

Patterns of morphological evolution in *Marmota* (Rodentia, Sciuridae): geometric morphometrics of the cranium in the context of marmot phylogeny, ecology and conservation

ANDREA CARDINI^{1,3*} and PAUL O'HIGGINS^{1,2}

¹Hull York Medical School and ²Department of Biology, The University of York, Heslington, York, UK

³The University of Hull, Cottingham Road, Hull, UK

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Marmots are of great interest for both sociobiologists studying the evolution of mammal societies and conservationists trying to protect them from extinction. In contrast, their phylogeny and morphological evolution are poorly understood and studied. Recently, a phylogenetic analysis using cytochrome *b* provided the first reconstruction of marmot evolutionary history and suggested that a high level of sociality evolved at least twice independently in the two proposed marmot subgenera. A morphological analysis of the marmot mandible supported this subgeneric classification and showed interesting, and unexpected, patterns in the evolution of marmot skeletal characters. In the present study we investigated a more complex, and potentially informative structure, the ventral cranium. Geometric morphometric techniques were applied in the first analysis of cranial morphology including all marmot species. Three main phenetic groups were found, which reflect phylogeny (subgenus *Petromarmota*, and Palaearctic subgenus *Marmota*) or geographical distribution (Palaeartic vs. Nearctic subgenus *Marmota*). Convergence in skeletal characters due to size similarities, a common finding in the sciurid skeleton according to traditional morphological analyses, did not occur in the marmot ventral cranium. Despite a genetic distance between *Marmota vancouverensis* and *Marmota caligata* similar to that among different populations of the latter species, the Vancouver Island marmot had the most atypical ventral cranium in the subgenus *Petromarmota*. This finding confirmed results obtained with the mandible, and emphasized the uniqueness of *M. vancouverensis* and the usefulness of complementing molecular analyses with morphological studies for a thorough characterization of population divergence, and a careful planning of conservation strategies. © 2004 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2004, 82, 385–407

ADDITIONAL KEYWORDS: convergence – genetic drift – ventral cranium.

INTRODUCTION

Marmots are rodents of the family Sciuridae, a highly diversified and cosmopolitan group that diverged early within the rodent clade retaining primitive morphological characters (Mercer & Roth, 2003). Contrary to the majority of species in this taxon, marmots and their closest relatives (*Ammospermophilus*, *Cynomys*, *Spermophilus* of the tribe Marmotini) do not have an

arboreal lifestyle and live exclusively, or prevalently, on the ground (hence the name terrestrial squirrels).

Marmots are found in mountain meadows and cold steppes all over the Holarctic (Barash, 1989). They often form large colonies, dig huge den systems and feed prevalently on dicots and grasses (Armitage, 2000). Among mammals, they are exceptional for being the largest true hibernating animals in this class. They are also noteworthy for having complex societies. Marmot characteristics such as size increase, reproductive skipping, hibernation and a high degree of sociality are adaptations to harsh envi-

*Corresponding author. E-mail: andrea.cardini@hyms.ac.uk

ronments with very short growing seasons (Armitage, 2000) typical of the periglacial habitat in which marmots evolved (Zimina & Gerasimov, 1973; cited in Armitage, 2000).

Marmots originated in the Nearctic 9.5 Mya from a ground-squirrel lineage, they colonized the Palaearctic at the beginning of (or immediately before) the Pleistocene (Armitage, 2000), and gave rise to two main lineages, according to the cytochrome *b* gene tree (Steppan *et al.*, 1999): the subgenus *Marmota* includes all Palaearctic species plus two North American species, *Marmota broweri* and *Marmota monax*, while the subgenus *Petromarmota* is composed exclusively of Nearctic species. (To avoid confusion between *Marmota* as a genus and *Marmota* as a subgenus, the latter will here be indicated with *Marmota*_{SG}.)

Marmots have a central position in the study of mammalian social evolution (Barash, 1974; Arnold, 1990; Armitage, 1999, 2000), and they are also of interest with regard to their morphological evolution (Hoffman, Koeppel & Nader, 1979; Cardini, 2003). For instance, it has been claimed that the sciurid skeleton has a propensity to morphological convergence (Hafner, 1984; Roth, 1996; Velaghen & Roth, 1997). In this respect, the first morphological analysis of the mandible that included all marmot species produced unexpectedly informative results with respect to phylogeny (Cardini, 2003). The shape of the mandible supported the monophyly of *Marmota*_{SG} and the close similarity of the two main species of *Petromarmota* (*Marmota flaviventris* and *Marmota caligata*), while the Vancouver Island marmot (*M. vancouverensis*) emerged as the most peculiar species with regard to mandibular morphology. Convergence due to size similarities was not found nor was congruence evident between mandibular shape clusters and the few ecological characters available for all species. Also, a basal position of *M. broweri* in *Marmota*_{SG}, suggested by the Steppan *et al.* (1999) gene tree, was corroborated by mandibular morphology. This observation gives further support to the rejection of disputed hypotheses about the origin of the Alaskan marmot, *M. broweri*, considered by different authors either as a recent offshoot of a Palaearctic lineage returned to the Nearctic (Gromov *et al.*, 1965; cited in Hoffmann & Nadler, 1968; Rausch & Rausch, 1971; Hoffmann *et al.*, 1979; Steppan *et al.*, 1999) or as a subspecies of the North American *M. caligata* (Hall, 1981).

The intriguing outcome of the analysis of the marmot mandible, with its simple anatomy, encouraged us to continue this study using potentially more informative structures. Thus, the anatomical complexity of the skull may offer stimulating insights into marmot morphological evolution and no analysis of the skull including all living species of *Marmota* has yet been carried out.

In this study we apply geometric morphometric techniques (Rohlf & Marcus, 1993; Adams, Rohlf & Slice, 2004) to the form of the ventral aspect of the cranium (VC) of all living marmot species, and compare the results with those for the mandible (Cardini, 2003) and with the cytochrome *b* gene tree (Steppan *et al.*, 1999). The VC is a particularly promising structure as anatomical landmarks are numerous. Further, much of this aspect of the cranium is directly involved in the mechanics of mastication and in another study we demonstrate that it covaries with the mandible during development in a highly integrated way (Cardini *et al.*, 2003). Furthermore, ecological and behavioural changes (especially, the increase in social and communicatory complexity) during the radiation of marmots may have affected the brain and the sense organs, with possible implications for VC morphology.

In particular we address three specific issues:

1. To what extent does VC morphological variation reflect phylogeny? To this end we compare the pattern of phenetic relationships obtained through a geometric morphometric study of shape with published phylogenetic (cytochrome *b* gene tree) analyses and the results of the previous morphological study of the mandible.
2. To what extent does VC morphological variation reflect size variability? Thus we consider if the patterns of phenetic relationships arising from our geometric morphometric study are congruent with patterns of size variability. The finding of a significant relationship would support hypotheses of sciurid propensity to skeletal homoplasy contrary to the findings from the mandible (Cardini, 2003), but congruent with previous studies on sciurids. Related to this question is the possible role of interspecific allometry in modelling the VC.
3. Is the *M. vancouverensis* VC atypical among marmots? *Marmota vancouverensis* is one of the most endangered mammal species, surviving in the wild with less than 50 specimens (Bryant, 2002; Wilson, 2002). Despite a strong effort to save this species from extinction (Bryant, 2002), its biological uniqueness has been questioned as cytochrome *b* studies have suggested that genetic differences between *M. vancouverensis* and its sister species, *M. caligata*, are of similar degree to those found among populations of *M. caligata* (Steppan *et al.*, 1999). Cardini (2003) showed that the morphological peculiarities of *M. vancouverensis* are not limited to its external morphology (it is the only melanistic marmot), and he interpreted the atypical features of its mandible as a by-product of geographical isolation on the Vancouver Island during the last 10 000–100 000 years. Genetic drift during severe population bottlenecks may have acted as an accelerator of morphological evolution making this young species the most peculiar marmot

for mandibular shape (Cardini, 2003). The investigation of uniqueness needs to be extended to other structures, like the VC. By detecting unique shape features despite very small genetic differences, morphological investigations may indeed help to underline the 'value' of a species for conservation policies, and may also improve our knowledge about models of accelerated

morphological evolution and speciation in peripheral isolates (the classical peripatric model by Mayr, 1963).

