

PHYLOGENETIC AND ENVIRONMENTAL COMPONENTS OF MORPHOLOGICAL VARIATION: SKULL, MANDIBLE, AND MOLAR SHAPE IN MARMOTS (*MARMOTA*, RODENTIA)

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Abstract.—The phenotype is a product of its phylogenetic history and its recent adaptation to local environments, but the relative importance of the two factors is controversial. We assessed the effects of diet, habitat, elevation, temperature, precipitation, body size, and mtDNA genetic divergence on shape variation in skulls, mandibles, and molars, structures that differ in their genetic and functional control. We asked whether these structures have adapted to environment to the same extent and whether they retain the same amount of phylogenetic signal. We studied these traits in intra- and interspecific populations of Eurasian marmots whose last common ancestor lived 2–5 million years ago. Path Analysis revealed that body size explained 10% of variation in skulls, 7% in mandibles, and 15% in molars. Local vegetation explained 7% of variation in skulls, 11% in mandibles, and 12% in molars. Dietary category explained 25% of variation in skulls, 11% in mandibles, and 9% in molars. Cyt *b* mtDNA divergence (phylogeny) explained 15% of variation in skulls, 7% in mandibles, and 5% in molars. Despite the percentages of phylogenetic variance, maximum-likelihood trees based on molar and skull shape recovered most phylogenetic groupings correctly, but mandible shape did not. The good performance of molars and skulls was probably due to different factors. Skulls are genetically and functionally more complicated than teeth, and they had more mathematically independent components of variation (5–6 in skulls compared to 3 in molars). The high proportion of diet-related variance was not enough to mask the phylogenetic signal. Molars had fewer independent components, but they also have less ecophenotypic variation and evolve more slowly, giving each component a proportionally stronger phylogenetic signal. Molars require larger samples for each operational taxonomic unit than the other structures because the proportion of within-taxon to between-taxon variation was higher. Good phylogenetic signal in quantitative skeletal morphology is likely to be found only when the taxa have a common ancestry no older than hundreds of thousands or millions of years (1% to 10% mtDNA divergence)—under these conditions skulls and molars provide stronger signal than mandibles.

Key words.—Geometric morphometrics, *Marmota*, maximum-likelihood, morphology, phylogeny.

Received February 28, 2005. Accepted September 8, 2005.

The phenotype is the product both of phylogenetic history and recent adaptation to local environments, but the relative importance of the two factors in explaining morphometric variation is contested (MacLeod and Forey 2002). Some studies have concluded that morphology is an unreliable indicator of phylogenetic relationships because of capricious, adaptation-driven homoplasy (e.g., Graur et al. 1997; Collard and Wood 2001; Stone and Cook 2002) or because of lack of differentiation among genetically distinct populations (e.g., Barratt et al. 1997; Mayer and von Helversen 2001; Roca et al. 2004). But other studies have found significant phylogeographic structuring in morphometric data among closely related taxa (Thorpe 1976; Straney and Patton 1980; Hausser 1984; Malhotra and Thorpe 1997; Polly 2003a,b). Although not thoroughly assessed, the difference in results appears partly due to recency of common ancestry. In the latter studies, which displayed a significant phylogenetic signal, the taxa were populations of the same species or members of recently diverged species groups whose mtDNA sequence divergence was no more than 5–10%; however, in the earlier studies, in which little phylogenetic signal was apparent, the species divergences were much deeper. This suggests that morphological traits probably have a finite optimum range for phylogeny reconstruction. The recent end of the range will be constrained by the minimum time required for taxa to evolve measureable differences in population means; the deeper end will be constrained by the time required for sta-

bilizing or adaptive selection to erase deeper phylogenetic history through convergence. The principle is the same as in genes that evolve at different rates depending on their functional role; the range of phylogenetic usefulness of a particular gene is determined by the rate of mutation, the sequence length, and selection on nonsynonymous sites (Lemos et al. 2005). For morphological traits, the range will be influenced by the trait's adaptive response, which is a function of its genetic control and the strength of selection. Despite the long history of morphological analysis, there have been few comparisons of morphological traits in this context, partly because complicated structures have been difficult to quantify.

In this paper, we systematically compared the environmental and phylogenetic components of variance in three morphological structures—skulls, mandibles, and teeth—belonging to Eurasian marmots. These skeletal structures were chosen because they are common in the fossil record, where morphology remains crucial for phylogenetic reconstruction, and because their genetics, development, and function differ in ways that could influence their adaptive responses. Marmots were chosen because they have mtDNA sequence divergences that fall within the 5–10% range, and because previous studies found phylogenetic patterning in all three skeletal structures (Cardini 2003; Polly 2003a; Cardini and O'Higgins 2004). We specifically focused on quantitative, geometric morphometric representations of morphology because of current interest in such traits. We assessed the effects of diet, habitat, elevation, temperature, precipitation, body size, and mtDNA genetic divergence on variance among pop-

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