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PALEOPHYLOGEOGRAPHY: THE TEMPO OF GEOGRAPHIC DIFFERENTIATION IN MARMOTS (*MARMOTA*)

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Quantitative analysis of molar shape may provide a metric for paleontological phylogeography or the study of intraspecific relationships in the fossil record. In this study, outlines of the lower 3rd molars (m3) of North American *Marmota* were analyzed as between-shape distances after ordination with eigenshape analysis. Based on comparisons with cytochrome *b*, quantitative divergence in molar shape appears to be a reasonable proxy for phylogenetic reconstruction at the level of populations, subspecies, and the most closely related species of marmots. Phylogeographic analysis of living North American marmots and middle Pleistocene fossils from Porcupine Cave, Colorado, revealed that the latter were more closely related to extant *Marmota monax* than they are to *M. flaviventris*, which currently inhabits the Porcupine Cave area, suggesting that the origin of living species occurred in regions different from those they inhabit today. Change in molar shape was significant from level to level through the Porcupine Cave section, which spans a glacial–interglacial cycle, but was not correlated with environmental change. The amount of morphological difference among conspecific populations of living *M. monax* suggested that they differentiated over many glacial cycles, whereas morphological differences between *M. caligata* and *M. flaviventris* were smaller and may have evolved over fewer cycles.

Key words: cytochrome *b*, eigenshape analysis, *Marmota*, molar evolution, phylogeography, Porcupine Cave

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The study of intraspecific evolutionary processes using mitochondrial DNA (mtDNA) has revolutionized research on mammals (and other organisms) because historical processes such as speciation, divergence, population changes, and migration leave their imprint on genealogies of sequences (Hewitt 2000; Klicka and Zink 1997; Slatkin 1987; Tajima 1983; Wakeley 1996a, 1996b). Phylogeography, the reconstruction of phylogenetic relationships among geographically distinct populations, uses such sequence data to gain insights into spatial patterns of evolutionary diversification. However, such studies exclusively concern the extant biota because interpopulation relationships require the precision of molecular data to resolve. Thus, phylogeography has had little impact on mammal paleontology, even though phylogeographic findings are usually interpreted in terms of past environments and geographic history.

The mammalian fossil record, which embodies direct evidence of the past, is extraordinarily rich but has usually been restricted to supraspecific problems because skeletal and dental remains often limit phylogenetic reconstruction to intraspecific levels; the smallest units diagnosable from fossilized bones and teeth are normally species-level taxa. Only in the study of lineages preserved

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in superpositional stratigraphic sequences has paleontology been able to address evolution within species, gaining on a temporal scale what it loses on a geographic one (Barnosky 1993; Bell et al. 1985; Gingerich 1976, 1993).

In the study of living mammals, the distinction between phylogenetic differentiation and geographic variation—evolutionary time and space—has been blurred by the phylogeographic approach (Avise 1994, 2000; Patton and Smith 1989). Phylogeography thus provides a powerful paradigm for paleontological research, offering a synthetic interpretation of geographic variation, temporal evolutionary change, and biogeography both above and below the species level (Hadly et al. 1998; Lister and Sher 2001; Martin 1993; Polly 2001). However, the phylogeographic paradigm is difficult to apply to fossil material because paleontology lacks a quantitative measurement of phylogenetic divergence that is informative at the level of species and populations like mtDNA. Molar tooth shape provides such a measurement because it is a trait that has a high additive genetic component (teeth do not grow or remodel once mineralized), varies among populations, has a form complex enough to make homoplasy less likely than in univariate traits such as size, and yet evolves quickly enough to be phylogenetically informative at the population and species level (Polly 2001). With such a ''morphological marker,'' paleontologists can study phylogenetic relationships among intraspecific fossil samples separated both geographically and stratigraphically, exploring morphological divergence through time and through space.

I assessed the potential of molar shape for paleophylogeographic reconstruction in *Marmota* and applied it to North American taxa, using it to ask how deep into the Quaternary inter- and intraspecific divergences go, at what rate intraspecific geographic differences evolved, and how the magnitude of stratigraphic evolution compares with intraspecific geographic variation in the modern world. Marmots are large terrestrial squirrels belonging to 6 recognized North American species: woodchuck (*Marmota monax*), yellow-bellied marmot (*M. flaviventris*), hoary marmot (*M. caligata*), Brower's marmot (*M. broweri*), Vancouver marmot (*M. vancouverensis*), and Olympic marmot (*M. olympus*—Barash 1989; Hall 1981; Steppan et al. 1999). I studied teeth from extant marmot populations and the middle Pleistocene Pit locality in Porcupine Cave, Colorado, which is estimated to be 750,000–800,000 years old (Barnosky and Rasmussen 1988; Barnosky et al. 1996; Bell and Barnosky 2000; Wood and Barnosky 1994). The Pit's strata span a single glacial–interglacial cycle, providing a temporal standard for assessing whether subspecific differences in living marmots are likely to have evolved since the most recent glaciation. Porcupine Cave also provides an opportunity to study the temporal scale of geographic species range changes because it lies within the current range of *M. flaviventris*. I used m3 shape to test whether the fossil marmots are closely related to a particular subspecies of *M. flaviventris* or to another species or whether they lie outside the common ancestry of living marmots altogether. To provide a scientific foundation for this study, I initially tested whether molar shape differs among populations of the same marmot subspecies, whether molar shape evolves on the same temporal scale as cytochrome-*b* (*Cytb*) mtDNA, and whether molar shape can be used to reconstruct inter- and intraspecific phylogeny with enough accuracy to address these questions.