MATERIAL AND METHODS

354 adult specimens of all 14 living marmot species were examined (Table 1; Appendix). Adults were dis-

Table 1. Marmots and related species examined

Species*		N_{females}	N_{males}	$N_{\text{total}}\ddagger$
Marmotini				
<i>Marmota</i> (MAR)				
subgenus <i>Marmota</i>				
<i>M. baibacina</i> (bai)	(Kastschenko, 1899)	6	5	17
<i>M. bobak</i> (bob)	(Müller, 1776)	8	9	18
<i>M. broweri</i> (bro)	(Hall & Gillmore, 1934)	1	1	2
<i>M. camtschatica</i> (cam)	(Pallas, 1811)	9	10	21
<i>M. caudata</i> (cau)	(Geoffroy, 1844)	18	14	35
<i>M. himalayana</i> (him)	(Hodgson, 1841)	12	15	31
<i>M. marmota</i> (mar)	(Linnaeus, 1758)	5	8	25
<i>M. menzbieri</i> (men)	(Kashkarov, 1925)	4	3	7
<i>M. monax</i> (mon)	(Linnaeus, 1758)	23	22	56
<i>M. sibirica</i> (sib)	(Radde, 1862)	6	11	18
subgenus <i>Petromarmota</i>				
<i>M. caligata</i> (cal)	(Eschscholtz, 1829)	27	19	47
<i>M. flaviventris</i> (fla)	(Audubon & Bachman, 1841)	32	24	59
<i>M. olympus</i> (oly)	(Merriam, 1898)	5	6	11
<i>M. vancouverensis</i> (van)	(Swarth, 1911)	4	3	7
'Outgroup'				
<i>Spermophilus</i>				
subgenus <i>Otospermophilus</i>				
<i>S. variegatus</i> (spev)	(Erxleben, 1777)	2		2
subgenus <i>Spermophilus</i>				
<i>S. beldingi</i> (speb)	(Merriam, 1888)	1	2	4
<i>S. citellus</i> (spec)	(Linnaeus, 1766)	2	3	5
<i>S. richardsoni</i> (sper)	(Sabine, 1822)	1	1	3
<i>S. undulatus</i> (speu)	(Pallas, 1778)	‡	‡	2
<i>Cynomys</i>				
subgenus <i>Cynomys</i>				
<i>C. ludovicianus</i> (cynl)	(Ord, 1815)	‡	1	4
subgenus <i>Leucocrossuromys</i>				
<i>C. leucurus</i> (cynle)	(Merriam, 1890)	1		1
Tamiini				
<i>Tamias</i>				
subgenus <i>Eutamias</i>				
<i>T. sibiricus</i> (tamsi)	(Laxmann, 1769)	1	2	3
subgenus <i>Neotamias</i>				
<i>T. amoenus</i> (tama)	(Allen, 1890)	2	1	3
subgenus <i>Tamias</i>				
<i>T. striatus</i> (tams)	(Linnaeus, 1758)	1	1	3
Sciurini				
<i>Sciurus</i>				
<i>S. vulgaris</i> (sciv)	(Linnaeus, 1758)	1	2	3

*Abbreviations for species names used in figures are given in parentheses. †Including specimens of unknown sex.

‡No available information on sex.

Table 2. Definition and numbering of ventral cranial landmarks

Number	Definition*
1	Anterior (midsagittal) tip of the premaxilla
2	Posterior extremity of the incisor alveolus
3–4	Extremities of incisive foramen
5	Tip of the masseteric tubercle
6	Anterior extremity of the toothrow
7	Posterior maxillary foramen
8	Posterior palatine foramen
9	Suture between maxilla and palatine along the midsagittal plane
10	Point of maximum curvature on the posterior edge of the palatine
11	Meeting point between basisphenoid and presphenoid where the anterior <i>foramen lacerum</i> typically opens
12	Anterior extremity of the suture between the alisphenoid and the zygomatic process of the squamosal
13	Posterior tip of the zygomatic arch
14–15	Anterior and posterior tip of the external auditory meatus
16	Posterior extremity of the foramen ovale
17	Meeting point between the basisphenoid, basioccipital and tympanic bulla
18	Anterior extremity of the jugular foramen
19–20	Lateral tips of the occipital condyle
21	Most posterior point on the ventral region of the occipital foramen
22	Upper extremity of the incisor alveolus
23	Most lateral point of the rostrum along the suture between the premaxilla and the maxilla
24	Most anterior point of the orbit (in the ventral view)
25	Marked change in curvature along the anterior region of the upper internal side of the zygomatic arch
26	Anterior region of the squamosal zygomatic process where it joins the zygomatic arch

*The terms 'anterior', 'posterior' and 'upper' or 'lower' are used with reference to Fig. 1.

tinguished as described by Cardini (2003) on the same sample using tooth wear and differences in mandibular size and shape between young and adults. The identification of adults is supported by a plot of PC1 of the VC shape variables against VC size in which putative young and adults form two distinct groups. A further 33 specimens belonging to four other sciurid genera are included in the present study to provide reference to an outgroup (Table 1; Appendix).

A set (configuration) of 26 landmarks (L), digitized on pictures taken under standardized conditions (Cardini & Tongiorgi, 2003), was employed to describe the VC (Table 2; Fig. 1). Landmarks were digitized only on the left side to avoid redundant information in symmetric structures. Landmark precision was tested. A subsample of specimens (representing all species) was digitized three times on three successive days by the same person. Profile plots of the landmark coordinates were used to detect landmarks with relatively large variation between repetitions. An unweighted pair-group method using arithmetic average (UPGMA) cluster analysis of the matrices of Procrustes distances (see below) among all specimens from the three repetitions was used to verify that variation in the landmark coordinates due to digitizing error was negligible compared to shape differences among specimens. Landmarks on the internal side of the

zygomatic arch (landmarks 24–26) were not always located with high repeatability, but the three repeats always clustered together and correlation between the matrices of Procrustes distances from each of the repetitions is very high (Mantel test $r \geq 0.960$). Digitizing error was, therefore, negligible compared to differences among specimens.

