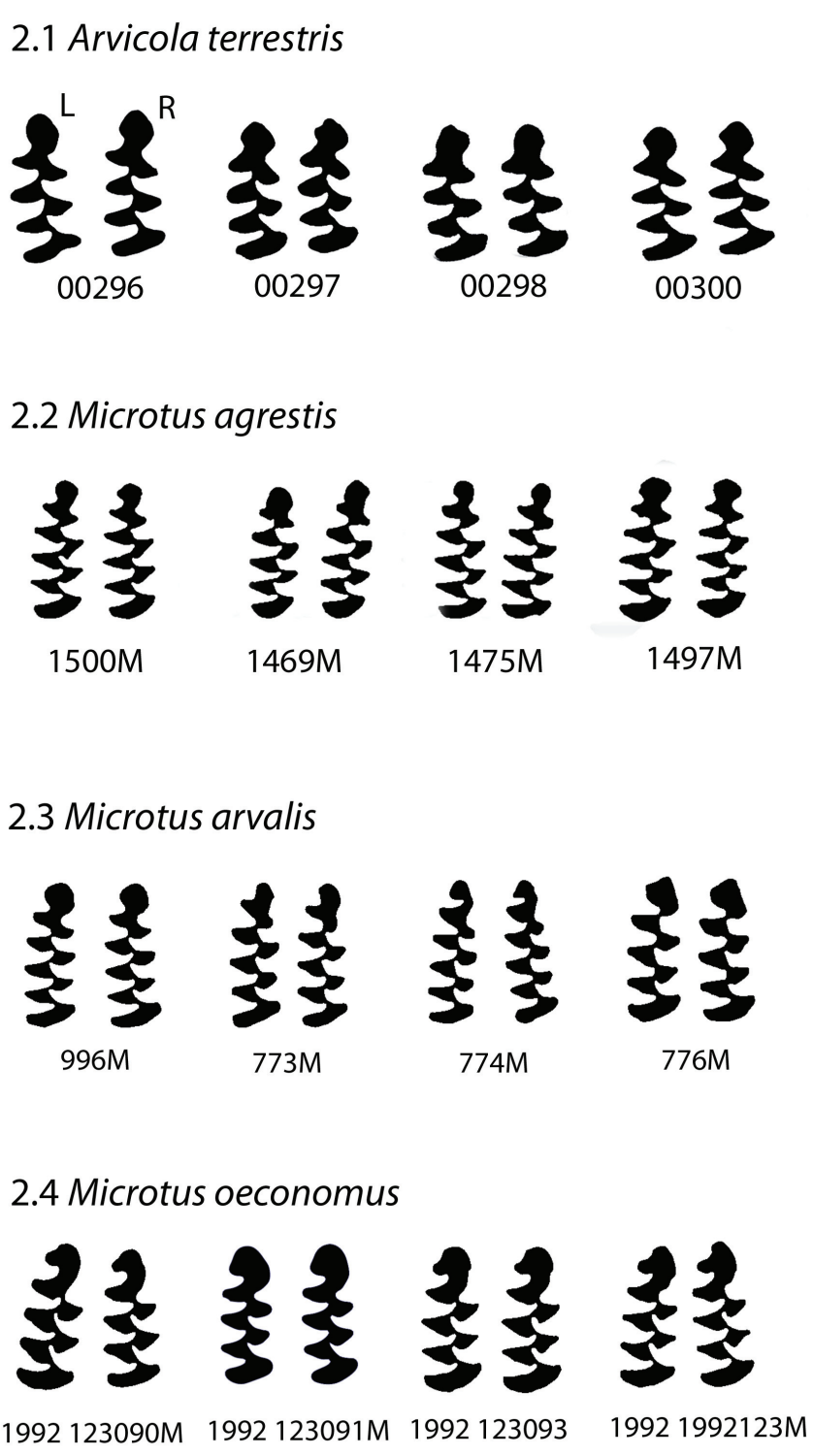

FIGURE 2. A representative sample of individual and left-right variation in the shape of the first lower molar of four arvicoline species. Outlines of the left and right teeth of *Arvicola terrestris* (2.1), *Microtus agrestis* (2.2), *M. arvalis* (2.3), and *M. oeconomus* (2.4) are illustrated. The left tooth was flipped to facilitate comparison with the right.