Materials and Methods

Molar shape was quantified using standard eigenshape analysis of the outline of the lower 3rd molar (m3). Eigenshape analysis is an ordination technique for outline data in which orthogonal vectors are calculated from a covariance or correlation matrix, allowing the objects to be projected into a multidimensional shape space (Lohmann 1983; Lohmann and Schweitzer

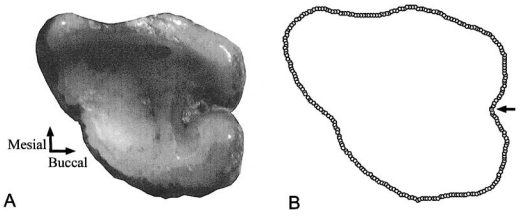

FIG. 1.—Molar shape quantified using outline analysis. A) Right m3 of *Marmota flaviventris engelhardti* in occlusal view showing its general morphology and shape. B) Two hundred fifty outline coordinates around the perimeter of the molar beginning at the junction of the buccal lobes (arrow) and continuing around the tooth clockwise.

1990; MacLeod 1999; MacLeod and Rose 1993). Marmot molars do not have many discrete landmarks, such as cusp tips or notches, and their features tend to lie along their periphery (Fig. 1A); therefore, a considerable amount of shape information is conveyed in the crown outline. Lower 3rd molars were chosen because they were the most common in the Porcupine Cave sample and because they can be unambiguously identified. Two-dimensional coordinates representing the outline were collected from digital images (Fig. 1B). Each outline started at the notch formed between the 2 buccal lobes of the tooth (Fig. 1B, arrow), continuing clockwise around the crown. Outlines were initially captured using 250 coordinates, which were reduced to 100 evenly spaced points, then converted to closed, unstandardized ϕ shape functions. In this study, analysis was performed on the covariance matrix of the ϕ functions. Euclidean distances among specimens were calculated from the projections onto the resulting eigenshape axes for use as an index of shape dissimilarity.

Four different eigenshape analyses were performed. Results of the 1st were used to test whether mean differences in m3 shape can be measured between conspecific populations. I compared samples of *M. m. monax* from northern Virginia ($n = 11$) and Indiana ($n = 20$). Specimens are housed in the National Museum of Natural History in Washington, D.C. Eigenshape scores for the first 30 of 100 eigenshape axes were submitted to multivariate discriminant function analysis. Axes higher than 30 have variances that are nearly zero and so do not describe significant shape variation.

Results of the 2nd analysis were used to compare m3 shape distance with *Cytb* sequence divergence to test whether molar shape can be used as a proxy for phylogenetic divergence or time since common ancestry. In this study, *Cytb* served as a proxy for time since common ancestry because more direct data were unavailable. Fourteen sequences were taken from Steppan et al. (1999), who studied several taxa whose locality and subspecific identity were known. Shape data were taken from corresponding museum samples (Appendix I). Kimura 2-parameter (K2P) distances were calculated from the sequences and plotted against m3 shape distance. Correlation between the 2 was tested using a Mantel test with 50,000 permutations (Thorpe et al. 1995). The relationship between the 2 is not expected to be linear because mtDNA does not have a direct causal influence on m3 shape; rather, there is a time series relationship with an expectation that the variance in m3 shape will increase proportional to the square root of time. This relationship was visually assessed by plotting an expected 50% confidence envelope around the observed data. To do this, the rate of m3 change per 1% sequence divergence (r_0) was estimated using log-rate/log-interval analysis (Gingerich 1993), which corrects for biases in rate introduced by evolutionary reversals. The envelope was calculated as $0.674r_0\sqrt{\text{K2P}}$.

Results of the 3rd eigenshape analysis were used to reconstruct a phylogenetic tree of extant and fossil *Marmota*. Shape data were collected from 25 geographically localized samples, comprising 333 total individuals, including 1 sample from level 4 of Porcupine Cave Pit locality (Fig. 2; Appendix II). All living North American species were included except *M. olympus*. In some cases, specimens from several localities were pooled to increase the sample size. No samples with $n < 5$ were considered. Eigenshape analysis was performed individually on each sample to calculate a mean shape; then, the mean shapes were submitted to a 2nd analysis for ordination. The scores were used to construct a maximum-likelihood tree using the continuous traits method of Felsenstein (1973). The tree was rooted along the branch connecting *M. monax* to the other species, the root identified by previous molecular phylogenies that used other squirrels as