Shape variables (see Bookstein, 1991; Dryden & Mardia, 1998; for computational details) were obtained as linear combinations of the original landmark coordinates after standardizing size and removing artefactual variation due to different positions of the specimens in the process of data collection (generalized Procrustes analysis, Rohlf & Slice, 1990). Size information was retained as centroid size (CS), that is the square root of the sum of squared distances between each landmark and the centroid of the landmark configuration. Shape differences were visualized with deformation grids in the style of Thompson (1917), where an object (reference) is deformed into another (target) and shape features can be described in terms of deformation grids depicting the differences between objects (Adams *et al.*, 2004). The thin plate spline (TPS) algorithm (Bookstein, 1991) was used to compute the deformation grid with least bending energy between reference and target landmark configurations. In all figures the average of the landmark

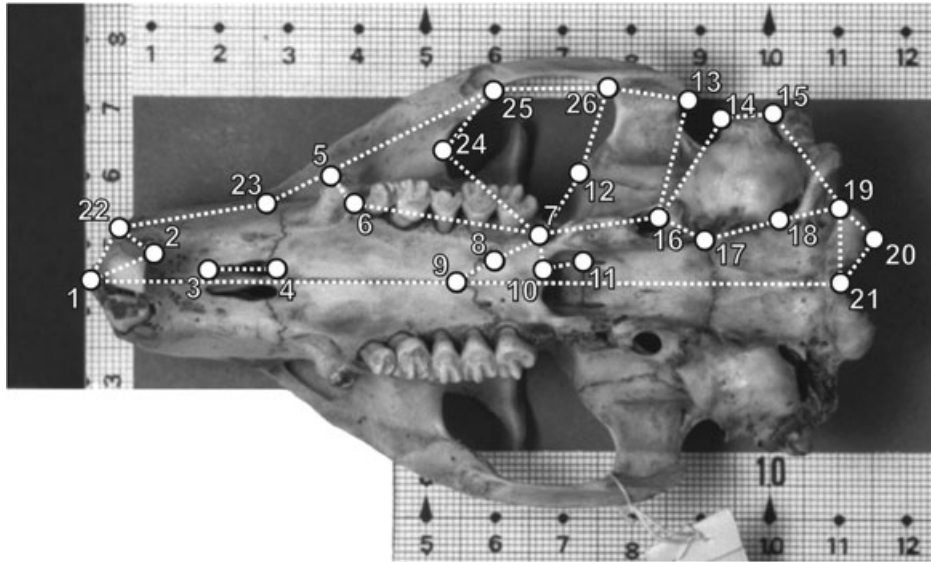


Figure 1. Landmark configuration for the ventral aspect of the cranium and wireframe used for 'stylized' drawings.

configurations (i.e. the configuration that is obtained by averaging specimen landmark coordinates in the generalized Procrustes analysis) is used as reference and shown in light grey, while the target configuration is shown in black.

Points representing landmark configurations are projected into a Euclidean tangent space that approximates the curved shape space to aid statistical analyses. This approach is satisfactory when variations are small (Rohlf, 2003), as in the present data (results not shown).

Size was compared between sexes and across species with a two-way (sex \times species) analysis of variance (ANOVA). Multivariate analysis of variance (MANOVA) and canonical variate analysis (CVA) were used for comparing shape among groups (sexes and species). *Marmota broweri* was excluded from analyses of variances and CVA with separate sexes because its sample size was inadequate ($N = 2$). Shape variables were regressed onto the first two CVA axes to illustrate shape changes along them. Interspecific shape differences were also analysed with principal component analysis (PCA) of the shape variables.

Heteroscedasticity in the ANOVA for CS was detected by means of Levene's test ($P = 5.5 \times 10^{-4}$) and ANOVA results must, thus, be interpreted with caution. Homoscedasticity in the multivariate comparisons (MANOVA and CVA) could not be verified as the number of variables is larger than sample size for most species, a common problem in taxonomic studies (Marcus, 1990).

Interspecific allometry was investigated with a multivariate regression of shape variables onto size, and slopes of allometric trajectories were compared among

species with a test for common slopes (TPSRegr 1.26, Rohlf, 2003). Size was not log-transformed as in Cardini (2003) because log-transformation leads to a negligible increase in the proportion of shape variance explained by size variation when only adults are analysed.

Phenetic relationships were investigated through cluster analysis and principal components analysis of the mean landmark configurations of each species. Cluster analysis was performed on the matrix of Procrustes distances. Procrustes distances measure multivariate distances between pairs of specimens computed directly in the shape space. UPGMA and the nearest neighbour clustering algorithms were chosen as they led to phenograms with the largest cophenetic correlations (Rohlf, 1970, 2002) to the original Procrustes distance matrix compared to other algorithms (complete linkage, unweighted pair-group method using centroid average, weighted pair-group method using arithmetic or centroid averages). A strict consensus tree was computed based on these methods. Lines proportional to mean VC size in each species were drawn in the phenograms to help detect size-related convergence. Information on social complexity (index described in Blumstein & Armitage, 1997) and the number of different alarm calls (communication complexity, Blumstein, 2003) are also shown on the phenograms. Behavioural data were not available for all species, and are thus presented only for a subset of the studied taxa.

Programs of the TPS Series (Rohlf, 2003), *Morpheus et al.* (Slice, 1999) and *morphologika* (O'Higgins & Jones, 1999) were used for geometric morphometric analyses. Statistical analyses were performed with

NTSYSpc (Rohlf, 2002) and STATISTICA (Statistica for Windows, 1997).

RESULTS

Sexual dimorphism is highly significant for both VC size and shape (Tables 3 and 4). Males are, on average, larger than females in all species. Interspecific differences are highly significant, while sex \times species interaction is not significant. The latter observation, and the much smaller F (size) and Wilks' λ (shape), suggests that sexual dimorphism is actually quite modest compared to interspecific differences. Indeed, a CVA of shape variables with separate samples for sexes shows that only *M. caligata* ($P < 0.01$) and *M. flaviventris* ($P < 0.05$) have significant sexual dimorphism. Different sexes of each species first group together (results not shown) in a cluster analysis of the mean VC shapes for males and females (all species included). Sexual dimorphism in VC shape is thus negligible in the interspecific comparison, and all further analyses are performed with pooled sexes.

Large differences between all studied species are confirmed in a CVA (all species included, pooled sexes: $F_{624,3733} = 10.414$, $P < 0.0001$, total hit ratio 99.4%). Pairwise comparison of Mahalanobis' distances is highly significant ($P < 0.000001$) for all species pairs, except a few comparisons involving *M. broweri* (very low statistical power in the smallest $-n_{broweri}=2$ -sample). Three main clusters are evident in the ordination of specimens along the first two CVA axes (Fig. 2A): *Petromarmota*, Palearctic *Marmota*_{SG} and *M. monax*. *Marmota broweri* is somewhat in between the latter two groups. TPS deformation grids for specimens at

the extremes of each axis are used in Figure 2A to describe the main features of the VC in the three groups. Generally, species of *Marmota*_{SG} have a relatively elongated VC, but *M. monax* is exceptional in its longitudinally compressed VC and relatively enlarged zygomatic arch and cranial base. *Petromarmota* is intermediate in shape between these two groups. The same three clusters are visible, although less clearly so, in a plot of PC1 vs. PC3 (Fig. 2B), and shape features similar to those described along CVA axes characterize the three groups.

Interspecific allometry, although highly significant ($\lambda_{\text{Wilks}} = 0.180$, $F_{48,305.0} = 29.040$, $P = 7.0 \times 10^{-88}$), explains a small percentage (8.3%, Goodall's $F_{48,16896} = 31.6872$, $P < 0.0001$) of shape differences among specimens of all marmot species. Magnified ($\times 2$) TPS deformation grids for shapes predicted by the linear regression model at the extremes of size variation in the genus *Marmota* are very similar to those that describe size-related shape changes during marmot VC development (results not shown). With increasing centroid size, relative to the landmark configuration as a whole, the zygomatic arch (L13, L23–26) enlarges and the snout (L1–4, L22–23) becomes longer. Additionally, the foramen magnum (L20–21) is relatively bigger in small individuals and negative allometry characterizes the palate (L7–11) and tympanic bulla (approximately, L14–19). Slopes of species-specific regression lines are not homogeneous (test for common slopes after exclusion of *M. broweri*: $\lambda_{\text{Wilks}} = 0.0683$, $F_{576,3296.5} = 1.482$, $P = 5.2 \times 10^{-11}$).

