

The Geometry of the Marmot (Rodentia: Sciuridae) Mandible: Phylogeny and Patterns of Morphological Evolution

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Abstract.—Marmots have a prominent role in the study of mammalian social evolution, but only recently has their systematics received the attention it deserves if sociobiological studies are to be placed in a phylogenetic context. Sciurid morphology can be used as model to test the congruence between morphological change and phylogeny because sciurid skeletal characters are considered to be inclined to convergence. However, no morphological study involving all marmot species has ever been undertaken. Geometric morphometric techniques were applied in a comparative study of the marmot mandible. The adults of all 14 living marmot species were compared, and mean mandible shape were used to investigate morphological evolution in the genus *Marmota*. Three major trends were observed. First, the phylogenetic signal in the variation of landmark geometry, which describes mandible morphology, seems to account for the shape differences at intermediate taxonomic levels. The subgenera *Marmota* and *Petromarmota*, recently proposed on the basis of mitochondrial cytochrome *b* sequence, receive support from mandible morphology. When other sciurid genera were included in the analysis, the monophyly of the genus *Marmota* and that of the tribe Marmotini (i.e., marmots, prairie dogs, and ground squirrels) was strengthened by the morphological data. Second, the marmotine mandible may have evolved as a mosaic of characters and does not show convergence determined by size similarities. Third, allopatric speciation in peripheral isolates may have acted as a powerful force for modeling shape. This hypothesis is strongly supported by the peculiar mandible of *M. vancouverensis* and, to a lesser degree, by that of *M. olympus*, both thought to have originated as isolated populations in Pleistocene ice-free refugia. [Geometric morphometrics; mandible; *Marmota*; morphological evolution; phylogeny; sciurid convergence.]

Marmots are large Holarctic rodents (Figs. 1, 2) with marked adaptations for living in cold climates (Barash, 1989; Armitage, 2000). Hibernation, size increase, suppression of reproduction, and sociality are among the evolutionary responses to the selective pressures of harsh environments (Barash, 1974; Armitage, 1981, 2000) such as those of the periglacial zone in which marmots are believed to have evolved (Zimina and Gerasimov, 1973, cited by Armitage, 2000). The genus appeared in North America about 9.5 million years ago and crossed the Bering Strait to colonize Eurasia at the end of the Pliocene or the beginning of the Pleistocene (Mein, 1992; Steppan et al., 1999). The increasing abundance and diversification of the fossils during the Pleistocene witness the marmot radiation in the Palaeartic (Lyapunova et al., 1992; Mein, 1992; Armitage, 2000). However, the fossil record is often fragmentary and of uncertain attribution (Rumiantsev and Bibikov, 1994) and thus of little help in supporting hypotheses on the vagaries of marmot evolution.

Despite a very large number of ecoethological studies on marmots and the centrality of this taxon for understanding the evolution of mammalian society, the phylogeny of the genus *Marmota* has been poorly studied. The lack of a reliable phylogeny may undermine any attempt to take into account the lack of independence in interspecific comparisons due to phylogenetic relationships (Felsenstein, 1985; Harvey and Pagel, 1991), thus preventing meaningful tests for hypotheses on the evolution of highly social behaviors (Blumstein and Armitage, 1998). Biogeographic questions of great interest for understanding the faunal interchange across the Bering Strait, such as the disputed geographic origins of the Alaskan marmot (*M. broweri*) and of the black-capped marmot (*M. camtschatica*), have remained unanswered.

Marmota broweri has been considered by different authors either as a recent offshoot of a Palaeartic lineage returned to the Nearctic (Gromov et al., 1965, cited by Steppan et al., 1999; Hoffmann and Nadler, 1968; Hoffmann et al., 1979) or as a subspecies of the North American *M. caligata* (Hall, 1981). *Marmota camtschatica* has been considered a possible member of the North American marmot group (Lyapunova et al., 1992), which became isolated from its Palaeartic relatives when Beringia was covered by the ocean.

Only recently have researchers tried to address many of the questions of marmot phylogeny using molecular techniques. Comparisons of cytochrome *b* (cyt *b*) sequences (Kruckenhauser et al., 1999; Steppan et al., 1999) have produced gene trees suggesting that there are two main marmot lineages in which complex societies have evolved independently. The subgenus *Petromarmota* includes western North American species (all Nearctic species except *M. monax* and *M. broweri*), and the subgenus *Marmota* is a large clade of Palaeartic marmots plus the two North American species, *M. monax* and *M. broweri*. This subgeneric classification has not yet been supported by the analysis of different sets of characters, and a large polytomy at the base of the predominantly Palaeartic clade has remained unresolved. Thus, the relationships among two Eurasiatic monophyletic groups, the Alpine marmot (*M. marmota*) and the two North American species belonging to the subgenus *Marmota*, are not fully understood. The basal position of the woodchuck (*M. monax*) in the subgenus *Marmota* is not surprising because it has the same chromosome number as the majority of Eurasiatic marmots ($2n = 38$), but the emergence of the Alaskan marmot at the root of this clade was completely unexpected. The Alpine marmot seems to be an ancient lineage, close to the ancestor of the



FIGURE 1. Young Alpine marmots (*Marmota marmota*) chewing flowers (top) and biting each other during play (bottom). (Photos by L. Gaudenzio.)

Palaeartic clade, which may help explain some unusual features of this species. All the Eurasiatic species except the Alpine marmot are parasitized by the flea *Oropsylla silantiewi* and are characterized by soft and fine black-tipped guard hairs. *Marmota marmota* also does not have a low-frequency alarm call component, which is present in all the other Palaeartic marmots (Rumiantsev and Bibikov, 1994). The peculiarities of the Alpine marmot, which are partially shared by North American marmots, might represent symplesiomorphies of the ancestor of all living marmots.

Morphometrics is becoming an increasingly important counterpart of molecular phylogenetics. The presumed propensity of the sciurid skeleton for convergence induced by ecological or size similarities (Hafner, 1984; Roth, 1996; Velhagen and Roth, 1997) has led scientists to apply the most modern morphometric techniques to study the correspondence between phenetics, based on quantitative osteological characters, and molecular cladistics (Swiderski, 1993; Swiderski and Jansa, 1998). The close agreement between molecular cladograms and phylogenetic hypotheses suggested by cranial characters for a group of terrestrial squirrels (Swiderski and Jansa,



FIGURE 2. Geographic distribution of the 14 *Marmota* species (modified from Barash, 1989).

1998) and the appearance of the sciurid scapula as a mix of distinct and integrated parts (Swiderski, 1993) have raised doubts about the hypothesis that the sciurid skeleton is a highly integrated structure, inclined to convergence (Roth, 1996).

However, despite several attempts to combine morphometric data with methods for phylogenetic inference, no consensus has been achieved among taxonomists about how this should be done, and splitting continuous morphometric data into meristic characters suitable for phylogenetic analysis is still considered problematic (various authors have addressed this issue; see MacLeod and Forey, 2002). Morphometrics is thus employed for the postcladistic morphological analysis of monophyletic groups (Smith, 1990) found in gene trees and for the analysis of patterns of morphological evolution.

Geometric morphometrics (Bookstein, 1991; Rohlf and Marcus, 1993; Corti et al., 2000; O'Higgins, 2000) allows comparisons of the geometric form of a structure as described by a set of topographically corresponding points (landmarks). This technique provides morphologists with a powerful tool for testing congruence between morphological and molecular data and for studying the ontogeny of organism shape (e.g., allometric growth) and the evolutionary forces modeling biological forms (e.g., size- or ecology-dependent homoplasies and the effects of genetic drift on the rate of morphological evolution). The application of geometric morphometric techniques to the study of the sciurid skeleton (Swiderski, 1993; Swiderski and Jansa, 1998) has produced results contrasting with those obtained with different analytical

methods (Hafner, 1984; Roth, 1996; Velhagen and Roth, 1997). Beyond methodological differences, the authors of these various studies have considered different characters (Velhagen and Roth (1997), analyzed the mandible; Swiderski (1993) compared the scapula) or have focused mainly on tree squirrels (Roth, 1996; Velhagen and Roth, 1997) rather than on terrestrial squirrels (Hafner, 1984; Swiderski and Jansa, 1998).

In spite of the recent interest in marmot phylogeny and the evolution of skeletal structures in the marmotines, a morphological study involving all marmot species has not been performed. A particularly suitable structure for comparing marmot form is the mandible. This bone is both simple and highly informative. The sciurid hemimandible is nearly flat and can be analyzed in two dimensions (Velhagen and Roth, 1997), but its trophic and possibly defensive function and its strict connection with the skull, which houses the brain and sense organs, make it a potential target for natural selection. For instance, changes in diet or in the agonistic interactions (sexual selection, defence from predators, etc.) may create selective pressures that contribute to shape the mandible (Thorington and Darrow, 1996; Cardini and Tongiorgi, in press). Body size increase to accumulate more resources for survival in harsh environments (Armitage, 1999) may imply morphological remodeling of the entire skeleton; functions could be lost if size changes happened without compensatory adjustments in shape (Emerson and Bramble, 1993). The rodent mandible has been the subject of several morphological and phylogenetic studies (Thorpe et al., 1982; Atchley et al., 1992; Corti et al., 1996; Velhagen and Roth, 1997; Swiderski et al., 1999; Astua de Morales et al., 2000; Duarte et al., 2000; Corti and Rohlf, 2001), with particular attention paid to the relationships between the mandible and the jaw muscles (Hiimae, 1971a, 1971b; Hiimae and Houston, 1971; Ball and Roth, 1995; Thorington and Darrow, 1996; Cardini and Tongiorgi, in press). The mandible ontogenesis and the genetic bases of its development also have been investigated (Atchley et al., 1992; Cheverud et al., 1997; Klingenberg and Leamy, 2001; Klingenberg et al., 2001).

Beyond the importance of marmots for sociobiologists and sciurid morphologists, the fur industry, and sanitation (control of plague foci), the recognition of marmot genetic and morphological peculiarities will allow detection of species uniqueness, helping conservationists to protect marmots. Marmot conservation is a hot issue for biologists trying to preserve biodiversity. The Vancouver Island marmot (*M. vancouverensis*) is threatened with extinction, surviving with a population of <50 individuals, and biologists are trying to breed some specimens in captivity for future reintroductions (Bryant, 1997). The Menzbier marmot (*M. menzbieri*) lives in small populations inhabiting a restricted area of the western Tian Shan, south of the Siberian steppe. Its biology and conservation status are poorly known, but it is considered among those vulnerable to extinction (Hoffmann et al., 1993). *Marmota caudata* and *M. himalayana* are in Appendix III of the Indian CITES.

We sought answers for the following questions. Are molecular and morphological data on marmots congruent? To answer this question, the main focus was on verifying whether the subgeneric classification of marmots is supported by the comparison of their mandibles; confirmation of the marmot subgenera would imply that the highest levels of sociality have independently evolved at least twice (Kruckenhauser et al., 1999). If morphological relationships among the studied species do not reflect their phylogeny, is the mandibular shape convergent because of size similarities? Does the mandible suggest any pattern of morphological evolution in the sciurids other than the presumed propensity for convergence of skeletal parts?