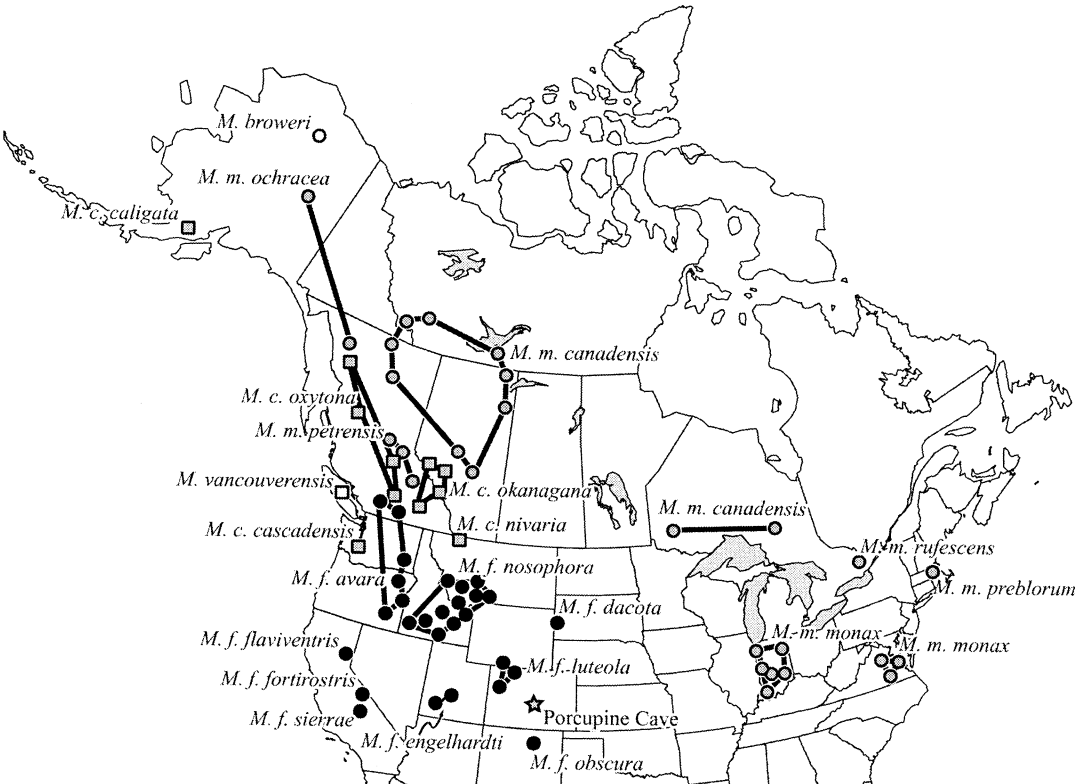

FIG. 2.—Location of samples used in this study (Appendix II). *Marmota broweri* samples are indicated with an open circle, *M. caligata* with gray squares, *M. flaviventris* with black circles, *M. monax* with gray circles, and *M. vancouverensis* with an open square. Where several localities were combined to create a single sample, they are connected with a heavy black line. The middle Pleistocene Porcupine Cave locality is symbolized with a star.

out-groups (Kruckenhauser et al. 1999; Steppan et al. 1999).

The 4th eigenshape analysis was used to study within- and between-sample variations. The data were the same as in the 3rd analysis, with the addition of samples from the remaining Porcupine Cave Pit levels (2, 3, 5, 6, and 7; total n = 89). All individuals were included rather than sample means. Distances between samples were calculated as the mean of pairwise distances between individuals in 2 samples:

$$d_{xy} = \frac{1}{n_x n_y} \sum_{i=1}^{n_y} \sum_{j=1}^{n_y} d_{ij}, \qquad (1)$$

where d_{xy} was the mean distance between samples x and y and d_{ij} was the Euclidean distance between specimen i in sample x and specimen j in sample y (Tajima 1983; Wakeley 1996a, 1996b). The distance d_{xy} is the same as the Euclidean distance between the multivariate mean of sample x and sample y. Variation within samples was calculated as the mean of pairwise distances between individuals in a sample:

$$d_x = \frac{2}{n(n-1)} \sum_{i=1}^{n-1} \sum_{i'=i+1}^{n} d_{ii'}, \qquad (2)$$

where $d_{ii'}$ was the multidimensional Euclidean distance between specimen i and i + 1 in sample x. This distance is analogous, but not equal, to the sample standard deviation; d_x is larger than the standard deviation. Evolutionary change in shape between Porcupine Cave Pit levels was

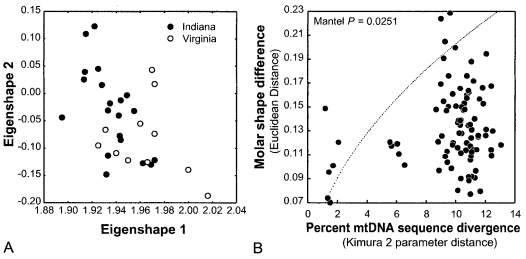

FIG. 3.—Relationship between molar shape and both population differentiation and phylogenetic divergence. A) An eigenshape plot of molar shape in 2 populations of *Marmota monax monax*, from Indiana and northern Virginia. B) Correlation between molar-shape divergence and mitochondrial cytochrome-*b* divergence. The curve is a 50% confidence envelope for the expected relationship based on a random-walk time-series model.

expressed as the ratio of d_{xy}/d_x or the proportion of mean differences between individuals in the 2 levels to the mean difference within a level.

RESULTS AND DISCUSSION

Molar shape as a phylogenetic proxy.—Paleontologists use molars to diagnose fossil mammalian species because of the morphological complexity of molars and because isolated teeth are the most common type of fossil specimen. In many cases, molar size alone may be enough to discriminate between closely related sympatric species (Gingerich 1974, 1979; Kurtén 1953), although size evolves quickly enough that relationships are rapidly obscured by homoplasy. In this study, shape also discriminated among closely related populations (as well as between species). In *M. m. monax* from Indiana and Virginia, m3 allowed 100% of individuals to be assigned correctly to their group, although the samples overlapped on each eigenshape axis (Fig. 3A). Divergence between geographically distinct populations of the same subspecies, although measurable, was small relative to the variation within populations. Because of this, it may be impossible to estimate the mean shapes of very small samples with enough precision to accurately assess distances between them. Smaller sample sizes are adequate when differences are large (i.e., when populations are distantly related), but larger samples are required when differences are small (i.e., when populations are closely related). No samples with $n < 5$ were considered for studying intraspecific relationships, and $n > 10$ was preferred (Appendix II).

Molar-shape distance was positively related to *Cytb* divergence (Fig. 3B) and had a significant matrix correlation ($P = 0.0251$). The distribution of m3 distances relative to *Cytb* divergence matched expectation under a random-walk time-series model. Most observations fell within the 50% confidence envelope, and all observations fell within a 95% envelope (not shown). It is unlikely that m3 evolution is random in the sense of neutral drift because there is likely to be active selection in relation to occlusion, diet, and other factors; however, the overall pattern appeared random over time and across lineages, a result that would be expected if the magnitude and direction of selection varied stochastically. Thus, shape distances scale in proportion to phylogenetic divergence and are distributed as assumed by maximum-likelihood tree algorithms.

Porcupine Cave marmots and living marmots.—How are the Pleistocene marmots from Porcupine Cave related to living North American marmots? The maximum-likelihood tree based on m3 grouped them comfortably within *M. monax*, rather than within *M. flaviventris* whose current range they inhabited (Fig. 4A).