Mean species shapes were also submitted to PCA and cluster analysis. The multidimensional shape relationships are better summarized by the PCA in that the Euclidean distance matrix based on the first

Table 3. ANOVA sex \times species for mandibular centroid size in *Marmota* (excluding *M. broweri*)

Effect	Sum of squares	d.f.	F	P
Sex	134 223	1	23.926	1.7×10^{-6}
Species	277 879	12	49.533	0*
Sex \times species	4 716	12	0.841	0.608
Error	5 610	282		

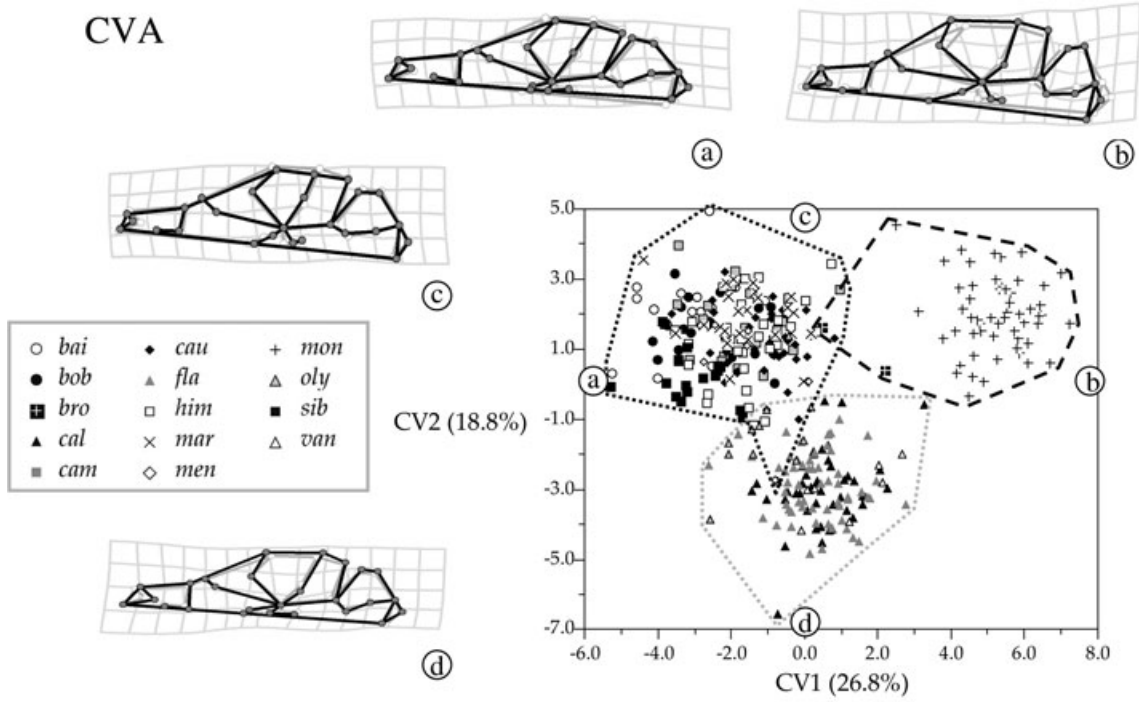
* P -values smaller than the minimum value ($P = 1 \times 10^{-6}$) that can be displayed by STATISTICA (Statistica for Windows, 1997).

Table 4. MANOVA sex \times species for the VC shape in *Marmota* (excluding *M. broweri*)

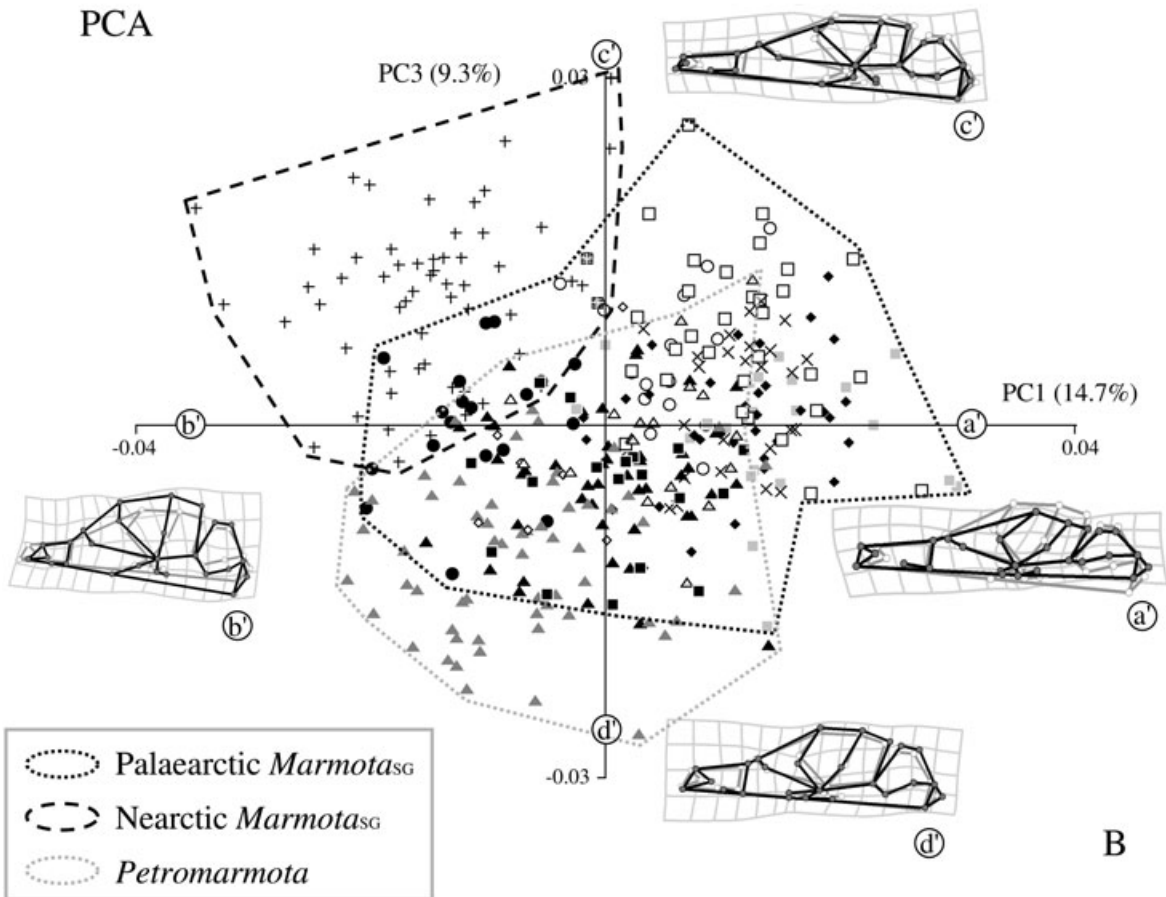
Effect	λ_{Wilks}	d.f.	P
Sex	0.715	48 235	6.1×10^{-4}
Species	3.0×10^{-6}	5762 783	0*
Sex \times species	0.124	5762 783	0.786

* P -values smaller than the minimum value ($P = 1 \times 10^{-6}$) that can be displayed by STATISTICA (Statistica for Windows, 1997).