METHODS

Specimens, Dental Measurements, and Digital Images

The left hemimandibles of 518 marmots were photographed. Young animals and possible outliers were removed from the sample, and the analysis was performed on 388 adult marmots belonging to all living species (Table 1). Specimens were chosen when possible to represent the entire geographic range. Thirty-one specimens of other sciurid genera were included as an outgroup (Table 1). The list of the specimens, their museum catalog number and indication of the geographic origin (when available) is given in Appendix 1.

To estimate age classes using premolar wear (Appendix 2), the distances between the paraconid and protoconid cusps of the lower left premolar were measured with digital calipers to the nearest 0.1 mm. Precision was tested as described by Cardini and Tongiorgi (in press).

All images were captured on film using a single-lens reflex camera with a 180-mm APO MACRO lens, locked to a copy stand. The mandible was placed on a horizontal plane whose inclination could be adjusted. A spirit level was used to check that the lens and the specimen plane were parallel. The mandible rested on the lingual side of the horizontal ramus and the coronoid and condylar processes, and the labial side of each specimen was photographed. The height of the camera was adjusted to bring into focus the diastema region of each mandible to maintain a constant focal distance of 1 m from the camera to that region. Digital images were scanned directly from the 35-mm negative film as grayscale images at a resolution of 480 dpi with 210% magnification.

Geometric Morphometrics

Marmot mandibles were analyzed using geometric morphometric procedures (Bookstein, 1991; Rohlf and Marcus, 1993; Dryden and Mardia, 1998; Rohlf, 1998a) and the computer programs of the TPS series (Rohlf, 1998b–1998d, 1999) and the program Morphue et al. (Slice, 1999). Landmarks were defined and digitized on the specimen images to capture their form. A geometric morphometric analysis involves three main steps (Bookstein, 1996, 2000) after the landmark coordinates have been recorded.

TABLE 1. Marmot and related species examined.

Species	Taxonomic authority	Males	Females	Total ^a
Marmotini				
<i>Marmota</i>				
<i>M. baibacina</i>	(Kastschenko, 1899)	5	6	19
<i>M. bobak</i>	(Müller, 1776)	10	9	21
<i>M. broweri</i>	(Hall and Gillmore, 1934)	2	1	3
<i>Petromarmota caligata</i>	(Eschscholtz, 1829)	17	25	44
<i>M. camtschatica</i>	(Pallas, 1811)	10	9	20
<i>M. caudata</i>	(Geoffroy, 1844)	13	19	35
<i>P. flaviventris</i>	(Audubon and Bachman, 1841)	26	36	62
<i>M. himalayana</i>	(Hodgson, 1841)	15	11	33
<i>M. marmota</i>	(Linneus, 1758)	11	8	51
<i>M. menzbieri</i>	(Kashkarov, 1925)	3	3	7
<i>M. monax</i>	(Linneus, 1758)	19	25	55
<i>P. olympus</i>	(Merriam, 1898)	5	5	10
<i>M. sibirica</i>	(Radde, 1862)	11	7	20
<i>P. vancouverensis</i>	(Swarth, 1911)	4	4	8
Outgroup				
<i>Spermophilus</i>				
<i>S. beldingi</i>	(Merriam, 1888)	2	b	3
<i>S. citellus</i>	(Linneus, 1766)	3	3	6
<i>S. richardsoni</i>	(Sabine, 1822)	1	1	3
<i>S. undulatus</i>	(Pallas, 1778)	?	?	2 ^b
<i>Otospermophilus variegatus</i>	(Erleben, 1777)	2	2	2
<i>Cynomys</i>				
<i>Leucocrossuromys leucurus</i>	(Merriam, 1890)		1	1
<i>Cynomys ludovicianus</i>	(Ord, 1815)	1	?	5 ^b
Tamiini				
<i>Tamias</i>				
<i>Eutamias sibiricus</i>	(Laxmann, 1769)	1	?	2 ^b
<i>Tamias striatus</i>	(Linneus, 1758)	1	1	3
Sciurini				
<i>Sciurus vulgaris</i>	(Linneus, 1758)	1	3	4

^aIncluding specimens of unknown sex.

^bNo information on sex available.

Computation of shape coordinates (generalized Procrustes analysis).—The landmark configurations are translated so that their centroids (center of gravity) are placed in the same spot and rescaled to unit centroid size (a measure of the overall size computed as the square root of the sum of squared distances from the landmarks to the centroid of the landmarks). The configurations are then rotated so that the sum of squared distances among corresponding landmarks is a minimum. The square root of the sum of squared distances between the corresponding landmarks of the iteratively computed average (or consensus) configuration and that of a specimen is called the Procrustes chord distance to consensus (Rohlf and Slice, 1990).

Multivariate analysis.—The realigned landmark configurations are projected into a Euclidean space tangent to the shape space. The sample mean shape is chosen as the point of tangency to minimize the error in the projection onto the tangent space. After testing the closeness of the tangent space to the curved shape space by comparing the Procrustes distances in the shape space with the Euclidean distances in the tangent space (Rohlf,

1998d), the shape coordinates can be analyzed with multivariate statistical techniques (e.g., regressed onto the size or other variables or summarized with ordination methods).

Visualization.—The results of the analysis of the shape coordinates must be brought back into the picture plane where the landmarks have been collected (Bookstein, 2000). An especially effective tool for displaying morphological features by means of deformation grids (Thompson, 1917; Bookstein, 1991) is the thin-plate spline (TPS), which expresses a shape change as the smoothest possible deformation from a reference configuration of landmarks to a target configuration. Shape variables are computed as linear combinations of the original landmark coordinates, and they can be subdivided into a uniform component (shape changes that leave the grid lines parallel) and a set of partial warps (localized shape modifications). The TPS can illustrate and emphasize the shape differences among the specimens, and multivariate regressions or principal component analysis (relative warp analysis) of shape variables can be realized and their results visualized with deformation grids.

Mandible Landmarks

The following topographically corresponding (Marcus et al., 2000) and reliable landmarks (Cardini and Tongiorgi, in press) were chosen on the labial side of the left hemimandible (Fig. 3): 1) upper extreme anterior part of the incisor alveolus; 2) anterior top of the mandibular symphysis; 3) anterior extremity of the maxillary tooththrow (premolar alveolus); 4) intersection of the dental ridge with the dorsal portion of the masseteric ridge (base of the coronoid process); 5) tip of the coronoid process; 6 and 7) anterior and posterior tips of the condyle; 8) posterior extremity of the angular process; 9) mental foramen.

Statistical Analyses

Sexual dimorphism and the significance of mandible size and shape differences among species were tested

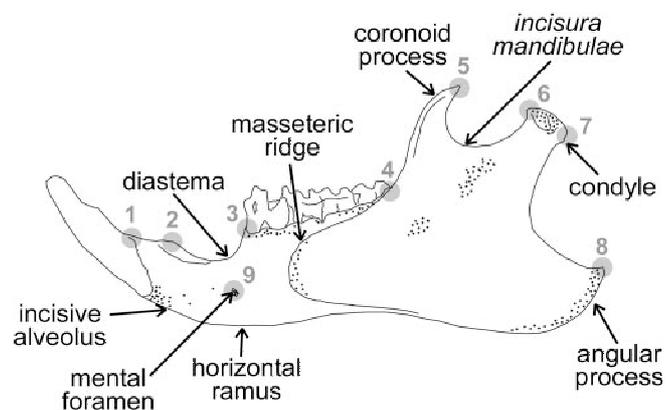


FIGURE 3. Marmot mandible anatomical regions and landmark configuration.

by means of two-way (sex \times species) analyses of variance for both centroid size (ANOVA) and shape variables (MANOVA). Canonical variate analysis (CVA) was also employed for testing shape differences between sexes and among species and for graphical illustrations of the MANOVA results. *Marmota broweri* was not included in analyses of differences with distinction between sexes because its very small sample of only two males and one female could lead to unstable results (e.g., the inclusion of *M. broweri* in the sex \times species MANOVA of shape variables resulted in *P* values for sex effect two orders of magnitude larger than those obtained without this species).

Univariate normality of the centroid size (CS) and shape variables was tested when the sample size was ≥ 10 . The Kolmogorov–Smirnov test led to *P* values always > 0.01 , but possible deviations from normality could be occasionally found in the histograms. Marcus (1990) remarked that the assumption of (multivariate) normality is especially difficult to test in taxonomy, where large samples are uncommon.

Heteroscedasticity was detected for CS in the sex \times species ANOVA (Levene's test: $F_{25,291} = 2.879$; $P = 1.1 \times 10^{-5}$). Variance-covariance matrices were not homogeneous ($\chi^2 = 1362.8$, $df = 945$, $P < 0.0001$; Box M = 1601.0, $F_{945,43978.6} = 1.344$, $P = 2.0 \times 10^{-11}$) as tested in a sample of species with $n > 14$ (the number of shape variables). This is another rather common problem in taxonomic comparisons. However, the ANOVA and the CVA are robust to violations of the assumption of homoscedasticity (Marcus, 1990; Hair et al., 1998). Furthermore, the analyses of size and shape variation one species at a time led to results consistent with those obtained for the entire sample.

The patterns of shape variation related to mandibular size were compared across species with a multivariate regression of the shape variables onto log-transformed CS (Rohlf et al., 1996). The CS was log-transformed because the allometric relationships in marmot mandibles are better described by a model that takes into account the progressive decrease of the rate of shape change during growth (Cardini and Tongiorgi, in press; Cardini and O'Higgins, unpubl.), and log-transformed CS led to a slightly larger proportion of shape variance explained by size variation. A test for common slopes was performed to assess whether the regression slope was the same for all the species or whether at least two groups differed in slope (Rohlf, 1998b).

Cluster analysis and ordination techniques were employed for reconstructing marmot mandible phenetic relationships. Both these procedures were applied to the matrix of Procrustes distances among the mean shapes of each species. The Procrustes distances express the morphological relationships among the species computed directly in the shape space and avoid the problem of using Mahalanobis distances when sample sizes are unequal and unlikely to reflect population structures. The cophenetic correlation coefficient (r_{cp}) was used to evaluate the efficiency of different clustering algorithms. The co-

TABLE 2. ANOVA of sex \times species for the mandible centroid size in *Marmota* (excluding *M. broweri*).

Effect	Sum of squares	df	<i>F</i>	<i>P</i>
Sex	28968.9	1	20.282	9.68×10^{-6}
Species	74090.6	12	51.872	0 ^a
Sex \times species	1462.8	12	1.024	0.426
Error	1428.3	291		

^a *P* values smaller than the minimum value that can be displayed by SPSS.

efficient r_{cp} measures the correlation between the original distance matrix and the cophenetic distance matrix, which mirrors the distances between all pair of species on the basis of the dendrogram topology (Rohlf, 1970, 1997; Fabbri, 1997). The UPGMA algorithm had the highest r_{cp} . Nonmetric multidimensional scaling (MDS) was applied to the mean shapes Procrustes distance matrix using the first three relative warps as the initial configuration (Rohlf, 1997; Hair et al., 1998). The MDS should preserve smaller interpoint distances better than does principal component analysis (Rohlf, 1997) and thus might help to elucidate relationships among the most similar species.

The computer programs SPSS 9.0.1 (1999, SPSS, Chicago, IL), Statistica 4.5 (1993, StatSoft, Tulsa, OK), NTSYS-pc 2.01d (Rohlf, 1997), and TpsRegr 1.20 (Rohlf, 1998b) were used for the statistical analyses.