TABLE 1. MANOVA results for the partition of variance between individuals. The sum of squared deviations for individual differences and left/right differences is reported along with the percentage of the total variance accounted for and the maximum estimate of h^2 for each species.

Eigenshape Analysis			
Source of variation	**Sum of squared deviations**	**Percentage of total**	**Proportion (Max h^2)**
Arvicola terrestris			
Individual differences (between groups)	748.5	88.6%	0.89
Left and right differences (within groups)	96.4	**11.4%**	
Microtus agrestis			
Individual differences (between groups)	566.4	71.5%	0.71
Left and right differences (within groups)	226.2	**28.5%**	
Microtus arvalis			
Individual differences (between groups)	1817.4	86.2%	0.86
Left and right differences (within groups)	289.8	**13.8%**	
Microtus oeconomus			
Individual differences (between groups)	498.2	77.6%	0.78
Left and right differences (within groups)	144.2	**22.4%**	

Semilandmark (Procrustes) Analysis			
Source of variation	**Sum of squared deviations**	**Percentage of total**	**Proportion (Max h^2)**
Arvicola terrestris			
Individual differences (between groups)	0.1930	88.3%	0.88
Left and right differences (within groups)	0.0257	**11.7%**	
Microtus agrestis			
Individual differences (between groups)	0.1483	76.6%	0.77
Left and right differences (within groups)	0.0454	**23.4%**	
Microtus arvalis			
Individual differences (between groups)	0.5070	89.0%	0.89
Left and right differences (within groups)	0.0628	**11.0%**	
Microtus oeconomus			
Individual differences (between groups)	0.1432	71.6%	0.72
Left and right differences (within groups)	0.0567	**28.4%**	

MANOVA and Components of Variance

The results presented visually above can be measured quantitatively by partitioning shape variation into between-individual and between-side components with MANOVA. Both Eigenshape and semilandmark analyses showed that between-individual variance was much greater than variance between left and right teeth (Table 1). *Microtus agrestis* and *M. oeconomus* had the greatest amount of asymmetry (22.4-28.5%), whereas *Arvicola terrestris* and *M. arvalis* had less (11.4-13.8%). These results suggest that within-species variation is only marginally inflated by random environmental effects.

Using left-right asymmetry as a minimum estimate of environmental variance (E), heritability (h^2) of tooth shape in the four species was estimated (Table 1). Heritabilities ranged from 0.71 to 0.89.