The tree grouped living marmots roughly as expected given our current knowledge of marmot phylogeny. All *M. monax* samples formed a single clade, and *M. flaviventris* plus *M. caligata* plus *M. vancouverensis* formed a 2nd clade. This arrangement agreed with mtDNA findings, which grouped *M. monax* plus Eurasian species into subgenus *Marmota* and *M. flaviventris* plus *M. caligata* plus *M. vancouverensis* together into subgenus *Petromarmota*

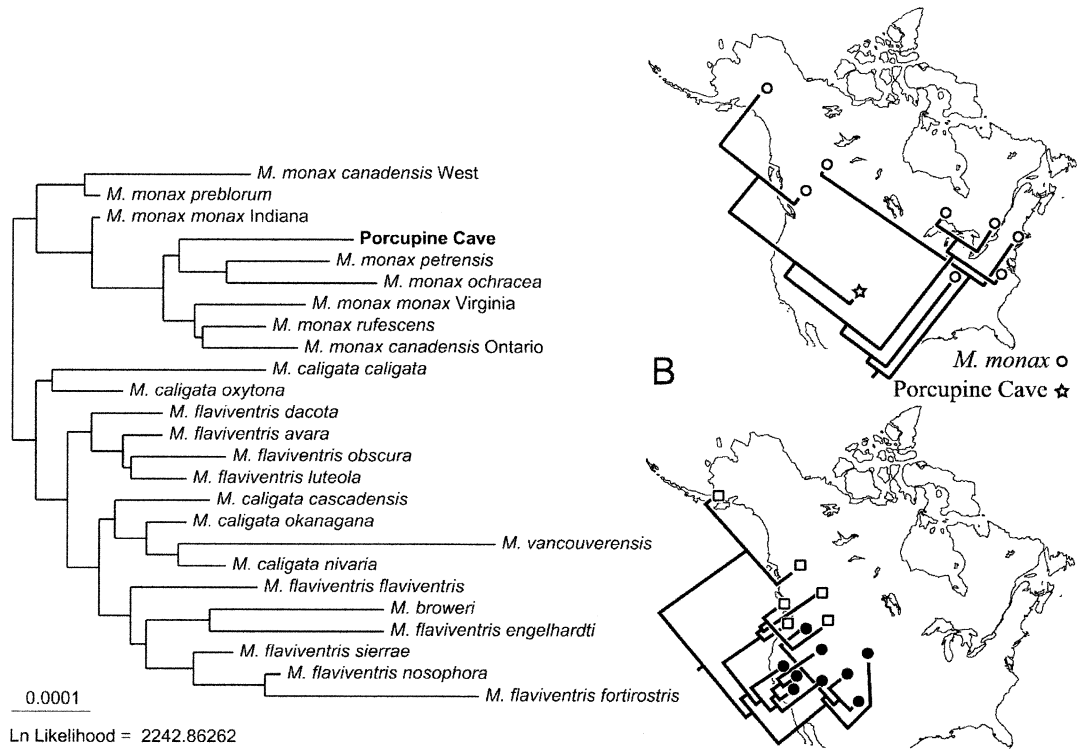

FIG. 4.—A) Maximum-likelihood tree based on m3 shape. The Porcupine Cave marmots fall within the *Marmota monax* group, well away from *M. flaviventris*, which occupies the Porcupine Cave area today. B) Phylogeographic map of *M. monax* based on the tree in A. C) Phylogeographic map of *M. caligata*, *M. flaviventris*, and *M. vancouverensis*.

(Kruckenhauser et al. 1999; Steppan et al. 1999). The m3 grouping was also consistent with karyotypic evidence: *M. monax* has a 2n = 38, whereas *M. flaviventris*, *M. caligata*, and *M. vancouverensis* all have 2n = 42 (Hoffmann and Nadler 1968; Rausch and Rausch 1971).

Samples of *M. flaviventris* and *M. caligata* were intermingled, with each species divided into 2 clades separated by 1 clade of the other species. It was not clear whether this reflects true phylogenetic relationships or whether m3 shape lacked the precision necessary to resolve relationships at this level. The sole molecular study applicable to relationships within *M. flaviventris* and *M. caligata* was consistent with the results found here: Steppan et al. (1999) found that *M. f. luteola* and *M. f. obscura* formed a clade that shared a common ancestor with one containing *M. c. caligata* and *M. vancouverensis*. The position of *M. vancouverensis* in the m3 tree was consistent with previous molecular and morphological studies, which placed it as a sister taxon to *M. caligata* (Hoffmann et al. 1979; Kruckenhauser et al. 1999; Steppan et al. 1999). *M. vancouverensis* is thought to be an isolated relict population in whose past such populations may have operated (Hoffmann et al. 1979; Nagorsen 1987). Interestingly, the branch leading to *M. vancouverensis* was long, suggesting that its molar shape is more divergent than other samples.

Such a situation could be caused by population bottlenecks or founder effects and deserves further study.

The only overtly controversial grouping in the m3 tree was the placement of *M. broweri* within *M. flaviventris*. mtDNA suggests that *M. broweri* is most closely related to *M. caudata* and *M. menzbieri* from Asia (Steppan et al. 1999). Even that finding was controversial, however. Morphological data have linked *M. broweri* to *M. camtschatica* from Siberia (Hoffmann et al. 1979); chromosomal, ecological, and behavioral data have linked *broweri* with *M. caligata* (Rausch and Rausch 1971). No previous studies have linked *broweri* to *M. flaviventris* broadly, much less directly, to the geographically remote subspecies *M. f. engelhardti*. If *M. broweri* is truly most closely related to *caudata* and *menzbieri*, then its closest relatives were not included in this study and *broweri* may be floating anomalously due to long-branch attraction.