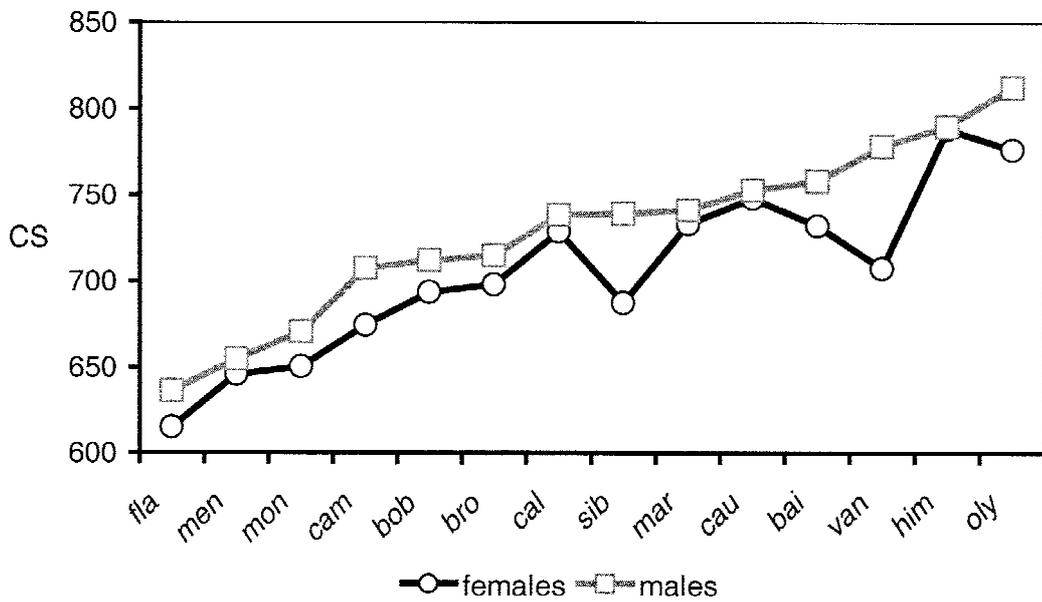
RESULTS

ANOVAs and CVA

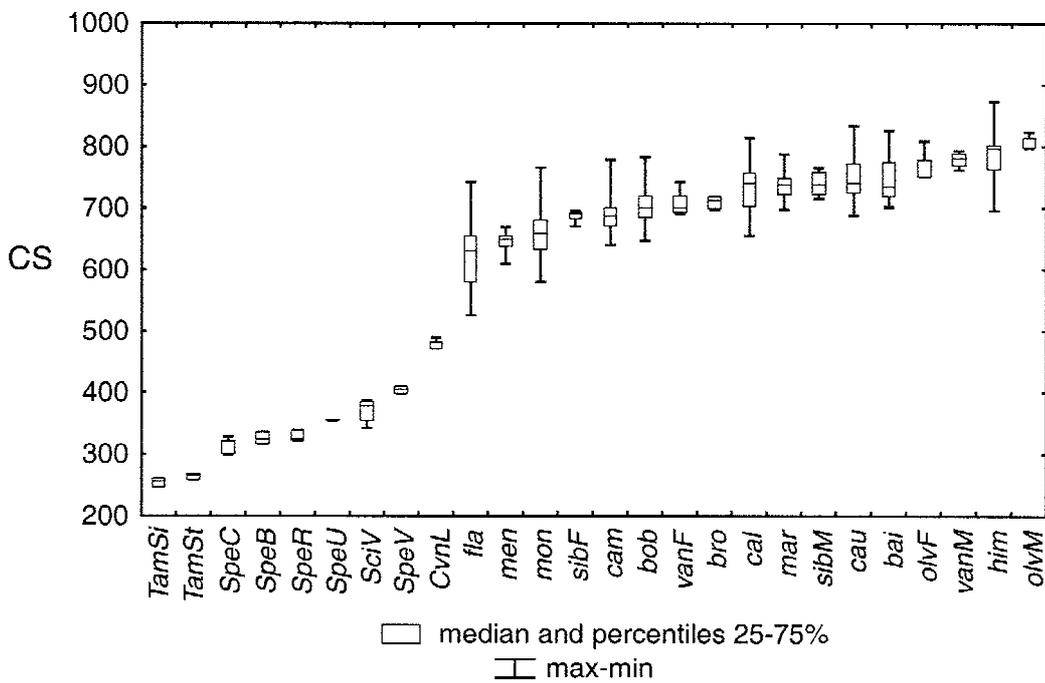
The linear tangent space closely approximates the shape space (TpsSmall 1.14; Rohlf, 1998d). The ANOVA sex \times species for the CS demonstrated that species differences are highly significant (Table 2), that male marmots are larger on average than females (Fig. 4a), and that interaction between sex and species is not appreciable. Sexual dimorphism of mandibular size was particularly remarkable in *M. olympus*, *M. sibirica*, and *M. vancouverensis* (Fig. 4a). In Figure 4b, the CS variation for each species, including the outgroup, is shown with a box-plot.

Either body mass at the beginning of hibernation or body length, as reported by Armitage (1999), were highly correlated with mandible size ($R^2 = 0.53$ in both the linear regressions), but body mass turned out to be a better predictor of mandible size ($R^2 = 0.70$) after excluding *M. caudata*, which has an atypically low mass for its body length.

As with size, mandibular shape differed significantly between sexes and across species, but the interaction between these two effects was negligible (the results of the sex \times species MANOVA for the matrix of shape variables are displayed in Table 3). When the MANOVA was performed after excluding *M. caligata*, *M. sibirica*, and *M. vancouverensis*, shape sexual dimorphism also became negligible ($P > 0.05$). *Marmota sibirica* and *M. vancouverensis* have the largest mandibular



(a)



(b)

FIGURE 4. (a) Average centroid size (CS) for males and females (CS is measured in pixels at a scale factor of 0.106 mm/pixel). Marmot species names are abbreviated with the first three letters of their specific epithets. (b) Box-plot of CS for marmot and outgroup species (abbreviated with the first three letter of the genus plus the initial of the specific epithet) with separated samples for males (M) and females (F) of *M. olympus*, *M. sibirica*, and *M. vancouverensis*, which show the largest sexual dimorphism for size.

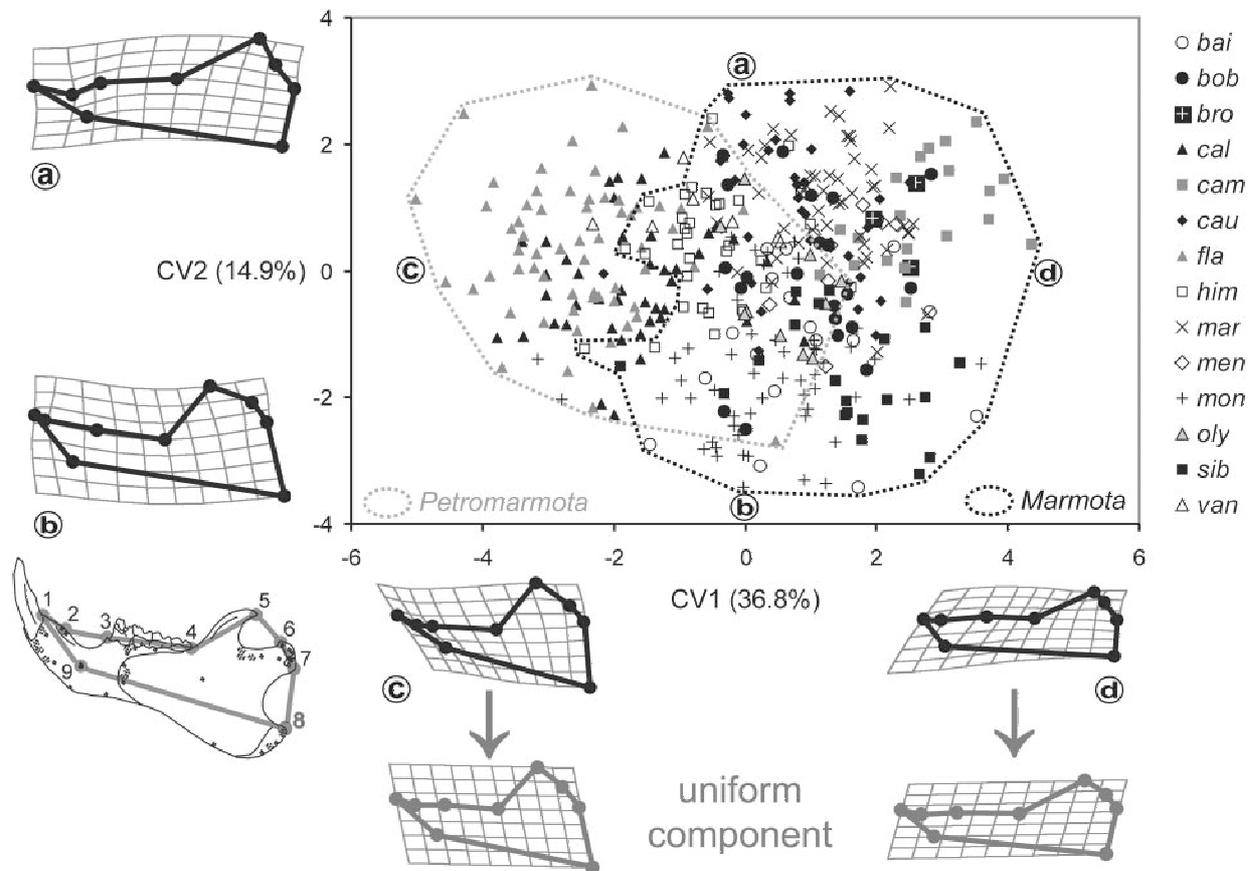


FIGURE 5. Ordination of the 14 marmot species in the space of the first two canonical axes (CV1, and CV2) based on the matrix of shape variables. The TPS deformation grids depicting the shape changes at the extremes of both the CV axes (CV2: a, b; CV1: c, d) are shown (for CV1, either deformation grids using both components of shape change or only the uniform component are displayed). The mandibles in the deformation grids are stylized representations obtained by linking pairs of landmarks (lower left).

cytochrome *b* gene tree proposed by Steppan et al. (1999). The diploid chromosome number (Kruckenhauser et al., 1999) is indicated by the dendrogram branches. The mandibular dendrogram of Figure 6 includes the out-group, whereas in Figure 7 the same tree is shown for marmots only. The TPS deformation grids describe the mandibular shape of each species compared with the mean of the genus *Marmota*; lines proportional to mean mandible size are displayed by species to help detect size-related convergence. The mandibles drawn in Figure 7 above the CS lines correspond to specimens closest to the mean of the respective marmot species, and hence they are the real specimens that most closely resemble the mean mandible of their species. In Table 5, the main mandibular clusters were related to ecological variables (habitat, age of dispersion/first reproduction, social system) to investigate possible convergent patterns.