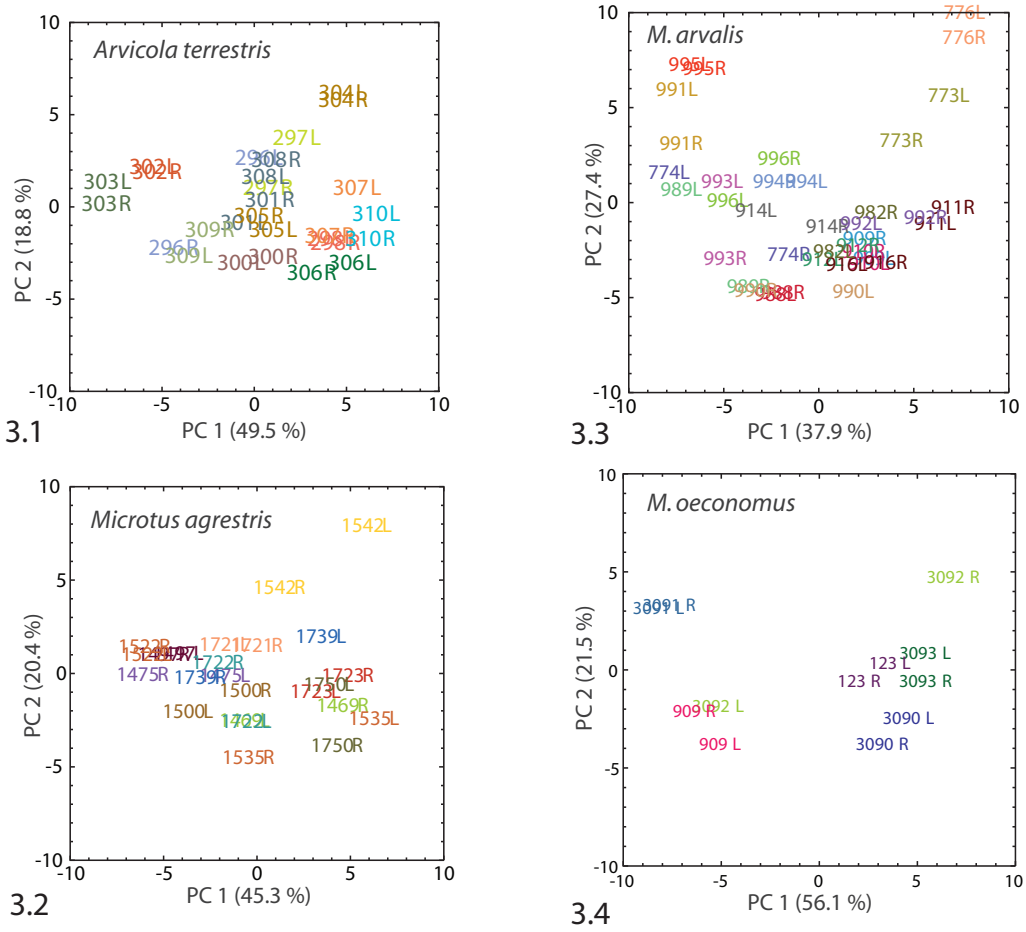

FIGURE 3. Scatterplots of the first and second principal components of tooth shape based on Eigenshape analysis. Labels are centred on the point occupied by each specimen in the shape space. L, left. R, right. Left and right teeth of the same individual are indicated with the same colour.

Matching Contralateral Teeth

In many cases, contralateral teeth from the same individual were more similar to the teeth of another individual than to each other. Using Procrustes distance, which is a form of nearest-neighbour matching, we found that in *Arvicola terrestris*, twoout of 28 (7.1%) teeth did not match to their contralateral counterpart; in *Microtus agrestis* 15 out of 24 (62.5%) did not match; in *M. arvalis* 20 out of 38 (52.6%) were mismatched; and in *M. oeconomus* four out of 14 (28.5%) were incorrectly matched. Procrustes distances between teeth of different individuals were often larger than between teeth of the same individual, but many teeth of different individuals had Procrustes distances that were as small as those between teeth of the same individual (Figure 5). Thus, teeth of the same individual cannot reliably be matched based on shape alone.

The Relative Merits of Eigenshape and Semilandmarks (Procrustes)

As discussed above, the PC plots of molar shape generated by Eigenshape and semilandmark analyses were broadly similar. The fact that corresponding plots had the same teeth as outliers on each of the two PC axes indicates that both methods are recovering the same variation (Figure 3). For example, the right and left molars of specimen 00303 of *Arvicola terrestris* lie at one end of the first PC extracted by both methods, and specimen 00304 lies at one end of PC2. The fact that the positive and negative ends of the axes are flipped can be ignored because shape does not have an inherent directionality. The percentages of within and between individual variation were roughly the same regardless of which method was used.

That the two methods yield similar results can be further tested by comparing Eigenshape and