The question of *broweri* aside, most points of comparison suggested that m3 shape does a reasonable job of reconstructing phylogenetic relationships, lending weight to the finding that Porcupine Cave marmots are not closely related to *M. flaviventris*. Although the possibility of long-branch attraction could not be discounted in explaining the position of Porcupine Cave marmots within *M. monax*, the tree quite clearly indicated that they do not lie within *M. flaviventris*. The exclusion of Porcupine Cave marmots from *M. flaviventris* was also supported by qualitative assessment of molar morphology: the mesial margin of the crown in *M. flaviventris* is curved distally just buccal to the parametaconid (adjacent to the margin of m2), whereas the curve is less pronounced in both *M. monax* and the Porcupine Cave marmots, and on the buccal side of the crown the hypoconid lobe is relatively larger than the protoconid lobe in Porcupine Cave marmots compared with *M. flaviventris*. These features combine to give the m3 of Porcupine Cave marmots a heart-shaped appearance, whereas the m3 outline of *M. flaviventris* is more irregular. *M. monax* has m3s that are similar in these respects to Porcupine Cave marmots.

The phylogenetic tree and the stratigraphic placement of the Porcupine Cave fossils suggest a phylogeographic scenario for North American marmots (Figs. 4B and 4C). *Marmota* probably originated in what is now the basin-and-range country of the North American west. The earliest incontrovertible fossils are *M. minor* from the late Miocene Hemphillian deposits (about 8.0 million years ago) at Thousand Creek, Nevada (Black 1963; Kellogg 1910; Webb 1984), and the closest living relatives of *Marmota* are western North American ground squirrels (Steppan et al. 1999; Thomas and Martin 1993). Previous to the late Miocene, the midcontinental region now inhabited by *M. monax* would have been drier and more seasonal, whereas the west would have had proportionally more broad-leaved deciduous forests (Potts and Behrensmeyer 1992). As the Sierra Nevada and Cascade ranges rose, the west became increasingly arid, forcing the broad-leaved forests out and leaving conifer forests in the comparatively moist uplands. If the habitats of extant marmots (Barash 1989; Frase and Hoffmann 1980; Kwiecinski 1998) are extrapolated into this paleoecological reconstruction, it seems likely that marmots initially occupied the cool, moist habitats of the west but were pushed either eastward into the plains or upward to higher elevations as the climate changed. A late Miocene timing is consistent with the deep separation between eastern lowland *M. monax* from the western highland dwelling North American species found by mtDNA studies. Porcupine Cave marmots lived several million years after this split. Fossil marmots attributed to *M. monax* are found in eastern areas for the 1st time during the Irvingtonian (Kurtén and Anderson 1980). Most records of *Marmota*, east of the plains, postdate Porcupine Cave, but at least 1, the Cheetah Room of Hamilton Cave in West Virginia, is thought to be roughly contem-

porary at 740,000–850,000 years old (Repenning and Grady 1988).

Subsequent glacial–interglacial cycles would have added to the complexity of marmot phylogeography. During the 10 or more glacial–interglacial cycles in North America, ice advanced and retreated over large sections, extending as far south as northern Missouri at its peak (Flint 1971; Richmond 1986). The separation of *M. monax* into eastern and western subclades (Fig. 4B) may have been facilitated by periodic isolation into eastern and western groups by the southern tip of the Laurentide ice sheet. Further to the west, Cordilleran ice extended south to present-day Washington, with glacial caps on more southern mountains and isolated refugia along the coast and in Beringia (Conroy et al. 1999; Heaton 1995; Hoffmann 1981). The phylogeographic pattern of *M. caligata* was consistent with periodic isolation in refugia, and the pattern of *M. flaviventris* suggests southern and coastal isolation coupled with postglacial colonization from the coast and southern refugia (Fig. 4C).

Change through the Porcupine Cave sequence.—The marmot-bearing strata of the Pit locality in Porcupine Cave record a climatic cycle that began with a warm and dry interval, became cooler and more humid, and finally changed back to warm and arid, probably recording a shift from interstadial to glacial and back to interglacial (Wood and Barnosky 1994; Fig. 5). The precise age and duration of the strata are difficult to ascertain, but levels 4 and 5 are probably 750,000–850,000 years old (Bell and Barnosky 2000). If so and if no cycles are missing from the section, then the glacial–interglacial sequence probably coincides with the transition from oxygen-isotope stage 22 to 21, stage 20 to 19, or stage 18 to 17 and the duration of the sequence was probably >60,000 years (Bell and Barnosky 2000; Harland et al. 1989).

Molar-shape change between adjacent levels was on the order of 1 d_x unit, meaning that the differences between levels were about the same as the average distance between individuals within each level. This order of magnitude difference was greater than would be expected by chance. There was little correlation between m3 change and climatic shifts (Fig. 5). The greatest change (1.08d_x units) was between levels 6 and 5, the transition between the warm dry period and the humid glacial period. The smallest change (0.96d_x units) was between levels 3 and 2. Barnosky et al. (in press) reported a similar lack of trend in univariate size measurements of the dentition of the Porcupine Cave marmots; however, the magnitude of change in tooth size between

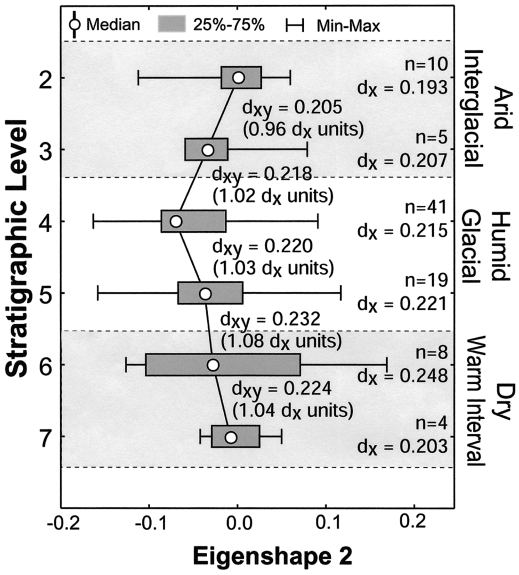

FIG. 5.—Molar-shape change through the middle Pleistocene Pit locality of Porcupine Cave. Eigenshape 2 values are graphed to convey a rough idea of the amount of shape change at each level relative to the variation at that level (the 2nd component usually summarizes the greatest percentage of variance among shapes in eigenshape analysis). The 2nd eigenshape only summarizes 1 dimension of a multidimensional shape space, so mean multidimensional distances between levels (d_{xy}) and mean multidimensional pairwise distances within each level (d_x) are also reported. There is no obvious pattern of molar-shape change relative to glacial–interglacial transitions.

levels was smaller than tooth shape on the order of 0.3 *SD*.