The congruence between molecular and morphological information is very low when marmot terminal branches are compared. However, the mandible morphology supported the mainly Palaearctic subgenus *Marmota*, typically composed of species with 38 chromosomes. A puzzling exception is *M. (Petromarmota) olympus*,

whose mandible curiously resembles those of members of the subgenus *Marmota* instead of being similar to those of other *Petromarmota* species. The majority of Eurasian marmots belong to the same cluster (black-capped marmot group; Fig. 7, cluster 2), and only *M. sibirica* and *M. baibacina*, whose mandibles are almost identical, are grouped in another cluster (woodchuck group; Fig. 7, cluster 1), which also includes the North American woodchuck (*M. monax*). *Marmota olympus* seems relatively close to the marmots of this second cluster, but this apparent similarity was not confirmed by ordination techniques. The main mandibular traits shared by the woodchuck group are the posteriorly elongated angular process and the coronoid process bent towards the toothrow. All other Eurasian species (Fig. 7, cluster 2) are characterized by a contraction of the ascending ramus with coronoid and angular processes getting closer. The Alaskan marmot (*M. browni*) does not belong to either of the two main clusters in the subgenus *Marmota*. The peculiar shape of the *M. browni* mandible, dorsoventrally stretched with a remarkable uplift of the toothrow, may be related to its presumably basal position in the subgenus *Marmota* (Fig. 6) and its unique karyotype ($2n = 36$).

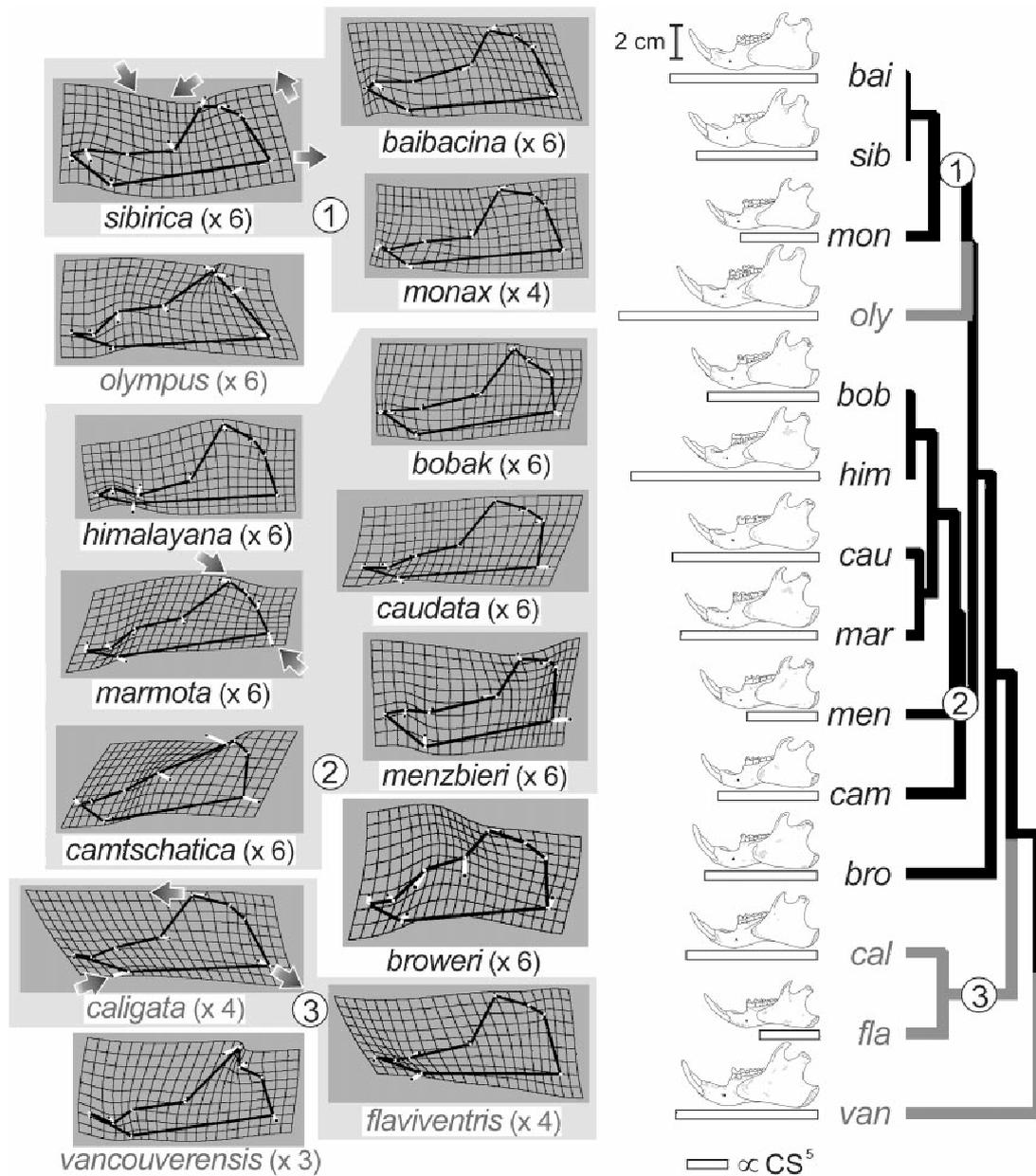


FIGURE 7. UPGMA dendrogram and magnified TPS deformation grids for the marmot mean mandibles (magnification factor in parentheses). The displacement vectors from the mean shape of the genus *Marmota* to that of a marmot species are shown (white lines) and the arrows (shaded) locate the main common shape features for three clusters: 1) woodchuck group, 2) black-capped marmot group, and 3) typical *Petromarmota* species. Lines proportional to the average mandible size for each species were traced next to the species name abbreviations in the mandibular dendrogram (first three letters of the specific epithet). The mandible drawings correspond to the specimens closest to the mean shape of their species.

with the mandibular dendrogram (rearranged in Fig. 8 for facilitating the comparison). The Vancouver Island marmot is isolated from all other marmots, and *M. caligata* and *M. flaviventris* are far from the cloud formed by the subgenus *Marmota* (plus *M. olympus*) but close to each other. The Alaskan marmot mandible is confirmed as the most peculiar one in the subgenus *Marmota*. On the contrary, *M. olympus*, although closer to *Marmota* than to *Petromarmota*, seems no more similar to the wood-

chuck group. The Olympic marmot is apparently near *M. himalayana*, with which it contends the primacy for the largest mandible, but its individuality is clearly recognizable along the vertical axis. A second difference between the diagram and the dendrogram is the similarity between *M. caudata*, the long-tailed marmot, and *M. menzbieri*, which is suggested by the MDS plot but not by the dendrogram and is congruent with both the *cyt b* cladogram (Fig. 6) and the geographic distribution (Fig. 2).

TABLE 5. Main *Marmota* mandibular clusters and ecological variables.

Species	Main cluster ^a	Habitat ^b	Age at dispersion (years) ^c	Age at first reproduction (years) ^c	Social system ^d
<i>M. baibacina</i>	1	HM, low mountains	≥3	2–4	EF
<i>M. sibirica</i>	1	HM, permafrost, xeric habitat	≥3	2	EF
<i>M. monax</i>	1	Plain meadows, forest	0	1	Solitary
<i>M. olympus</i>	<i>oly</i>	HM	2	3	Restricted family
<i>M. bobak</i>	2	Steppe	≥3	3	EF
<i>M. camtschatica</i>	2	HM, permafrost	≥3	3	EF
<i>M. caudata</i>	2	HM	≥3	3	EF
<i>M. himalayana</i>	2	HM, xeric steppe	?	?	EF
<i>M. marmota</i>	2	HM	2–3	2–3	EF
<i>M. menzbieri</i>	2	HM	?	3–4	EF
<i>M. broweri</i>	<i>bro</i>	HM, permafrost	≥3		EF
<i>M. caligata</i>	3	HM, xeric habitat	2	3	Restricted family
<i>M. flaviventris</i>	3	HM, low mountains, xeric habitat	1	2	Female kin group
<i>M. vancouverensis</i>	<i>van</i>	HM	2	3	Restricted family

^aIndicated as in Figure 6.

^bHM = high mountain meadows; variations from this typical marmot habitat are indicated with no abbreviation (Barash, 1989; Armitage, 2000).

^cBlumstein and Armitage, 1998, 1999; Armitage, 1999, 2000; Rymalov, pers. com.

^dEF = extended family (Armitage, 2000).

DISCUSSION

Sexual Dimorphism

Male mandibles are larger than those of females in all marmot species. This dimorphism mirrors similar

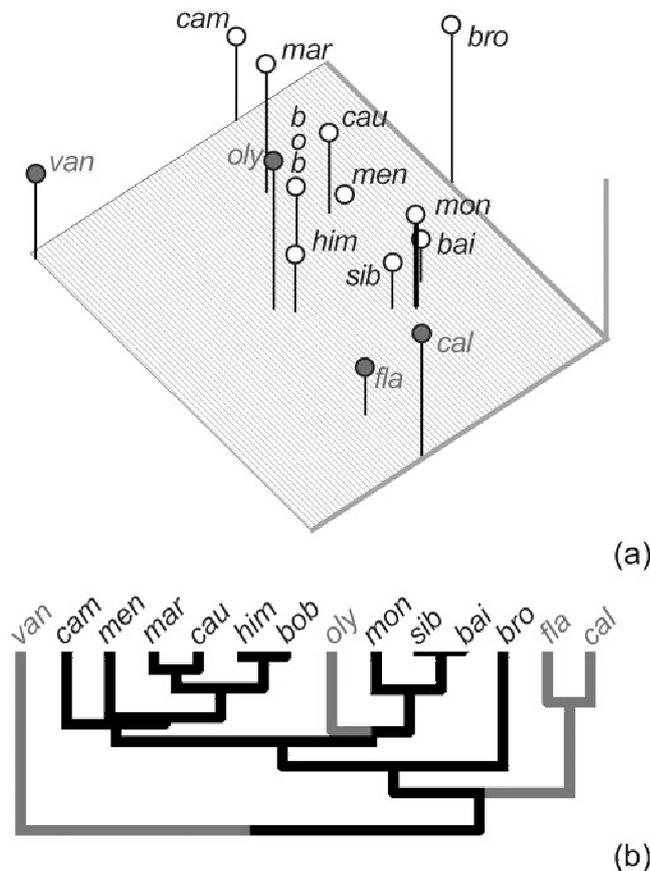


FIGURE 8. Ordination (MDS) of the mean marmot mandibles (a) compared with the dendrogram (tree topology rearranged to emphasize size congruencies) (b).

observations on body size (Barash, 1989) and is related to sexual selection. In contrast, sexual dimorphism for mandible shape is modest and negligible if compared with interspecific differences. These findings are in agreement with observations of the yellow-bellied marmot (*M. flaviventris*) (Cardini and Tongiorgi, in press). The CVA indicated that mandible shape differences between sexes are conspicuous only in *M. caligata* and *M. sibirica*. A moderate degree of sexual dimorphism also may be present in mandible shape of *M. vancouverensis*, but it was difficult to detect because of small sample size. Sexual dimorphism is not significant in the sex \times species MANOVA of shape variables only when the *M. vancouverensis*, *M. caligata*, and *M. sibirica* are excluded from the analysis. Sexual dimorphism in the hoary marmot and the Vancouver Island marmot is, nevertheless, negligible compared with interspecific differences. A cluster analysis (not shown) of mean mandibles performed with separate means for sexes showed dendrogram topology almost unchanged, and average shapes for males and females of each species grouped together. An exception is represented by *M. sibirica*, which clusters with *M. baibacina*; males of *M. baibacina* are more similar to females of *M. sibirica* than to their conspecific females. Because this is the only exception, the analysis was performed with common samples for males and females. Because some specimens were of unknown sex, this approach also increased sample sizes.