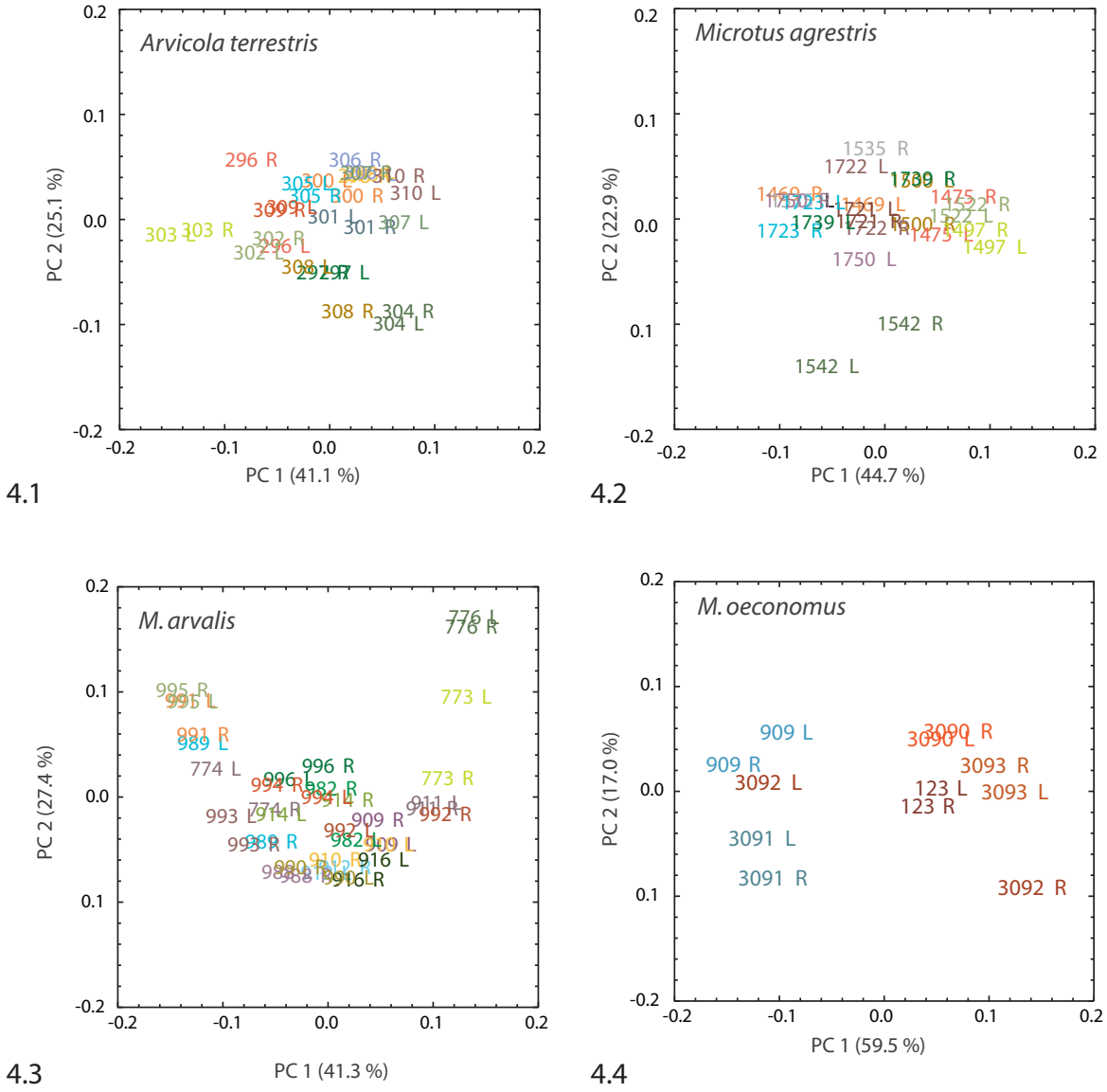

FIGURE 4. Scatterplots of the first and second principal components of tooth shape based on semilandmark (Procrustes) analysis. Labels are centred on the point occupied by each specimen in the shape space. L, left. R, right. Left and right teeth of the same individual are indicated with the same colour.

Procrustes distances between pairs of teeth (Figure 6). We calculated all possible pairwise distances using both methods for each of the four species. The tight correlation between the two distances again indicates that each is measuring the same differences in shape and that one method can safely be substituted for the other.

CONCLUSIONS

The proportion of environmental variance identified through fluctuating asymmetry was relatively small (11.0%-28.5% of the total variance), implying that heritabilities (h^2) of tooth shape range from 0.71 to 0.89. These h^2 values are somewhat higher than in previous studies of heritability in dental characters, but not surprisingly so. Leamy and Bader (1968) found h^2 values that ranged between 0.60 and 0.66 for the linear size of field mouse molars. Hlusko and Mahaney (2003) found h^2 to be as high as 0.725 for the presence of cingular remnants in baboon molars, though in most cases h^2 was around 0.60 for that trait.