How does the scale of change through the Porcupine Cave section compare with differences between geographically distinct subspecies of marmot? This is a concern for paleontologists because what appears to be evolutionary change through a stratigraphic sequence may be an illusion created by geographical shifts among allopatric populations (Lillegraven et al. 1981; McKenna et al. 1977). Change through the Pit sequence is unlikely to be a range-shift artifact because the differences between levels are smaller than average geographic differences between living populations and subspecies. Mean d_{xy} in molar shape between Porcupine Cave levels was 0.216, lower than the mean d_{xy} between subspecies (or populations) of *M. caligata* (Fig. 6A), *M. flaviventris* (Fig. 6B), or *M. marmota* (Fig. 6C). Among living marmots, within-species differentiation was smallest in *M. caligata* (mean d_{xy} = 0.229), and the differences among Pit levels were smaller than those among subspecies of *M. caligata*, although not dramatically so. Pit level differences were substantially smaller than differences among *M. flaviventris*. Interestingly, even the smallest between-population differences in *M. monax* were larger than the largest change between Porcupine Cave levels. Pit changes were significantly less than between-species differences (Fig. 6D), although the smallest between-species differences overlapped the largest between-level changes. On balance, the best interpretation was that the Porcupine Cave sequence records in situ evolution. If geographic range shifts played a role, they were shifts among minimally divergent populations.

Geographic differentiation, gene flow, and history.—Shape change through the Pit sequence can be used to judge the timescale of divergences among extant *Marmota*. The expectation for change through a single glacial–interglacial sequence was d_{xy} = 0.216, assuming that rates measured in the Pit are representative. Differences in *M. caligata* were only slightly greater than this (d_{xy} = 0.235), whereas those in *M. flaviventris* were substantially larger (d_{xy} = 0.241) and those in *M. monax* greater still (d_{xy} = 0.255). This suggested that the differentiation of *M. caligata* could have happened over roughly the same time span as a long glacial–interglacial cycle, but the differentiation of *M. flaviventris* and *M. monax* must have occurred over several cycles.

Not only was m3 shape differentiation in *M. monax* greater than in the other species but also its phylogeographic pattern was more interwoven (Fig. 4). The level of differentiation in *M. monax* is surprising because the mountainous basin-and-range habitat occupied by *M. caligata* and *M. flaviventris* is usually thought to be more amenable to population subdivision and isolation than is the flatter region inhabited by *M. monax*. Subspecies of *M. monax* lie in broad belts that should favor long-distance gene flow, *M. m. monax* running across half the continent in the southern part of the species range, *M. m. rufescens* in an even longer belt just south of the Canadian border, and *M. m. canadensis* running for thousands of miles across most of Canada; subspecies of *M. flaviventris*, on the other hand, have a patchy distribution that should favor local isolation (Frase and Hoffmann 1980; Hall 1981; Kwiecinski 1998). Why then are the subspecies of *M. flaviventris* and *M. caligata* more morphologically homogenous than *M. monax*? The answer must be historical, with the species having different times of origin or different responses to Pleistocene history.

The data analyzed in this study establish that the last common ancestor of *M. monax* taxa lived more than 750,000 years ago, and they suggest that the last common ancestors of *M. caligata* taxa and *M. flaviventris* taxa lived more recently. The differentiation of *M. monax* almost certainly occurred over many glacial cycles, whereas those of *M. caligata* and *M. flaviventris* may have been over 1 or 2 cycles. If *M. monax* subspecies were the result of a single episode of post-