Allometry

Interspecific allometry in *Marmota* is either negligible or follows complex nonlinear models. The test for common slopes was highly significant and only a small fraction of the shape variation in the marmot sample was explained by size, even when mean shapes for each marmot species were regressed onto the average mandibular size (7.5% of shape variation explained by size). However, when the outgroup specimens were included, a

larger percentage of shape differences was size related (12.3% including all specimens or 38.5% using averages for each species). This increase may be partly due to marmots being much larger than other sciurids, which results in two relatively separated clouds of points representing ingroup and outgroup specimens.

Ontogenetic allometry is an important factor in modeling yellow-bellied marmot mandibles during postnatal growth (Cardini and Tongiorgi, in press), and the same is likely to hold for the majority of marmot species (Cardini and O'Higgins, unpubl.). Allometry also may have played a significant role in shaping the mandible during sciurid evolution, but new studies involving more species, employing nonlinear models, and possibly taking into account the effects of taxonomic hierarchy in the statistical tests will be needed (Felsenstein, 1985; Harvey and Pagel, 1991).

INTERSPECIFIC COMPARISONS: CONVERGENCE VERSUS PHYLOGENETIC SIGNAL

Size

Marmot mandibles are much larger than those of the outgroup species, which is congruent with marmots being the largest living sciurids (Hafner, 1984). The size of marmot mandibles reflects fairly well their body size and cranial dimensions (Bibikov, 1996; Armitage, 1999). Comparisons of mandible size with body size (length and mass) and condylobasal length in *Marmota* are not simple, because the data reported by different authors are not fully concordant. Very large species, such as *M. himalayana* and *M. olympus*, and very small ones, such as *M. flaviventris* and *M. menzbieri*, have respectively the largest and smallest mandibles. However, the small mandible of *M. monax* is in agreement with Bibikov's (1996) observations of the woodchuck as one of the smallest marmots, but it is not in agreement with the observations of Armitage (1999), who considered it to be intermediate in size. Beyond these inconsistencies, only two major discrepancies between body and mandible measurements are evident. Despite the fact that *M. bobak* is among the largest species, its mandibles are of intermediate size. The opposite holds for *M. broweri*, which is a little species according to Bibikov (1996) and Hoffmann et al. (1979), but it does not have particularly small mandibles, at least in the three specimens available for the present study.

Morphological Convergence Hypothesis

Mandible size and shape are unlikely to be strongly related to dietary differences. All marmots are generalist herbivores, and their diets, consisting primarily of dicots and grasses, are relatively similar (Armitage, 2000). The relationship between mandible size and shape in the genus *Marmota* seems very weak. Interspecific allometries are negligible, and size does not produce convergent shapes. No clusters clearly reflecting size similarities were found in the mandibular dendrogram (Fig. 7).

The outgroup supports the lack of size-related convergence in the mandible. The small chipmunks clustered with the large rock squirrel and the large marmots clustered with the smaller ground squirrels and not with the intermediate-size prairie dogs. Roth's hypothesis (1996) that the sciurid skull is inclined to convergence and the observation that clusters based on sciurid skeletal characters often reflect size (Hafner, 1984; Roth, 1996; Velhagen and Roth, 1997) do not hold for the Marmotini mandible. Hafner (1984) suggested that ecological similarities also may play an important role in shaping the sciurid skeleton, but a preliminary analysis of marmot habitats, life-history traits (age at dispersion/first reproduction), and social systems did not show evident convergent patterns in mandible shape (Table 5). Thus, the hypothesis of sciurid skeletal convergence is rejected in the case of the Marmotini mandible size and shape. The occurrence of convergent morphology due to ecological similarities is not evident but needs to be tested using more detailed ecological information.

Phylogenetic Signal in Mandible Shape

If the mandible is not a convergent structure in marmots and the other sciurids in the sample, does this bone contain a phylogenetic signal detectable with geometric morphometric techniques? Analysis of the marmot mandible produces phenetic groups that match the main sciurid genera and tribes, even if these mandibles were deliberately sampled from geographically distant populations to increase the intrageneric variability. Only the rock squirrel (*Spermophilus variegatus*) clusters far from its congeneric relatives, possibly reflecting the ancient evolutionary history of the subgenus *Otospermophilus* (Hoffmann, pers. com.). Compared to Hafner's (1984) morphometric analysis of the sciurid skeleton, where ground squirrels are interspersed in different sciurid tribes, the mandible efficacy in discriminating sciurid taxonomic groups is surprising. A more problematic issue is whether the relationships among genera and tribes shown in the mandibular clusters match phylogeny. The moderate resemblance between chipmunks and the common tree squirrel is unlikely to reflect phylogeny because the Tamiini are traditionally regarded as relatives of the Marmotini (Hoffmann et al., 1993), a position supported by genetic analyses (Hafner, 1984; Roth, pers. com.). The relative position of the Marmotini genera is more difficult to interpret in the absence of a consolidated phylogeny for this tribe. However, marmot mandibles are fairly similar to those of *Spermophilus*, and this finding might be consistent with Thomas and Martin's (1993) hypothesis of a recent divergence of marmots from true ground squirrels.

The most evident and interesting outcome in the mandible analysis of the genus *Marmota* is the corroboration given to the recently proposed marmot subgenera (Steppan et al., 1999). The support is weaker for the subgenus *Petromarmota*, because the Olympic marmot mandible more closely resembles those of members of the subgenus *Marmota*, and the Vancouver Island

marmot is isolated from all other species by its peculiar mandibular shape. Nonetheless, the hoary marmot and the yellow-bellied marmot, both of which occupy almost all of the Rocky Mountains and comprise several subspecies each, share many mandibular traits and are clearly separated from representatives of the subgenus *Marmota*. The CVA (Fig. 5) indicates that *Petromarmota* (excluding the Olympic marmot) and *Marmota* can be discriminated fairly well along the first canonical axis, which mainly corresponds to uniform shape changes. The uniform shape differences between the two subgenera are similar to the uniform dorsoventral stretching and longitudinal compression that occur during marmot postnatal growth (Cardini and Tongiorgi, in press; Cardini and O'Higgins, unpubl.). The usefulness of the uniform component for providing characters that separate *Petromarmota* and *Marmota* is corroborated by the relative warp analysis (RWA) of the mean mandibles (not shown). When the uniform component is included in the analysis, the species belonging to *Petromarmota* are easily recognizable for having the lowest values along the second relative warp (RW1 and RW2 explain 33.7% and 19.2%, respectively, of the shape variation). However, if an RWA is performed on the matrix of the partial warps alone, marmot subgenera are no more separated along the first two RWA axes (31.3% and 23.6%, respectively, of the variance).

Marmota vancouverensis and *M. olympus* mandibles do not resemble those of the typical *Petromarmota* species. Both of these atypical *Petromarmota* species survive with small populations in extremely restricted ranges (Fig. 2), and they are considered relict populations that differentiated in isolation during the Pleistocene (Hoffmann et al., 1979; Steppan et al., 1999). In this respect, the Vancouver Island marmot is of great interest. *Marmota vancouverensis* is believed to have originated between 100,000 and 10,000 years ago from a population that colonized the Vancouver Island via land bridges present during the glaciations (Bryant, 1997). Marmots survived glacial maxima on Vancouver Island nunataks or coastal refugia. The available evidence on *M. vancouverensis* genotype (karyotype and *cyt b*) points to a close relationship with *M. caligata* (Hoffmann et al., 1979; Kruckenhauser et al., 1999; Steppan et al., 1999). Steppan et al. (1999) showed that the similarity between the two species is so high that their *cyt b* interspecific distance overlaps the range of values found in the intraspecific comparisons. Despite the apparent low level of genetic divergence and the young age of the Vancouver Island marmot, its melanistic fur and characteristic vocalizations and behavior (Barash, 1989) make this species unique among all marmots. Hoffmann et al. (1979) observed some peculiarities of the Vancouver Island marmot skull and lower jaw but found it to be relatively similar to the hoary marmot. Hence, they considered *M. caligata*, *M. olympus*, and *M. vancouverensis* as members of the super-species *caligata*. In the present analysis, the Vancouver Island marmot mandible, with its recurved coronoid process (already noted by Hoffmann et al., 1979), forward

bent condyle apex (landmark 6), and inconspicuous mandibular symphysis ridge (landmark 2), emerges as the most atypical of the entire genus. Genetic bottlenecks during the short evolutionary history of the Vancouver Island marmot may have acted as powerful accelerators of the rate of morphological and behavioral evolution, which led to unique phenotypic features in this isolated population.

The Olympic Peninsula is similar to Vancouver Island with respect to geography and Pleistocene history, but marmots endemic to these two regions evolved differently. The Olympic marmot is a basal member of *Petromarmota*, which originated in an early to mid-Pleistocene nunatak (Steppan et al., 1999). The pronounced genetic divergence of *M. olympus* is suggested not only by the *cyt b* sequences (Steppan et al., 1999) but also by its karyotype of 40 chromosomes instead of the 42 found in the other *Petromarmota* species. Interpreting the anatomical traits that make the Olympic marmot mandible more similar to those of members of the subgenus *Marmota* is a difficult task. The lower jaw of *M. olympus* bears some resemblance to those of the typical *Petromarmota* in the ventral part of the mandible. However, the posteriorly bent coronoid process and the remarkable uplift of the tooththrow make the Olympic marmot manifestly different from its closest relatives. These mandibular characters may be a by-product of *M. olympus* evolution as a peripheral isolate or they could represent plesiomorphic traits, present in the ancestor of all living marmots and partially conserved either in the Olympic marmot or in members of the subgenus *Marmota*. In fact, the *M. olympus* mandible displays a mosaic of characters: the ventral half resembles the typical *Petromarmota* mandible, the relatively long angular process is found also in the woodchuck group, and the posteriorly inclined coronoid process is also seen in the black-capped marmot group.

The subgenus *Marmota* includes two main mandibular clusters plus *M. broweri*. The Alaskan marmot is the most peculiar species for mandible shape in this subgenus and is the only species with 36 chromosomes (all others have 38 except *M. camtschatika*, with 40). Steppan et al. (1999) pointed out that the Alaskan marmot might represent an ancient lineage that originated at the same time as the radiation of the Palearctic marmots. A strict relationship with *M. camtschatika* or *M. caligata* is rejected by the *cyt b* sequence data. The mandibular morphology is consistent with this view, and perhaps the uplift of the tooththrow in the Alaskan marmot represents a primitive mandibular trait apparent, also although less pronounced, in the Olympic and Alpine marmots.