Figure 2. Scatterplot of canonical variate (CV)1, CV2 (A) and principal component (PC)1, PC3 (B) (percentage of variance in parentheses). For both ordination plots, thin plate spline deformation grids for the extreme points (letters) of each axis are shown (deformation grids are magnified $\times 3$); these are superimposed on the shapes predicted when the average landmark configuration of all specimens is deformed into that of a hypothetical specimen positioned at the extreme point of an ordination axis. In this Figure, and in Figures 3–5, both the reference (grey) and target (black) are shown in each deformation plot. (See Table 1 for expanded species abbreviations.)



A



B

three PCA axes has a 0.932 correlation to the matrix of the original Procrustes distances vs. only 0.734–0.713 of UPGMA or nearest neighbour phenograms.

Three major groups are visible in the plot of the first three PCA axes (Fig. 3). Palaeartic species of *Marmota*_{SG} are separated from *Petromarmota* and Nearctic *Marmota*_{SG} species along PC2 and PC3. *Petromarmota* species are relatively close to one another and not far (especially *Marmota olympus*) from the cluster of Eurasian marmots. Nearctic *Marmota*_{SG} are clearly distant from all other species. The general pattern of morphological differences outlined in the CVA is confirmed by the deformation grids for the average VC of the three main clusters (Fig. 3).

The consensus phenogram of marmot mean shapes (Fig. 4) emphasizes the peculiarity of *M. broweri* and *M. monax*, but also indicates that *M. vancouverensis* has some unique features, especially affecting the maxillary (L24) and squamosal processes (L12) of the zygomatic arch, and the tympanic bulla (L14). The effect of sampling error on phenogram topology is investigated by splitting each species sample into two equal halves. In each subset mean VC shapes are computed for each species and these are compared by examining the resultant UPGMA phenograms. Four clusters, among those found in the complete dataset, are found from both subsets (branches drawn with thicker lines in Fig. 4).

Outgroup mean shapes are computed as were the marmots in this study and submitted to UPGMA clustering following joint GPA with the overall marmot generic mean (marmot species cluster together if analysed with outgroup taxa). The resulting phenogram is presented in Figure 5. Congeneric species always cluster together, and the tribe Marmotini is clearly discriminated by VC morphology. *Spermophilus* is fairly similar to *Marmota*, but *Spermophilus variegatus* is atypical in possessing a relatively long maxilla (L23) and compressed zygomatic arch (L13, L25–26).

No clusters clearly reflecting size similarities in the VC are evident in either phenogram (Figs 4 and 5). Further, behavioural variables (where we have data on these) do not seem to be congruent with species clusters. For instance, in *Petromarmota*, *M. caligata* is closer to *M. flaviventris* for VC shape, despite closer phylogenetic relationships and similarities in size, complexity of social behaviour and number of alarm

calls between *M. caligata*, *M. vancouverensis* and *M. olympus*. The clustering of *Marmota camtschatica* with *Marmota caudata* is the only case that might reflect similarities in social system and communication complexity.

DISCUSSION

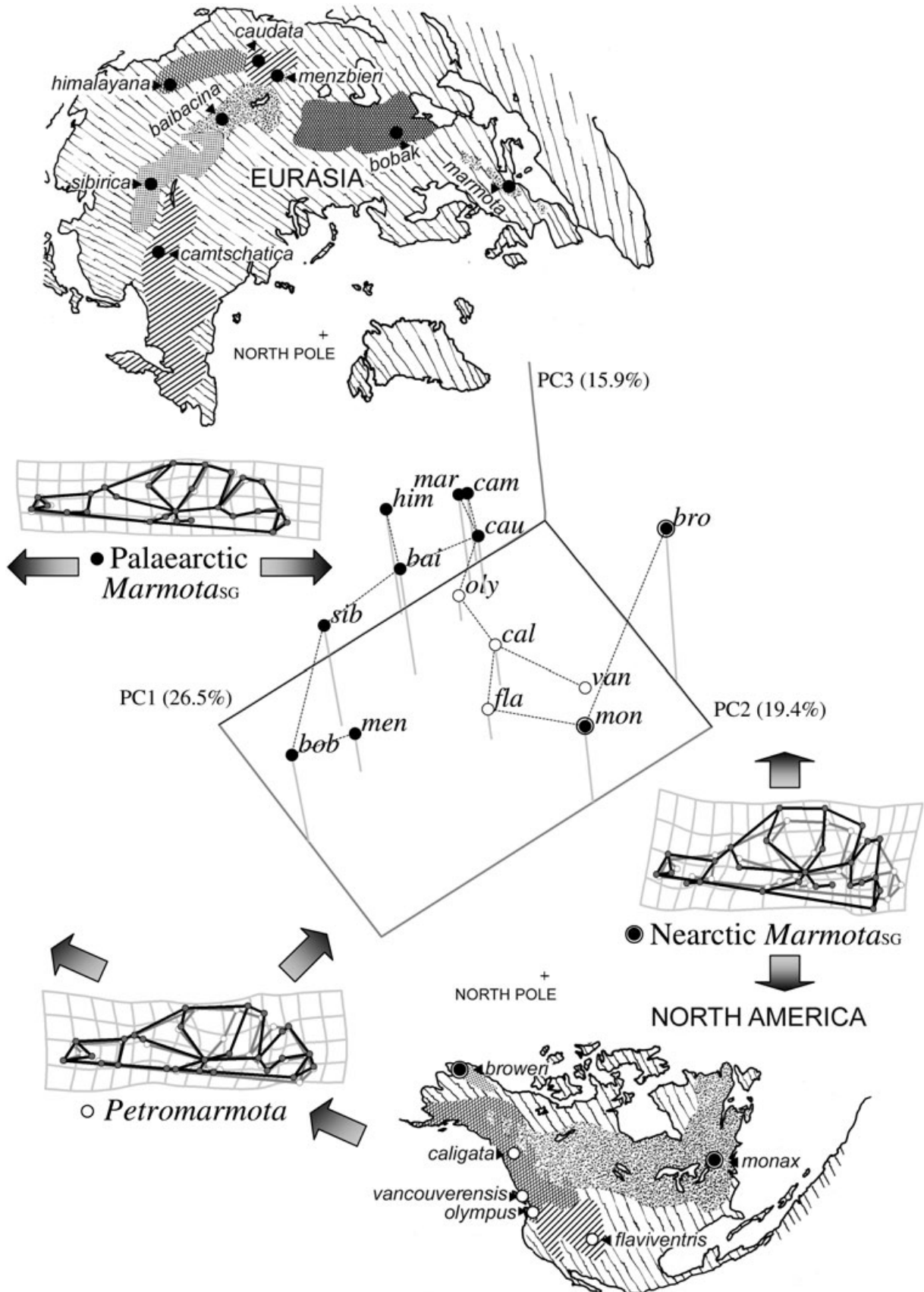
The present study is a phenetic rather than phylogenetic study. This is because our aim is not to reconstruct phylogeny but rather to examine variations in VC shape in the context of phylogeny and other possible factors contributing to these variations. These other factors include allometric effects, homoplasy, accelerated evolution, genetic drift and, of course possible sampling or measurement errors. These kinds of morphometric studies on patterns of morphological evolution have been termed (Smith, 1990) 'postcladistic morphological analysis of monophyletic groups'. In particular, this study focuses on three main questions.