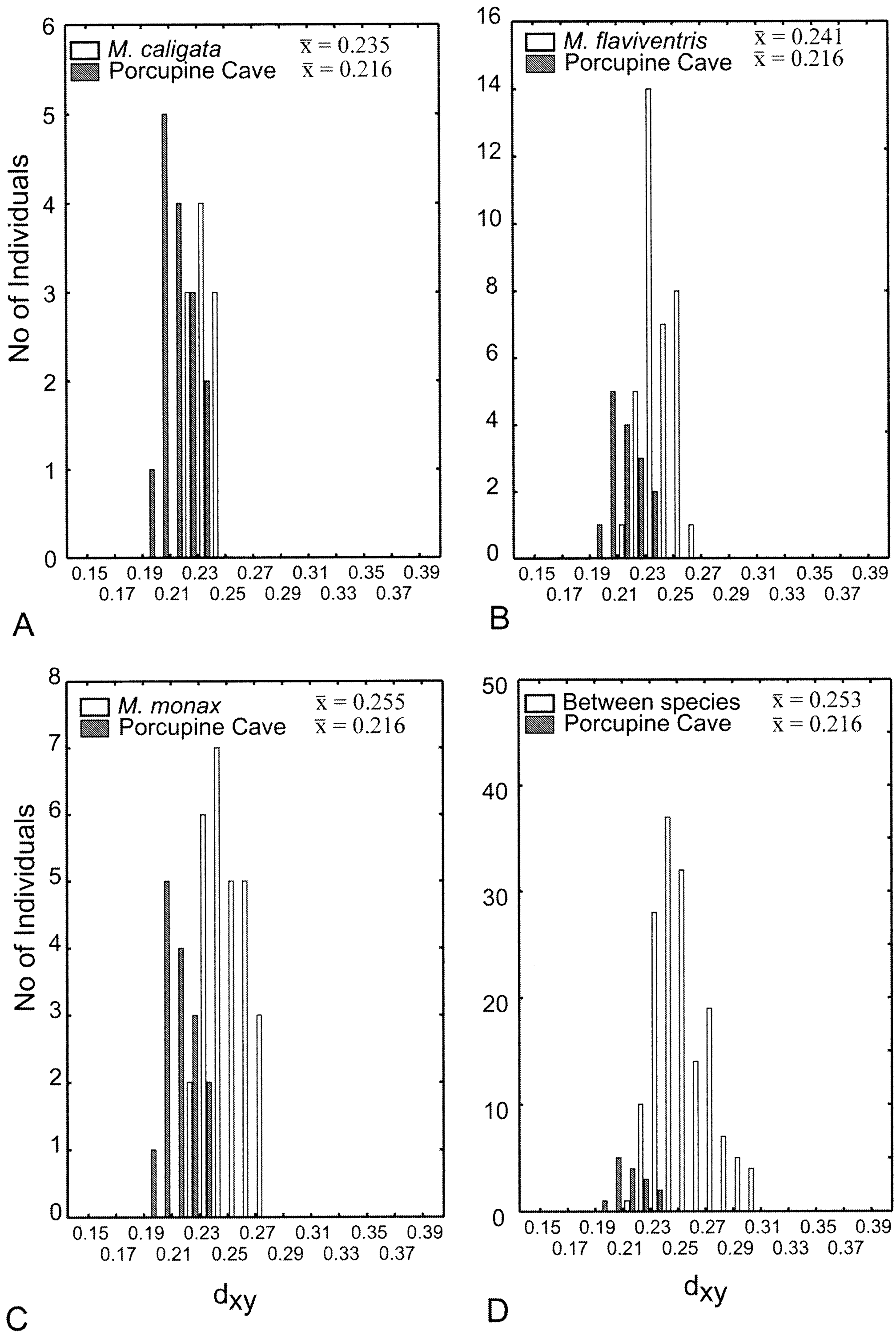

FIG. 6.—Comparison of between-level changes in Porcupine Cave with between-population divergences in extant marmots. Between-level changes compared with subspecific divergences in A)

glacial expansion in the last 20,000 years, they would be expected to be more homogenous than they are. When a species rapidly expands from a relatively small geographic center, it is expected to have increasingly lower genetic diversity—and by extension morphological diversity—along the margin of expansion (Hewitt 1999, 2000; Ibrahim et al. 1995). The diversity of molar morphology in *M. monax* is not consistent with such a pattern. Geographic fragmentation and morphological differentiation may have been higher in *M. monax* during glacial periods than today. Today the species inhabits widespread coniferous and deciduous forest biomes of Canada and the eastern United States, but faunal provinciality was greater during glacial periods (Graham et al. 1996; Martin and Hoffmann 1987). The current geographic continuity of *M. monax* subspecies may be recent, and differences built up during glacial isolation may still be moving toward genetic equilibrium. The situation in *M. caligata* and *M. flaviventris* is the opposite. The low level of differentiation and the geographic proximity of taxa on the tree suggest that they may have radiated rapidly in the recent past. Although their ranges are geographically fragmented today, they would have been less so at the height of glaciation, having been spread more continuously over what are now desert valleys, many of which contained rivers and large lakes (Potts and Behrensmeyer 1992). Population continuity and gene flow may have been highest during glacial cycles. The last glaciation may have homogenized variation in *M. caligata* and *M. flaviventris* over much of their range, although some differentiation may have been heightened by isolation in northern or southern refugia (Conroy et al. 1999; Heaton 1995). The possibility exists, then, that all 3 species have a roughly contemporary origin but that climatic history and geography have conspired to reduce variation in *M. caligata* and *M. flaviventris* but not in *M. monax*.

The possibility that all marmots may have endured many cycles of isolation and differentiation followed by increased contact and homogenizing gene flow is supported by the observation that within-population variation is high ($d_x = 0.238$) relative to between-population differences ($d_{xy} = 0.261$). In some marmot samples the within variation is greater than that between them. One mechanism for building up and maintaining such high variance is isolation, which fosters between-population divergence, with intermittent migration and gene flow, which spreads the isolation-induced diversity across populations (Avise 2000; Slatkin 1987; Wakeley 1996a, 1996b). Because marmots commonly migrate long distances when they disperse from the nest (Armitage 1974, 1984; Barash 1989), this seems worth considering.

Conclusions

The data considered in this study showed that high-altitude sites in Colorado were home to the ancestors of *M. monax* 750,000 years ago, and expansion of *M. flaviventris* into Colorado may be more recent. The origin of North American marmot species probably took place in geographic areas different from the ones they inhabit today. The data presented in this study also showed that at least some of the divergence within *M. monax* happened more than 750,000 years ago and cannot be explained by a single episode of postglacial recolonization. Phylogenetically, Porcupine Cave Pit marmots were placed within *M. monax* popu-

←

Marmota caligata, B) *M. flaviventris*, and C) *M. monax*. D) Between-level changes compared with between species differences in living marmots. Histograms show number of observations (and percentage of total) on the *y*-axis and multidimensional between-sample distances (d_{xy}) on the *x*-axis. (Note differences in scale of *y*-axes.)

lations, indicating an older divergence for these populations, and the m3 shape differences among living populations were substantially greater than those that accumulated through a single glacial cycle. *M. flaviventris* and *M. caligata* populations appeared to have diverged over much less time either because these species originated later or because their genetic diversity was homogenized during the last glacial cycle. Finally, the m3 shape evolution through Pit strata appears to genuinely be in situ evolution rather than an artifact of geographic range shifts because the differences between layers are much smaller than would be expected between contemporary geographic variants.