The species belonging to either the woodchuck group or the black-capped marmot group display subtle differences in mandible shape. The majority of these marmots, the black-capped marmot group, are characterized by a relative displacement of the angular and coronoid process, a contraction opposite to the enlargement found in the typical *Petromarmota*. The morphological divergence produced by the radiation of the Eurasiatic marmots is relatively modest. The North American woodchuck's

close phenetic relationship to *M. baibacina* and *M. sibirica* is unlikely to be of phylogenetic significance, but the mandible supports *M. monax* proximity to Eurasiatic marmots. In the black-capped marmot group, the Alpine marmot mandible does not show highly specific traits despite its presumed ancient origin and the uniqueness of this species among the Palaearctic species in fur morphology and its parasitic relationship with fleas. *Marmota caudata* clusters with the Alpine marmot in the dendrogram but is next to *M. menzbieri* in the ordination, a close relationship that reflects the *cyt b* tree and the geographic proximity of the long-tailed and Menzbier marmots.

The lack of correspondence between the dendrogram and *cyt b* tree terminal branches may be due to several factors: (1) sampling error (either in the collection of specimens or in the choice of landmark configuration), (2) the retention of plesiomorphic mandibular traits, which can obscure the interspecific differences and make the detection of the phylogenetic signal more difficult (which may be the case for the strong resemblance of the woodchuck to *M. baibacina* and *M. sibirica*), (3) genetic drift and morphological convergence in the past evolutionary history of *Marmota*, which could have masked the mandible phylogenetic signal, and (4) misrepresentation of true marmot phylogeny by the *cyt b* gene tree. For example, *M. baibacina* and *M. sibirica* could be more closely related. Their mandibles are almost indistinguishable. The main differences between these species are the larger size of *M. baibacina* and the more pronounced sexual dimorphism of *M. sibirica*; subtler shape differences are localized at the base of the coronoid process and at the anterior tip of the incisor alveolus. *Marmota baibacina* and *M. sibirica* are very similar also in external morphology, and hybridization may occur in the contact area between the two species (as discussed by Barash, 1989; Steppan et al., 1999). This observation could indicate a close phylogenetic relationship between *M. baibacina* and *M. sibirica* that would be consistent with their mandibular similarities. However, Potapova et al. (1997) found significant cranial differences in a morphometric comparison of these two species, and hybridization has also been reported between *M. baibacina* and *M. bobak* (Steppan et al., 1999). The study of *M. baibacina* skeletal morphology is further complicated by the variation of mandible phenotypic frequency determined by plague epidemics (Pole and Bibikov, 1991, cited by Armitage, 2000). Given the complex morphological patterns and the limited molecular data for the Eurasiatic marmots, an extensive analysis of morphological and molecular characters sampling the entire distribution range will be needed to assess fully the phylogenetic relationships in this clade.

Morphological Patterns

The role of allometry in producing morphological novelties during marmot evolution seems negligible, while its possible relevance in sciurid radiation should be investigated further. Each marmot species has its anatomical peculiarities, and although a distinction can be found

between mandibles of the two marmot subgenera, morphological traits may be mixed. The mandible could have evolved as a mosaic of characters. The complexity of the morphological patterns can also be related to genetic drift greatly speeding the rate of morphological evolution as a result of severe bottlenecks, as described for the Vancouver Island marmot.

Swiderski (1993) and Swiderski and Jansa (1998), applying geometric morphometrics techniques, found that sciurid skeletal characters do not behave as highly integrated structures nor are they prone to convergence. As in the present study, these authors mainly focused on marmotines. Different outcomes were obtained by Hafner (1984), Roth (1996), and Velhagen and Roth (1997), who considered the sciurid skeleton inclined to convergent evolution. The partially conflicting views on the usefulness of sciurid skull morphology in phylogenetic research and on the role of size and ecological specialization in determining squirrel cranial shape, may have several sources, among these are the choice of morphometric technique and the selection of species studied. Roth (1996) and Velhagen and Roth (1997) focused on tree squirrels, and Hafner (1984) mainly analyzed terrestrial squirrels, but none of these researchers used geometric morphometrics techniques, which may be more effective in capturing the phylogenetic signal in marmotine morphology. The results obtained from the mandible should be tested with other skeletal characters. Extensive investigations of tree and flying squirrel skeletal morphology are needed to assess whether convergent osteological patterns characterize other sciurid lineages.

CONCLUSIONS

A phylogenetic signal at intermediate taxonomic levels is detectable in the marmot mandible. Mandible shape clearly discriminates the genera and tribes and supports the recently proposed subgeneric classification of marmots. This outcome also implies that the high degrees of sociality found in several marmot species evolved independently at least twice (Kruckenhauser et al., 1999).

The hypothesis of sciurid propensity to morphological convergence caused by size similarities is rejected for marmots.

Interspecific allometry has not played an important role in shaping the mandible during the evolution of marmots. Genetic drift can greatly accelerate morphological evolution and may have contributed to the origin of morphological novelties in marmot skeletal structures. The mandible is likely to have evolved as a mosaic of characters mixing plesiomorphies with derived traits.

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APPENDIX 1. Museum catalog number and locality of collection for the adult specimens. ? = unknown.

Species/Subspecies	Museum ^a	Catalog no.	Locality ^b
<i>Marmota baibacina</i>			
<i>centralis</i>	BMNHL	12.4.1.41	Alatau
<i>centralis</i>	BMNHL	12.4.1.39	Alatau
<i>centralis</i>	BMNHL	12.4.1.40	Alatau
<i>centralis</i>	BMNHL	12.4.1.38	Altaj
<i>centralis</i>	BMNHL	14.5.10.74	centr. Asia
<i>centralis</i>	BMNHL	14.5.10.73	centr. Asia
<i>centralis</i>	BMNHL	8.3.2.74	Thian Shan
<i>centralis</i>	BMNHL	9.4.3.110	Turkestan
<i>centralis</i>	BMNHL	92.1.1.6	W Turkestan
?	BMNHL	98.12.15.1	NW Mongolia
?	USNM	175424	Altaj
?	USNM	175426	Altaj
?	USNM	102577	NW Mongolia
?	ZIN	63932	Altaj
?	ZIN	63933	Altaj
?	ZIN	63931	Altaj
?	ZIN	63930	Altaj
?	ZIN	31871	E Kazakhstan
?	ZIN	50165	E Kazakhstan
?	ZIN	84028	E Kazakhstan
?	ZIN	84029	E Kazakhstan
?	ZIN	84030	E Kazakhstan
?	ZIN	46147	E Kazakhstan
?	ZIN	39242	Thian Shan

APPENDIX 1. Continued

Species/Subspecies	Museum ^a	Catalog no.	Locality ^b
<i>M. bobak</i>			
	BMNHL	19.7.7.3325	Russia
	BMNHL	594a	Russia
	BMNHL	37.6.12.6	Russia
	ZIN	44227	N centr. Kazakistan
	ZIN	44236	N centr. Kazakistan
	ZIN	44218	N centr. Kazakistan
	ZIN	44204	N centr. Kazakistan
	ZIN	44212	N centr. Kazakistan
	ZIN	44238	N centr. Kazakistan
	ZIN	44208	N centr. Kazakistan
	ZIN	44229	N centr. Kazakistan
	ZIN	11987 oc	S centr. Europ. Russia
	ZIN	50300	S centr. Europ. Russia
	ZIN	50292	S centr. Europ. Russia
	ZIN	50283	S centr. Europ. Russia
	ZIN	50297	S centr. Europ. Russia
	ZIN	50293	S centr. Europ. Russia
	ZIN	50285	S centr. Europ. Russia
	ZIN	50287	S centr. Europ. Russia
	ZIN	50289	S centr. Europ. Russia
	ZIN	15459 oc	SE Europ. Russia
<i>M. broweri</i>			
	USNM	290276	Alaska
	USNM	583154	Alaska
	USNM	583155	Alaska
<i>M. caligata</i>			
<i>caligata</i>	USNM	74996	Alaska
<i>caligata</i>	USNM	96533	Alaska
<i>caligata</i>	USNM	96207	Alaska
<i>caligata</i>	USNM	98154	Alaska
<i>caligata</i>	USNM	271698	Alaska
<i>caligata</i>	USNM	271699	Alaska
<i>caligata</i>	USNM	271701	Alaska
<i>caligata</i>	USNM	48580	Alaska
<i>caligata</i>	USNM	96206	Alaska
<i>caligata</i>	USNM	146449	Alaska
<i>caligata</i>	USNM	135161	Yukon
<i>caligata</i>	USNM	135163	Yukon
<i>caligata</i>	USNM	88005	British Columbia
<i>caligata</i>	USNM	88006	British Columbia
<i>caligata</i>	USNM	42638	Washington
<i>caligata</i>	USNM	42793	Washington
<i>caligata</i>	USNM	90132	Washington
<i>caligata</i>	USNM	226719	Washington
<i>caligata</i>	USNM	233212	Washington
<i>caligata</i>	USNM	90134	Washington
<i>caligata</i>	USNM	221012	Alberta
<i>caligata</i>	USNM	114833	Idaho
<i>caligata</i>	USNM	72222	Montana
<i>caligata</i>	USNM	72225	Montana
<i>caligata</i>	USNM	72235	Montana
<i>caligata</i>	USNM	72223	Montana
<i>caligata</i>	USNM	81913	Alberta
<i>caligata</i>	USNM	66696	British Columbia
<i>caligata</i>	USNM	66697	British Columbia
<i>caligata</i>	USNM	66698	British Columbia
<i>caligata</i>	USNM	67073	British Columbia
<i>caligata</i>	USNM	174503	Alberta
<i>caligata</i>	USNM	174502	Alberta
<i>caligata</i>	USNM	53595	British Columbia
<i>caligata</i>	USNM	170741	British Columbia
<i>caligata</i>	USNM	101300	British Columbia
<i>caligata</i>	USNM	202790	British Columbia
<i>caligata</i>	USNM	226148	British Columbia
<i>caligata</i>	USNM	137319	Alaska
<i>caligata</i>	USNM	97952	Alaska