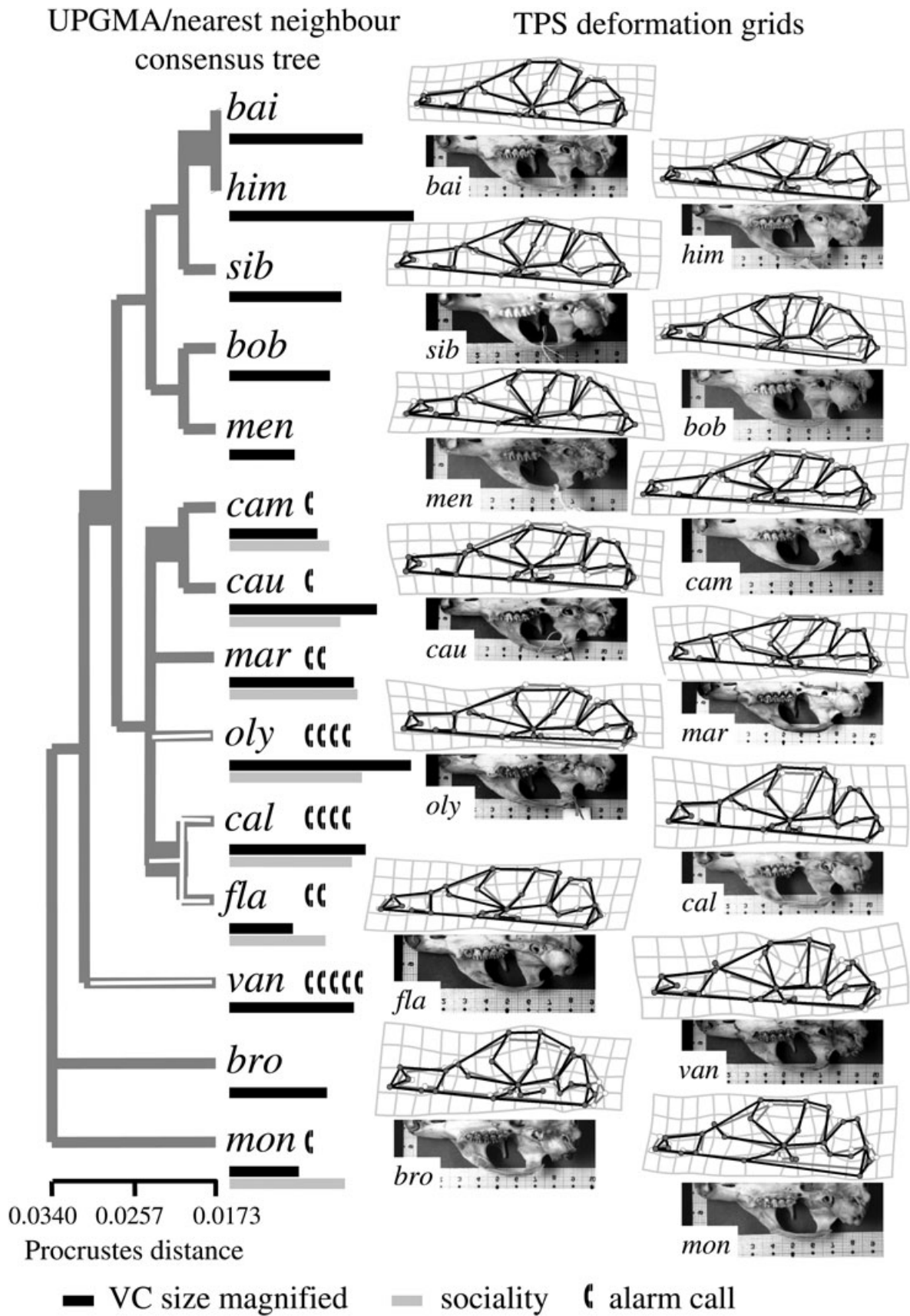
TO WHAT EXTENT DOES VC MORPHOLOGICAL VARIATION REFLECT PHYLOGENY?

In common with the results obtained for the mandible, there are strong shape similarities in the VC between the two most important (for geographical range and population size) *Petromarmota* species (*M. flaviventris* and *M. caligata*). Thus these species are in close proximity in the ordinations of Figures 2 and 3, in the cluster analyses (Fig. 4). *Marmota flaviventris*, the smallest living marmot, manifests some juvenile-like traits (a relatively short rostrum, enlarged bulla and occipital foramen, see inset, Fig. 4). However, the observation that *M. flaviventris* is similar to *M. caligata* despite large size differences suggests that shape similarities due to phylogeny are of greater importance than possible size-related shape differences.

In contrast to Cardini's (2003) findings from the mandible, the VC does not produce a *Marmota*_{SG} cluster. The main difference in the current study is the separation of *Marmota*_{SG} into two groups according to geographical distribution (Palaeartic and Nearctic groups, see ordinations in Figs 2 and 3). The North American representatives of *Marmota*_{SG} are highly peculiar species with relatively laterally enlarged (*M. broweri* and *M. monax*, see inset Fig. 3) and

Figure 3. First three axes of the principal component analysis (PCA) of mean ventral aspect of the cranium shapes with minimum spanning tree superimposed (Rohlf, 1970). Thin plate spline deformation grids for average shapes of the three main groups (Palaeartic *Marmota*_{SG}, Nearctic *Marmota*_{SG} and *Petromarmota*; magnified $\times 8$); arrows indicate the most pronounced shape differences between each group and the average of all marmot species. Marmot geographical distribution is shown (Barash, 1989; modified). (See Table 1 for expanded species abbreviations.)





longitudinally compressed (*M. monax*, see inset Fig. 4 with region defined by L1, L20–22 shrinking compared to the reference) VC.

In general, the overall differences in VC shape between Nearctic *Marmota*_{SG} and Palaeartic *Marmota*_{SG} appear larger than those between the latter and *Petromarmota*. Why is this? First, the results for *M. broweri* should be interpreted with caution because of the very small sample size. However, Cardini (2003) found that *M. broweri* was the most peculiar species in the subgenus *Marmota*_{SG} for mandibular shape, and related this finding to the hypothesized (Steppan *et al.*, 1999) ancient origin of *M. broweri* and its unique karyotype. Cardini's sample for the analysis of the mandible of *M. broweri* was small, but further studies including more specimens (A. Cardini, unpubl. data) support the finding that *M. broweri* possesses an unusual mandible that bears some similarities to those of *M. caudata* and *Marmota menzbieri*. If unusual features in the *M. broweri* cranium are confirmed in future studies, they may be due to accumulation of shape changes during a long, distinct, evolutionary history (Cardini, 2003), but geographical isolation and survival in small populations in the Brooks Range may also have contributed to the shaping of the skeletal characters of *M. broweri*. Second, a large sample was available for *M. monax*, and it is thus unlikely that its atypical VC is an artefact of sampling error. *Marmota monax* is also a basal lineage of *Marmota*_{SG} (Steppan *et al.*, 1999) and it manifests unique ecological characters among marmots. It is a solitary species, sexually mature as a yearling and lives at the boundary between meadows and forests. Thus, adaptations to an environment unusual for marmots may account for the evolution of peculiar traits of the VC in this species.