While the differences between contralateral teeth are often as great as between individuals of the same species, they were much, much smaller than differences between species (Figure 7). In

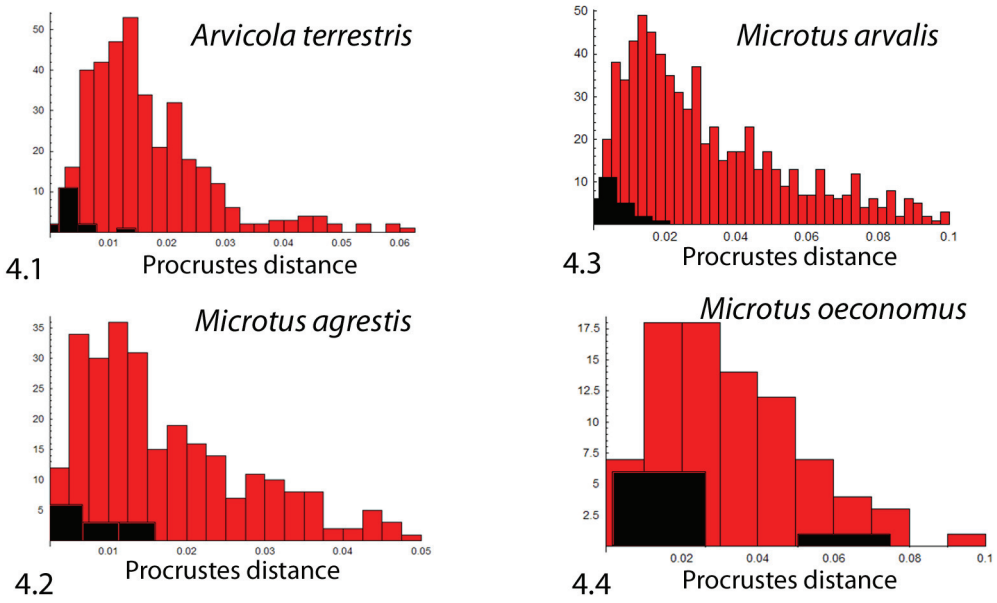

FIGURE 5. Histograms of Procrustes distances between teeth from the same individual (black bars) and between teeth from different individuals (red bars). While the largest differences are between teeth from different individuals, the distribution of distances between sides overlaps with distances between individuals in all four species.