APPENDIX 1. Continued

Species/Subspecies	Museum ^a	Catalog no.	Locality ^b
<i>vigilis</i>	USNM	97953	Alaska
<i>vigilis</i>	USNM	235255	Alaska
<i>vigilis</i>	USNM	235257	Alaska
?	BMNHL	593.a	Hudson Bay
		(45.7.4.9)	
<i>M. camtschatica</i>			
<i>bunpei</i>	BMNHL	1937.6.12.10	Jakutia
		(15084)	
?	BMNHL	58.11.18.3	Kamtschatka
?	BMNHL	69.4.20.1	Kamtschatka
?	ZIN	57873	E Transbaikal Region
?	ZIN	57874	E Transbaikal Region
?	ZIN	57872	E Transbaikal Region
?	ZIN	57880	E Transbaikal Region
?	ZIN	57879	E Transbaikal Region
?	ZIN	57877	E Transbaikal Region
?	ZIN	78912	E Transbaikal Region
?	ZIN	41505	Jakutia
?	ZIN	41449	Jakutia
?	ZIN	41531	Jakutia
?	ZIN	41550	Jakutia
?	ZIN	41475	Jakutia
?	ZIN	41502	Jakutia
?	ZIN	41503	Jakutia
?	ZIN	41514	Jakutia
?	ZIN	13561 oc	Jakutia
?	ZIN	78913	Kamtschatka
<i>M. caudata</i>			
<i>aurea</i>	USNM	62114	Pamir
<i>aurea</i>	USNM	62115	Pamir
<i>aurea</i>	USNM	62118	Pamir
?	USNM	35499	Kashmir (N India)
?	USNM	62112	Kashmir (N India)
?	USNM	173377	Kashmir (N India)
?	USNM	173380	Kashmir (N India)
?	USNM	173381	Kashmir (N India)
?	USNM	173382	Kashmir (N India)
?	USNM	173383	Kashmir (N India)
?	USNM	35500	Kashmir (N India)
?	USNM	173384	Kashmir (N India)
?	USNM	298212	N Pakistan
?	USNM	327143	N Pakistan
?	USNM	353196	N Pakistan
?	USNM	353197	N Pakistan
?	USNM	353199	N Pakistan
?	USNM	353200	N Pakistan
?	BMNHL	10.12.2.25	E Uzbekistan or W Pamir
?	BMNHL	69.493	E Pakistan
?	BMNHL	88.3.20.25	Kashmir (N India)
?	BMNHL	5.10.8.2	Kashmir (N India)
?	BMNHL	8.7.6.27	Kashmir (N India)
?	BMNHL	1937.6.12.7	Kirghizistan
?	BMNHL	91.5.16.2	Pamir
?	BMNHL	92.1.1.7	Pamir
?	BMNHL	9.4.3.112	Turkestan (E Uzbekistan)
?	BMNHL	76.3.9.3	?
?	BMNHL	97.10.3.54	?
?	BMNHL	8.10.3.16	?
?	ZIN	40555	Pamir
?	ZIN	40553	Pamir
?	ZIN	27912	Pamir-Alai
?	ZIN	51537	Pamir-Alai
?	ZIN	22535	Pamir-Alai
<i>M. flaviventris</i>			
<i>avara</i>	USNM	99759	British Columbia
<i>avara</i>	USNM	99760	British Columbia
<i>avara</i>	USNM	221898	Idaho
<i>avara</i>	USNM	221896	Nevada

APPENDIX 1. Continued

Species/Subspecies	Museum ^a	Catalog no.	Locality ^b
<i>avara</i>	USNM	79365	Oregon
<i>avara</i>	USNM	212471	Oregon
<i>avara</i>	USNM	242645	Oregon
<i>avara</i>	USNM	89312	Washington
<i>avara</i>	USNM	234960	Washington
<i>avara</i>	USNM	274340	Washington
<i>dacota</i>	USNM	168884	South Dakota
<i>dacota</i>	USNM	191366	South Dakota
<i>dacota</i>	USNM	191367	South Dakota
<i>dacota</i>	USNM	191369	South Dakota
<i>dacota</i>	USNM	468884	South Dakota
<i>dacota</i>	USNM	65920	Wyoming
<i>engelhardti</i>	USNM	157828	Utah
<i>engelhardti</i>	USNM	158033	Utah
<i>engelhardti</i>	USNM	158980	Utah
<i>engelhardti</i>	USNM	232665	Utah
<i>engelhardti</i>	USNM	244551	Utah
<i>engelhardti</i>	USNM	244552	Utah
<i>engelhardti</i>	USNM	158500	Utah
<i>flaviventris</i>	USNM	100532	California
<i>flaviventris</i>	USNM	100533	California
<i>flaviventris</i>	USNM	88243	California
<i>flaviventris</i>	USNM	23951	Nevada
<i>flaviventris</i>	USNM	80360	Oregon
<i>flaviventris</i>	USNM	89311	Oregon
<i>flaviventris</i>	USNM	211232	Oregon
<i>luteola</i>	USNM	139082	Colorado
<i>luteola</i>	USNM	74057	Colorado
<i>luteola</i>	USNM	25523	Wyoming
<i>luteola</i>	USNM	25524	Wyoming
<i>luteola</i>	USNM	25527	Wyoming
<i>luteola</i>	USNM	186520	Wyoming
<i>nosophora</i>	USNM	575170	Colorado
<i>nosophora</i>	USNM	156923	Idaho
<i>nosophora</i>	USNM	168477	Montana
<i>nosophora</i>	USNM	229842	Montana
<i>nosophora</i>	USNM	233382	Montana
<i>nosophora</i>	USNM	291192	Montana
<i>nosophora</i>	USNM	243663	Utah
<i>nosophora</i>	USNM	243664	Utah
<i>nosophora</i>	USNM	147183	Wyoming
<i>nosophora</i>	USNM	168799	Wyoming
<i>nosophora</i>	USNM	180918	Wyoming
<i>nosophora</i>	USNM	177297	Wyoming
<i>obscura</i>	USNM	72565	New Mexico
<i>obscura</i>	USNM	128750	New Mexico
<i>obscura</i>	USNM	128753	New Mexico
<i>obscura</i>	USNM	128754	New Mexico
<i>obscura</i>	USNM	228271	New Mexico
<i>obscura</i>	USNM	228273	New Mexico
<i>obscura</i>	USNM	133505	New Mexico
<i>parvula</i>	USNM	93688	Nevada
<i>parvula</i>	USNM	93689	Nevada
<i>parvula</i>	USNM	93690	Nevada
<i>parvula</i>	USNM	41914	California
<i>parvula</i>	USNM	42368	California
<i>parvula</i>	USNM	42112	California
<i>parvula</i>	USNM	108792	California
<i>sierrae</i>	BMNHL	40.823	California
<i>M. himalayana</i>			
<i>himalayana</i>	USNM	62122	Chinese Turkestan
<i>himalayana</i>	USNM	84099	Kashmir (N India)
<i>himalayana</i>	USNM	84100	Kashmir (N India)
<i>himalayana</i>	USNM	84101	Kashmir (N India)
<i>himalayana</i>	USNM	84104	Kashmir (N India)
<i>himalayana</i>	USNM	198637	Kashmir (N India)
<i>himalayana</i>	USNM	198638	Kashmir (N India)
<i>robusta</i>	USNM	144038	China
<i>robusta</i>	USNM	144039	China

APPENDIX 1. Continued

Species/Subspecies	Museum ^a	Catalog no.	Locality ^b
<i>robusta</i>	USNM	240674	Kansu (NW China)
<i>robusta</i>	USNM	240675	Kansu (NW China)
<i>robusta</i>	USNM	240677	Kansu (NW China)
<i>robusta</i>	USNM	102576	Tibet
<i>robusta</i>	USNM	255960	Tibet
?	USNM	576183	Kunlun Shan (China)
?	USNM	576184	Kunlun Shan (China)
?	USNM	573031	Kunlun Shan (China)
?	USNM	573037	Chinese Turkestan
?	BMNHL	96.11.4.9	Sichuan (centr. China)
?	BMNHL	96.11.4.2	Sichuan (centr. China)
?	BMNHL	91.10.7.98	Sikkim (N India)
?	BMNHL	23.9.1.41	Tibet
?	BMNHL	5.12.5.2	Tibet
?	BMNHL	5.12.5.3	Tibet
?	BMNHL	23.9.1.38	Tibet
?	BMNHL	23.9.1.40	Tibet
?	BMNHL	22.9.1.82	Yunnan, Mekong- Yangtze (S China)
?	BMNHL	11.2.1.95	Kansu (NW China)
?	BMNHL	11.2.1.94	Kansu (NW China)
?	BMNHL	99.3.1.13	?
?	BMNHL	8.2.29.1	?
?	BMNHL	8.7.6.20	?
?	BMNHL	8.7.6.30	?
<i>M. marmota</i>			
<i>marmota</i>	BMNHL	8.8.10.65	French Alps
<i>marmota</i>	BMNHL	8.8.10.145	French Alps
<i>marmota</i>	BMNHL	2.8.4.33	Swiss Alps
<i>marmota</i>	BMNHL	7.1.1.195	Swiss Alps
<i>marmota</i>	BMNHL	2.8.4.31	Swiss Alps
<i>marmota</i>	BMNHL	2.8.4.30	Swiss Alps
<i>marmota</i>	BMNHL	2.8.4.32	Swiss Alps
<i>marmota</i>	DBA UMR	not in catalog	Appennini
<i>marmota</i>	DBA UMR	not in catalog	Appennini
<i>marmota</i>	DBA UMR	not in catalog	Appennini
<i>marmota</i>	MSNM Ma	4532	Italian Alps
<i>marmota</i>	MSNM Ma	4799	Italian Alps
<i>marmota</i>	MSNM Ma	6103	Italian Alps
<i>marmota</i>	PNGP	not in catalog	Italian Alps
<i>marmota</i>	SC	165	Swiss Alps
<i>marmota</i>	SC	12	Swiss Alps
<i>marmota</i>	SC	173	Swiss Alps
<i>marmota</i>	SC	175(I)	Swiss Alps
<i>marmota</i>	SC	178	Swiss Alps
<i>marmota</i>	SC	26B	Swiss Alps
<i>marmota</i>	SC	168	Swiss Alps
<i>marmota</i>	SC	159 (I)	Swiss Alps
<i>marmota</i>	SC	167	Swiss Alps
<i>marmota</i>	SC	21B	Swiss Alps
<i>marmota</i>	SC	25B	Swiss Alps
<i>marmota</i>	SC	17	Swiss Alps
<i>marmota</i>	SC	171	Swiss Alps
<i>marmota</i>	SC	39	Swiss Alps
<i>marmota</i>	SC	34B	Swiss Alps
<i>marmota</i>	SC	159 (II)	Swiss Alps
<i>marmota</i>	SC	161	Swiss Alps
<i>marmota</i>	SC	149	Swiss Alps
<i>marmota</i>	SC	40	Swiss Alps
<i>marmota</i>	SC	29B	Swiss Alps
<i>marmota</i>	SC	158	Swiss Alps
<i>marmota</i>	SC	164	Swiss Alps
<i>marmota</i>	SC	15	Swiss Alps
<i>marmota</i>	SC	166	Swiss Alps
<i>marmota</i>	SC	35B	Swiss Alps
<i>marmota</i>	SC	36B	Swiss Alps
<i>marmota</i>	SC	32	Swiss Alps
<i>marmota</i>	SC	38B	Swiss Alps
<i>marmota</i>	SC	45	Swiss Alps