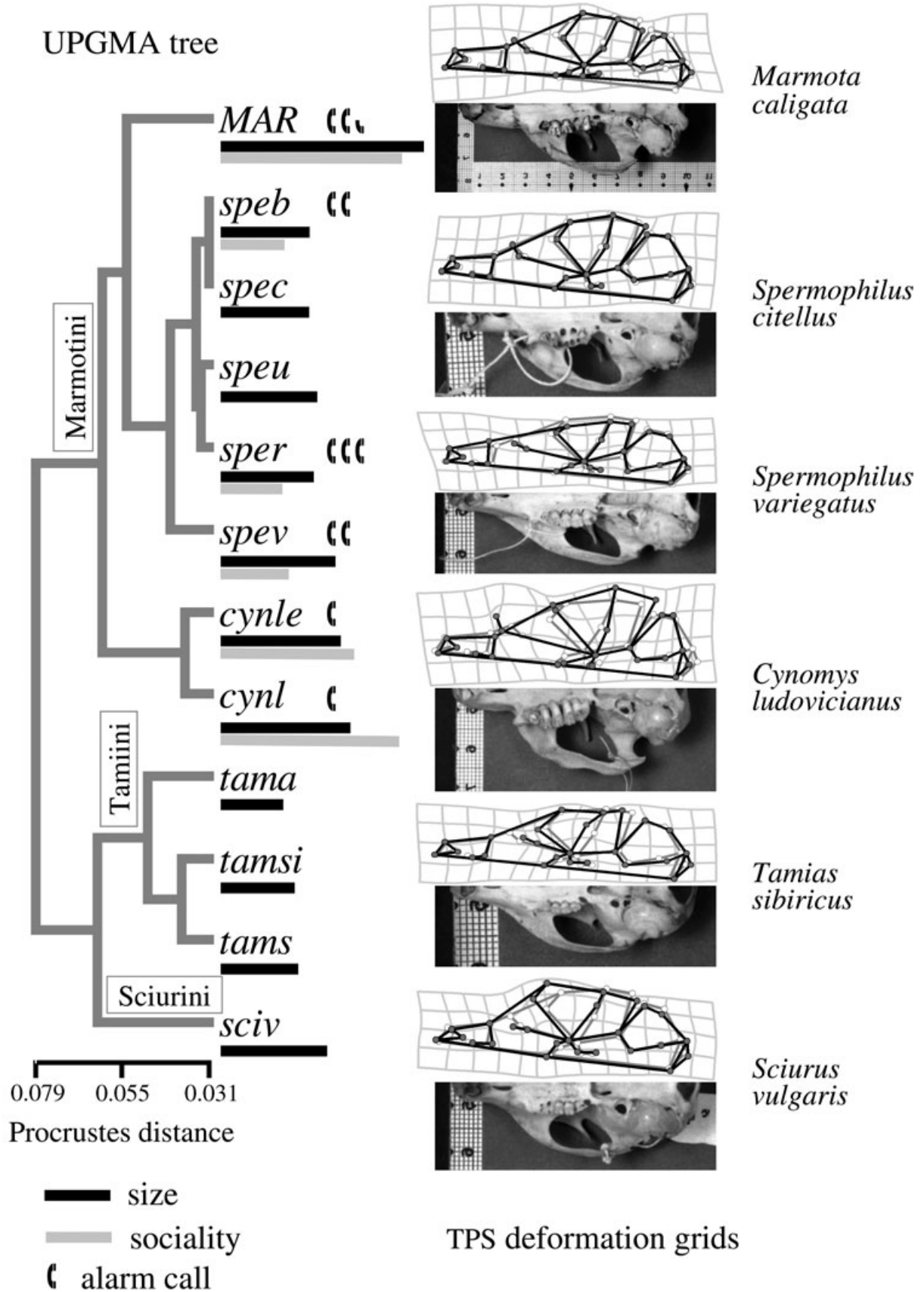
The patterns of shape variability among some of the other marmot species belonging to the main groups, *Petromarmota* and Palaeartic *Marmota*_{SG}, deserve discussion. Thus, *M. olympus* seems to possess VC morphology intermediate between typical *Petromarmota* (*M. caligata* and *M. flaviventris*, *sensu* Cardini, 2003) and Palaeartic *Marmota*_{SG} (Figs 3 and 4). A similar finding was made by Cardini (2003) who showed that *M. olympus* displays a combination of mandibular skeletal characters of the two marmot subgenera. Retention of 'plesiomorphic' traits (conser-

vative characters already present in the ancestor of all living marmots) and/or genetic drift may explain the observed skeletal features. Indeed, the present population of *M. olympus* consists of just a few thousand specimens, and genetic bottlenecks cannot be excluded during its long evolutionary history (Steppan *et al.*, 1999).

Among phenetic clusters found in the Palaeartic *Marmota*_{SG} group, similarities between *Marmota baibacina* and *Marmota sibirica* are interesting in a phylogenetic context. *Marmota baibacina* and *Marmota bobak* are sister species in the cytochrome *b* gene tree (Steppan *et al.*, 1999), while *M. sibirica* belongs to a different but related clade of central Asiatic species (together with *Marmota himalayana* and *M. camtschatica*). Cardini (2003) showed that mandibles of *M. baibacina* and *M. sibirica* are almost identical, and the two species represented the only case where sexual dimorphism was not negligible compared to interspecific differences. The VC is also very similar between *M. baibacina* and *M. sibirica*, although the latter is actually closer to *M. himalayana*. Further studies will be needed to explain why *M. baibacina* is similar to *M. sibirica* in craniomandibular morphology whilst apparently being more closely phylogenetically related to *M. bobak* (cytochrome *b* sequence) and to investigate the consequences of hybridization reported in the contact area between *M. baibacina* and either *M. sibirica* or *M. bobak* (Barash, 1989; Steppan *et al.*, 1999).

Cardini (2003) identified characters for the mandible that are approximately diagnostic of the two marmot subgenera. Thus, relative to *Marmota*, *Petromarmota* tends to have an enlarged ascending mandibular ramus, a relatively narrow diastema and a posteriorly displaced mental foramen. The situation with regard to the ventral cranium is less clear. Thus, *Petromarmota* turns out to be somewhat intermediate in VC shape between Nearctic *Marmota*_{SG} and Palaeartic *Marmota*_{SG} (Fig. 3). Further, if landmarks located in the zygomatic arch are excluded from the analysis (not presented), the pattern of clustering and the PCA plots no longer reflect phylogeny. Thus, an enlarged zygomatic arch (and an elongated angular process of the mandible) could be synapomorphic characters present in the ancestor of *Petromarmota*.

Figure 4. Strict consensus tree of UPGMA and nearest neighbour phenograms computed on the matrix of Procrustes distances among mean ventral aspect of the cranium (VC) shapes of marmot species. Lines proportional to VC size, thin plate spline (TPS) deformation grids (mean of *Marmota* to mean of *Marmota* sp.; magnified $\times 4$), and pictures (left sides reflected; not to scale) of real specimens most similar to the average shape of their own species are shown. For a subset of species, lines proportional to the index of social complexity and alarm call complexity (each 'phone' represents a different type of alarm call) are reported (data from Blumstein & Armitage, 1997; Blumstein, 2003). (See Table 1 for expanded species abbreviations.)



Geographic isolation in small populations may have modified these synapomorphies such that *M. olympus* retained a long angular process but evolved a compressed zygomatic arch, while the opposite occurred in *M. vancouverensis*. In noting this apparent phylogenetic signal in angular and zygomatic morphology we are aware that most ontogenetic modifications in the shape of the VC and mandible occur in regions directly involved in the mechanics of mastication (primarily, the zygomatic arch and the angular process). Thus it will be worth investigating in future studies the interaction between the epigenetic influences of muscle development and phylogeny in the zygomatic region.