Paleontological data have much to offer the study of phylogeographic patterns. Fossils are the only positive evidence that animals (or plants) inhabited a particular area at a particular time, and they are the most direct evidence for studying the temporal pattern of change. However, the precision required for phylogeographic analysis, which considers differentiation among closely related populations and species, presents a challenge. Traditional discrete-character phylogenetics performs at too coarse a scale because traits are ''discrete'' only when relatively distantly related taxa are compared. Size traits have been used effectively at the population level in paleontology, but the rate of evolution and the simplicity of the trait make convergence (or homoplasy) an issue when broad geographic or temporal scales are considered. Molar shape is a complex quantitative trait that holds considerable promise as a metric for paleophylogeography. The evidence presented in this study and elsewhere (Polly 2001) suggests that within-species differences are statistically detectable using molar shape and that the rate of evolutionary change is constant enough that between-population distances are a reasonable proxy for phylogenetic divergence when times of separation are between a few thousand and a few million years. I do not pretend that molar shape is as versatile or precise a tool as DNA sequence analysis, but it may provide a mechanism for bringing paleontological and neontological analyses onto similar temporal and geographic scales. The addition of genuinely historical data on place and time is worth some loss in precision. Considerable opportunity exists for testing molecule-based hypotheses and generating new hypotheses that can be tested with sequence data.

The practice of paleophylogeography requires a minor paradigm shift for paleontological systematics. The basic units of paleophylogeographic analysis must necessarily be temporally and geographically restricted samples, similar to those used in stratophenetics (Gingerich 1976, 1979), stratocladistics (Fisher 1991, 1994; Polly 1997), or likelihood approaches (Huelsenbeck and Rannala 2000). Links between phylogeographic units, across time and space, are made by way of phylogenetic analysis rather than geographic proximity. This, in particular, puts paleontological analyses of migration and geographic range shifts on a strong footing. It also strengthens hypotheses about the geographic history of living populations. Alpha taxonomy, the identification and classification of individual specimens, must necessarily come after phylogenetic analysis rather than before. Traditional cladistic analysis proceeds 1st with alpha taxonomy, followed by phylogenetic analysis (Smith 1994). The use of particular quantitative morphological traits (or discrete characters, for that matter) should be tested against other data (such as molecular sequence divergence or temporal ordering) to determine whether they are appropriate for the temporal and taxonomic scales of the analysis. Just as with different genes, different morphological traits are likely to evolve at different rates: rapidly evolving traits will be useful for studying shallow divergences, whereas slowly evolving traits will be useful for deep divergences. Also, like genetic data, the likelihood that convergence (or homoplasy) in mor-

phological traits will obscure relationships increases as a function of time since divergence, particularly with quantitative data (Berg 1993; Gingerich 1993; Polly 2001; Schluter et al. 1997). A paleophylogeographic study must take care not to work beyond the ''saturation point'' of its morphological metric. In this phylogeographic context, geographic, stratigraphic, and biological data can be freely mixed, with potentially productive results.

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Special Feature Editor was D. M. Leslie, Jr.

Appendix I

Marmot samples used to compare molar-shape distance with mitochondrial cytochrome-*b* (*Cytb*) divergence. Localities of the *Cytb* and morphological samples are reported along with the sample size (*n*) of the latter.

Taxon	*Cytb* sample	Molar-shape sample	*n*
M. baibacina kastschnkoi	Russia, Novosibirsk	Russia, Tchegan-Burgazi Pass, and Mongolia, Khovd River	3
M. broweri	Alaska, Anaktuvuk Pass	Alaska, Anaktuvuk Pass	6
M. caligata caligata	Alaska, Fairbanks	Alaska, Becharof Lake	13
M. caudata caudata	Pakistan, Khunjerab Pass	Kashmir and NE Pakistan	22
M. caudata aurea	Kazakhstan, Dzhambul	Pamir, Tagdumbash	7
M. flaviventris luteola	Colorado, Gunnison County	Colorado, Garfield, Grand, and Rio Blanco counties	15
M. flaviventris obscura	New Mexico, Taos County	New Mexico, Taos County	5
M. himalayana robusta	China, Qinghai Province	W China, including Qinghai Province	17
M. marmota marmota	Switzerland, Canton Grisons	Switzerland, Canton Grabunden	8
M. monax ochracea	Yukon, Ethel Lake	Alaska and British Columbia	5
M. monax rufescens	New York, Tompkins County	S Ontario	15
M. monax monax	North Carolina	Virginia, northern counties	11
M. sibirica caliginosus	Russia, Gusinoe Lake	Mongolia, Ulan Bataar	15
M. vancouverensis	British Columbia, Vancouver Island	British Columbia, Vancouver Island	9
Total			151

Appendix II

Marmot samples used in the phylogeographic analysis of North American taxa. Most samples included marmots from a single geographic locality, but a few included several localities that were close to one another. All localities are plotted in Fig. 2.

Taxon	Locality	*n*
M. broweri	Alaska	5
M. caligata caligata	Alaska	13
M. caligata cascadensis	Washington	6
M. caligata nivaria	Montana	11
M. caligata okanagana	British Columbia and Alberta	17
M. caligata oxytona	British Columbia and Alberta	9
M. flaviventris avara	Oregon, Washington, and British Columbia	18
M. flaviventris dacota	South Dakota	11
M. flaviventris engelhardti	Utah	11
M. flaviventris flaviventris	California	5
M. flaviventris fortirostris	California	6
M. flaviventris luteola	Colorado	15
M. flaviventris nosophora	Montana	25
M. flaviventris obscura	New Mexico	5
M. flaviventris sierrae	California	16
M. monax canadensis	Alberta, British Columbia and Northwest Territones	10
M. monax canadensis	Ontario	25
M. monax monax	Indiana	20
M. monax monax	Virginia	11
M. monax ochracea	Alaska and British Columbia	5
M. monax petrensis	British Columbia	11
M. monax preblorum	Massachusetts	13
M. monax rufescens	Ontario	15
M. vancouverensis	Vancouver Island, British Columbia	9
Porcupine Cave (level 4)	Colorado	41
Total		333