APPENDIX 1. Continued

Species/Subspecies	Museum ^a	Catalog no.	Locality ^b
<i>marmota</i>	USNM	14336	Swiss Alps
<i>marmota</i>	USNM	115219	Swiss Alps
<i>marmota</i>	USNM	115220	Swiss Alps
<i>marmota</i>	USNM	115221	Swiss Alps
<i>marmota</i>	USNM	115222	Swiss Alps
?	BMNHL	1087.b	?
?	MSNM Ma	6084	?
?	MSNM Ma	6085	?
<i>M. menzbieri</i>	ZIN	45476	E Uzbekistan
	ZIN	45474	E Uzbekistan
	ZIN	65848	E Uzbekistan
	ZIN	31704	Kirghizistan
	ZIN	57912	NW Tagikistan
	ZIN	45472	Uzbekistan
	ZIN	65852	Uzbekistan
<i>M. monax</i>			
<i>canadensis</i>	USNM	72186	Minnesota
<i>canadensis</i>	USNM	72187	Minnesota
<i>canadensis</i>	USNM	243949	New Scotland
<i>canadensis</i>	USNM	191345	North Dakota
<i>ignava</i>	USNM	291554	Labrador
<i>ignava</i>	USNM	293895	Labrador
<i>monax</i>	USNM	77924	District of Columbia
<i>monax</i>	USNM	244482	Illinois
<i>monax</i>	USNM	337132	Indiana
<i>monax</i>	USNM	347752	Indiana
<i>monax</i>	USNM	242724	Maryland
<i>monax</i>	USNM	53920	Missouri
<i>monax</i>	USNM	96574	Pennsylvania
<i>monax</i>	USNM	396279	Pennsylvania
<i>monax</i>	USNM	259345	Virginia
<i>monax</i>	USNM	283359	Virginia
<i>ochracea</i>	USNM	243607	Alaska
<i>ochracea</i>	USNM	77142	British Columbia
<i>ochracea</i>	USNM	77143	British Columbia
<i>ochracea</i>	USNM	202785	British Columbia
<i>petrensis</i>	USNM	291786	British Columbia
<i>petrensis</i>	USNM	291787	British Columbia
<i>petrensis</i>	USNM	101295	British Columbia
<i>petrensis</i>	USNM	203532	British Columbia
<i>preblorum</i>	USNM	78357	Massachusetts
<i>preblorum</i>	USNM	78356	Massachusetts
<i>preblorum</i>	USNM	78355	Massachusetts
<i>preblorum</i>	USNM	78354	Massachusetts
<i>preblorum</i>	USNM	78358	Massachusetts
<i>preblorum</i>	USNM	96140	Massachusetts
<i>preblorum</i>	USNM	23033	New Hampshire
<i>rufescens</i>	USNM	35361	Minnesota
<i>rufescens</i>	USNM	43560	Minnesota
<i>rufescens</i>	USNM	186521	Minnesota
<i>rufescens</i>	USNM	67692	New York
<i>rufescens</i>	USNM	67693	New York
<i>rufescens</i>	USNM	25184	Ontario
<i>rufescens</i>	USNM	174594	Ontario
<i>rufescens</i>	USNM	227256	Wisconsin
<i>rufescens</i>	USNM	228929	Wisconsin
<i>rufescens</i>	USNM	233345	Wisconsin
<i>rufescens</i>	USNM	234703	Wisconsin
<i>rufescens</i>	USNM	243073	Wisconsin
<i>rufescens</i>	MSNM Ma	4550	?
?	BMNHL	19.7.7.2552	Canada
?	BMNHL	36.11.6.31	Labrador
?	BMNHL	36.11.6.32	Labrador
?	BMNHL	36.11.6.30	Labrador
?	BMNHL	36.11.6.34	Labrador
?	BMNHL	592.a	Missouri
		(43.9.14.9)	
?	BMNHL	6.1.6.6	West Virginia

APPENDIX 1. Continued

Species/Subspecies	Museum ^a	Catalog no.	Locality ^b
?	BMNHL	592.c	?
?	BMNHL	592.e	?
?	BMNHL	592.d	?
		(51.8.16.19)	
?	BMNHL	1.989.337	?
<i>M. olympus</i>	USNM	66950	Washington, Olympic P.
	USNM	67611	Washington, Olympic P.
	USNM	67612	Washington, Olympic P.
	USNM	90516	Washington, Olympic P.
	USNM	241657	Washington, Olympic P.
	USNM	241658	Washington, Olympic P.
	USNM	241947	Washington, Olympic P.
	USNM	241948	Washington, Olympic P.
	USNM	241659	Washington, Olympic P.
	USNM	242102	Washington, Olympic P.
<i>M. sibirica</i>	USNM	175599	Mongolia
	USNM	175600	Mongolia
	USNM	175601	Mongolia
	USNM	259440	Mongolia
	USNM	268752	Mongolia
	ZIN	81139	Tuva (S centr. Siberia)
	ZIN	81137	Tuva (S centr. Siberia)
	ZIN	78671	Tuva (S centr. Siberia)
	ZIN	78672	Tuva (S centr. Siberia)
	ZIN	78663	Tuva (S centr. Siberia)
	ZIN	78670	Tuva (S centr. Siberia)
	ZIN	78666	Tuva (S centr. Siberia)
	ZIN	78680	Tuva (S centr. Siberia)
	ZIN	78682	Tuva (S centr. Siberia)
	ZIN	78689	Tuva (S centr. Siberia)
	ZIN	78687	Tuva (S centr. Siberia)
	ZIN	78690	Tuva (S centr. Siberia)
	ZIN	78679	Tuva (S centr. Siberia)
	ZIN	81142	Tuva (S centr. Siberia)
	ZIN	78686	Tuva (S centr. Siberia)
	ZIN	78684	Tuva (S centr. Siberia)
<i>M. vancouverensis</i>	MVZ	12091	Vancouver Island
	MVZ	12092	Vancouver Island
	MVZ	12090	Vancouver Island
	MVZ	12099	Vancouver Island
	MVZ	12100	Vancouver Island
	MVZ	12098	Vancouver Island
	MVZ	12093	Vancouver Island
	MVZ	12095	Vancouver Island
<i>Spermophilus beldingi</i>	BMNHL	38.4.1.39	California
	BMNHL	2.4.1.137	California
	BMNHL	98.12.27.1 (88754)	California
<i>S. citellus</i>			
<i>gravojerici</i>	BMNHL	33.4.4.3	Bosnia
<i>gravojerici</i>	BMNHL	31.11.11.40	Greece
<i>gravojerici</i>	BMNHL	31.11.11.37	Greece
<i>karamani</i>	BMNHL	471.105	Yugoslavia
<i>karamani</i>	BMNHL	471.106	Yugoslavia
<i>karamani</i>	BMNHL	471.110	Yugoslavia
<i>S. richardsoni</i>	BMNHL	1938.4.1.53	North Dakota
	BMNHL	1938.4.1.45	North Dakota
	BMNHL	1938.4.1.46	North Dakota
<i>S. undulatus</i> ^c			
	BMNHL	12.4.1.21	Siberia
	BMNHL	5.4.8.10	Thian Shan
<i>S. variegatus</i>			
<i>grammurus</i>	BMNHL	92.11.1.10	Colorado
<i>grammurus</i>	BMNHL	55.275	Messico

APPENDIX 1. Continued

Species/Subspecies	Museum ^a	Catalog no.	Locality ^b	
<i>Cynomys leucurus</i>	BMNHL	40.829	Wyoming	
<i>C. ludovicianus</i>	BMNHL	19.7.7.2841	Kansas	
	BMNHL	60.513	Kansas	
	BMNHL	67.7.8.34 (1433.b)	?	
	BMNHL	77.436	?	
	BMNHL	1433.a	?	
<i>Tamias sibiricus</i> ^d	USNM	200614	Jakutia	
	USNM	200617	Jakutia	
<i>Tamias striatus</i>	USNM	36950	Tennessee	
	USNM	47413	Tennessee	
	USNM	306058	Virginia	
<i>Sciurus vulgaris</i>				
	<i>infuscatus</i>	BMNHL	7.10.17.1	Spain
	<i>infuscatus</i>	BMNHL	25.7.1.9	Spain
	?	BMNHL	471.115	Yugoslavia
	?	BMNHL	1937.3.22.108	Yugoslavia

^aBMNHL = British Museum of Natural History (London, U.K.); MVZ = Museum of Vertebrate Zoology (Berkeley, CA); USNM = National Museum of Natural History (Washington, DC); ZIN = Zoological Institutes of the Russian Academy of Sciences (St. Petersburg, Russia), oc = osteological collection; PNGP = National Park Gran Paradiso (Torino, Italy); SC = collection of Dino Scaravelli; DBA UMR = Department of Animal Biology, University of Modena and Reggio Emilia; MSNM Ma = Museo di Storia Naturale di Milano.

^bGeographic position of mountain ranges. Alatau: Kazakhstan, Kirghizistan, Uzbekistan; Altaj: Mongolia, south Siberia; Thian Shan: Kirghizistan, China; Alai: Kirghizistan; Pamir: Tagikistan.

^c*Spermophilus undulatus* (Pallas, 1778) is a senior synonym of *S. eversmanni* (Hoffmann et al., 1993), which is the species name in the BMNHL collection.

^dThe specimens were classified as *Eutamias sibiricus* in the USNM collection, but *Eutamias* was considered a subgenus of *Tamias* by Hoffmann et al. (1993).

APPENDIX 2 ADULT IDENTIFICATION

The age of *Marmota flaviventris* specimens was estimated using Van Vuren and Salsbury's (1992) linear regression of age onto the paraconid–protoconid distance of the lower left premolar (Cardini and Tongiorgi, in press). Because no similar technique was available for evaluating age in the other marmot species (unless it has been published in the extensive but not easily accessible Russian literature), a method was developed to approximately recognize the adult speci-

mens. The mandible morphology and the dental measurements were combined to identify clusters of homogeneous specimens that roughly correspond to young and adults. In yellow-bellied marmots, young and adults have markedly different mandibles, but size and shape changes are extremely limited after sexual maturation (Cardini and Tongiorgi, in press). The gap between premolar cusps increases with age until yellow-bellied marmots are 4 years old (Van Vuren and Salsbury, 1992). Similar morphological trends are likely to hold for all marmot species, and the mandible form and the premolar wear were thus chosen for identifying adult specimens. The adult discrimination proceeded in three steps. First, unweighted pair-group average (UPGMA) cluster analysis of the matrix of squared Procrustes distances was used to find groups with marked differences in mandibular shape (the distances were squared to emphasize the separation between the main clusters). Then, a scatterplot of lower left premolar wear vs. mandibular size was employed to establish the correspondence between mandibular clusters and age groups. Clusters characterized by modest wear and small size corresponded to putative young, and large values of the two variables identified putative adults. Third, eventually, whenever the sample size was adequate and the statistical assumptions were not violated, a logistic regression of the two putative age groups (young and adult clusters) onto the mandible size and the paraconid–protoconid distance was performed to introduce a second criterion that may correct for possible misclassified specimens. Logistic regression was chosen over discriminant analysis because it is less sensitive to violations of the statistical assumptions and more suitable when the sample size is small or differs greatly in the two compared groups (Manly, 1994; Fabbri, 1997; Hair et al., 1998). The efficiency of the three-step method in discriminating adult marmots was tested in the yellow-bellied marmot sample. In four random subsamples of the same species, the results were compared with the age estimates of Van Vuren and Salsbury (1992). The adult hit ratio (adults correctly classified/total adults) was >95% in three samples and 75% and 62% in the other two. The misclassified young were never >4.6% of the specimens in the predicted group of adults. Because two other measures of premolar wear were available (paraconid–metaconid and protoconid–metaconid distances), other combinations of variables/techniques were tried to discriminate the two main age classes, but none of them worked as well as or better than the three-step method in recognizing the adults of *M. flaviventris*. Although the adult discrimination is rough and the method could not be tested on animals of known age or verified in other marmot species, it is likely to provide groups of morphologically homogeneous specimens. The classification outcome was partially confirmed by the putative adults having fully erupted teeth (Hoffmann et al., 1979; Pole, unpubl.). For premolar wear, mandibular size, and shape variables, differences between the groups of presumed young and adults were tested in all marmot species, always leading to significant results. The specimens of the outgroup species were chosen among those with fully erupted teeth to minimize age variability.