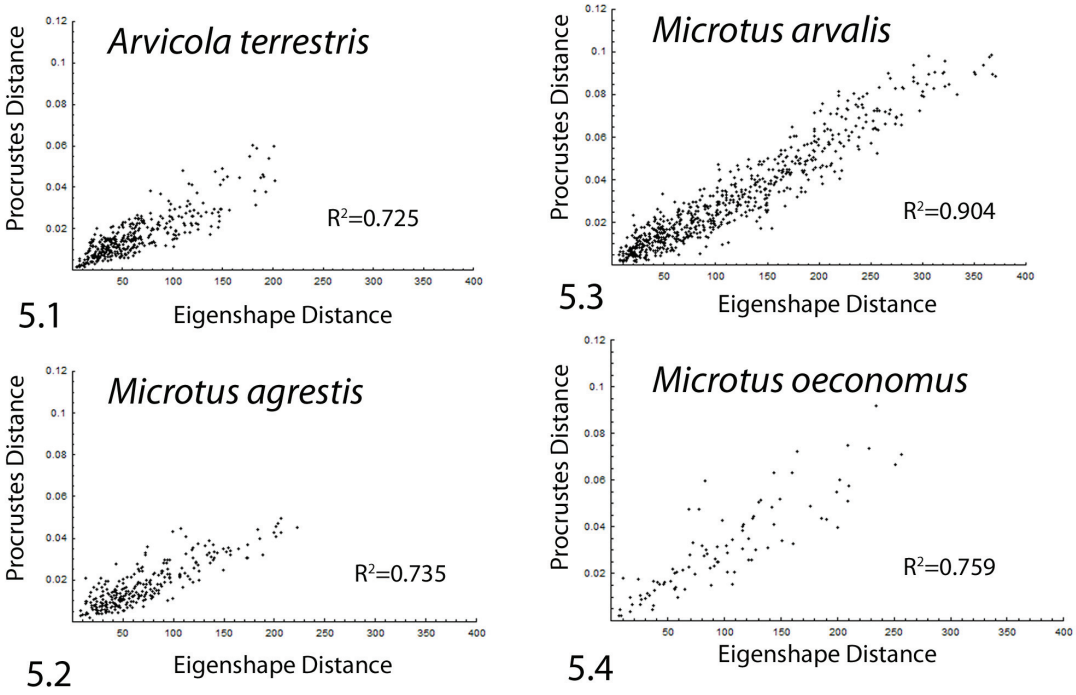

FIGURE 6. Comparison between Eigenshape and semilandmark (Procrustes) analysis. For each of the four species a scatterplot shows the relationship between the morphometric distance between pairs of teeth calculated using Eigenshape (y-axis) and Procrustes superimposition of semilandmarks (x-axis). R^2 is the proportion of variance in Procrustes distance that is explained by Eigenshape distance.

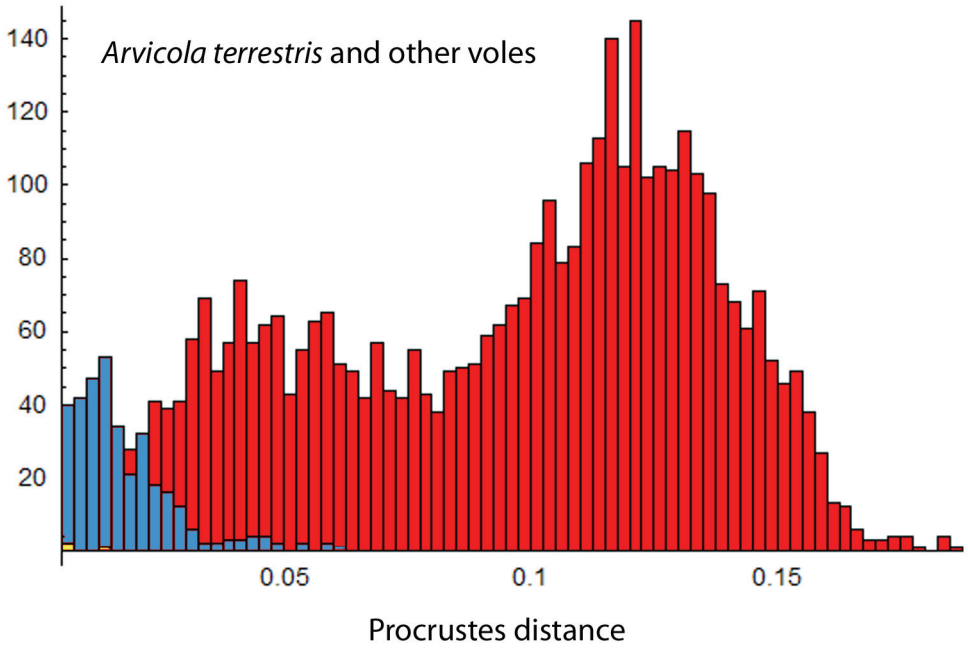

FIGURE 7. Comparison of the magnitude of between-side, between-individual, and between-species differences in lower molar shape. Histograms show the frequency of between-side distances (yellow bars), between-individual distances within *Arvicola terrestris* (blue bars), and between individual distances for individuals belonging to different species (red bars). The red histogram may be visually compared with the histograms for the other three species in Figure 5.

Arvicola terrestris the maximum Procrustes distance between teeth from two sides of the same individual was 0.015 units. The mean distance between teeth belonging to different species was nearly an order of magnitude greater at 0.095 units.

Arvicoline rodents may have especially variable teeth, and they may vary within species and between species, but the magnitude of variation between species is so much greater than that within species that variation is not likely to confound palaeontological interpretations. The amount of ecophenotypic environmental variance within the species we measured appears to be negligible compared to the differences we observed between species.

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