We leave considerations of the phenetic relationships of *M. vancouverensis* to the last section of the Discussion. Finally we note here that an apparent phylogenetic signal in VC shape is found at intermediate levels of taxonomic hierarchy. Thus in Figure 5 not only are clusters found that correspond to genera and tribes, but also *S. variegatus* apparently possesses unusual traits among true ground squirrels. These may reflect its ancient evolutionary history (R. S. Hoffmann, pers. comm.). These results closely mirror Cardini's (2003) analysis of the mandible. It is noteworthy that the finding of better correspondence between cranial morphological variation and phylogeny at intermediate and higher taxonomic levels rather than at lower taxonomic levels concurs with studies of craniofacial homoplasy and its consequences for phylogenetic reconstruction in primates (Collard & Wood, 2000; Collard & O'Higgins, 2001).

TO WHAT EXTENT DOES VC MORPHOLOGICAL VARIATION REFLECT SIZE VARIABILITY?

Similarity in shape due to size similarities is not evident in the genus *Marmota* and, in general, in the Marmotini. This outcome corroborates Cardini's (2003) findings on the mandible and suggests that the sciurid skull may not be as conservative and inclined to convergence as is believed (Hafner, 1984; Roth, 1996; Verlaghen & Roth, 1997). However, incongruencies between phenetic relationships based on skeletal characters and presumed marmot phylogeny (Steppan *et al.*, 1999) are present, and they may have several, not mutually exclusive, explanations. (a) VC clusters may reflect ecological similarities. This issue has not

been addressed (except in a very preliminary way) in the present study due to the lack of availability of detailed eco-ethological variables. Changes in social complexity and alarm communication during marmot evolution might have affected the brain and sense organs (especially the ear), and indirectly the shape of the cranium. Our preliminary, and partial, data do not support convergence driven by similarity in social and communicative complexity. Furthermore, if the rough habitat classification followed by Cardini (2003) is adopted, again there are no clear signs of homoplasy (for instance, *M. broweri*, *M. camtschatica* and *M. sibirica* all live in mountain habitats with permafrost, but they are remarkably different in VC shape). Among the outgroup species, *Tamias* is the only candidate for possible ecology dependent homoplasy. *Tamias* is the adelphotaxon of the Marmotini in molecular phylogenies (Mercer & Roth, 2003), it mainly lives on the ground but it is an excellent climber and has more arboreal habits than other ground squirrels. The phenogram shows some similarities between *Tamias* and the only arboreal species in our study, the tree squirrel *Sciurus vulgaris*. (b) 'Plesiomorphic' characters and 'autoapomorphic' traits may have obscured the phylogenetic signal at lower taxonomic levels. (c) Sampling and measurement errors may have led to misrepresentation of phenetic relationships. To mitigate against these, photographic distortions and measurement errors were minimized by choosing almost coplanar landmarks and by taking pictures at a distance (1 m) more than ten times the length of a skull. Nonetheless, a relatively flat structure such as the hemimandible employed by Cardini (2003) may be more suitable for the application of two-dimensional geometric morphometric techniques, and this may contribute to the explanation of differences between VC, mandible and cytochrome *b* analyses. However, given the clear functional basis and anatomical localization of many of the shape differences presented in Figures 2–5 we would argue that the errors due to photographic projection are slight.

IS THE *M. VANCOUVERENSIS* VC ATYPICAL AMONG MARMOTS?

In contrast to the mandibular study (Cardini, 2003) *M. vancouverensis* is not as clearly atypical in VC.

Figure 5. An unweighted pair-group method using arithmetic average (UPGMA) phenogram computed on the matrix of Procrustes distances among mean ventral aspect of the cranium (VC) shapes of the genus *Marmota* and outgroup species. Lines proportional to VC size, thin plate spline (TPS) deformation grids (mean of *Marmota* + outgroup to mean of a species; magnified $\times 2$) and pictures of real specimens (reflected; not to scale) are shown for at least some of the analysed taxa. Lines proportional to the index of social complexity and alarm call complexity (each 'phone' represents a different type of alarm call) are reported for a subset of species (data from Blumstein & Armitage, 1997; Blumstein, 2003). Average values of marmot species (see Fig. 4) are used for the genus *Marmota*. (See Table 1 for expanded species abbreviations.)

Thus, it is close to *M. caligata* in the PCA of VC mean shapes, but clearly distinguishable along PC3. The phenogram (Fig. 4) suggests some peculiarities of the *M. vancouverensis* VC, and both UPGMA and nearest neighbour cluster analyses indicate that only the two Nearctic *Marmota*_{SG} species may have more unusual traits than those of *M. vancouverensis*. The divergence between *M. caligata* and *M. vancouverensis* is likely to have started at the end of the last glacial maximum (about 12 000 years ago) as Vancouver Island was previously largely covered by glaciers and continuous occupancy by *M. vancouverensis* during glaciations seems unlikely (D. W. Nagorsen, pers. comm.). This recent origin is congruent with the observation by Steppan *et al.* (1999) of a very small genetic distance between the two species. From this perspective, the morphological differentiation of the *M. vancouverensis* VC is exceptional, and supports Cardini's (2003) view that 'genetic drift . . . can greatly accelerate morphological evolution and may have contributed to the origin of morphological novelties in marmot skeletal structures'. *Marmota vancouverensis* may represent a case of morphological fluctuation of uncertain fate (Gould, 2002) in a peripheral population of *M. caligata*. Alternatively *M. vancouverensis* might be regarded as an incipient new species or a genuine biological species, if mechanisms of reproductive isolation have already arisen to prevent interbreeding with other populations (i.e. to prevent genetic amalgamation and loss of differentiation).

Skeletal morphology, melanistic fur, characteristic vocalizations and behaviour (Barash, 1989; Blumstein, 1999, 2003) point to remarkable peculiarities of *M. vancouverensis*, and emphasize the importance of conservation efforts to save *M. vancouverensis* from extinction (Bryant, 2002).

CONCLUSIONS

Three main conclusions can be drawn from the present study:

1. Three main marmot groupings are described by VC shape: *Petromarmota*, Palaeartic *Marmota*_{SG} and Nearctic *Marmota*_{SG}. The first two groups reflect the marmot classification into two subgenera and their geographical distribution, while the separation of Nearctic *Marmota*_{SG} may be related to the ancient origin of the North American representatives of this subgenus. The uncommon habitat of *M. monax* (the boundaries between meadows and forests on plains), and its unique solitary behaviour, could have contributed to the remodelling of its highly 'autoapomorphic' cranium. In contrast, its mandible may have retained 'plesiomorphic' traits as a consequence of apparently modest dietary differences from other marmots.

2. Marmots and outgroup species do not cluster according to similarities in VC size. Hence, the presence of significant size-related homoplasy in the VC is not supported. Future studies applying geometric morphometric techniques to skeletal characters in other sciurid taxa, and possibly also employing detailed ecological information, will be needed to decide whether the hypothesis of sciurid propensity to morphological convergence holds only in some lineages and/or anatomical structures. A negative answer to this question might suggest that previous findings were due to the inadequacy (problems of size standardization for shape comparisons, low statistical power, absence of information about geometry) of traditional morphometrics and might lead to the definitive rejection of the 'skeletal convergence hypothesis'.
3. Remarkably divergent morphological characters are found in *M. vancouverensis* despite its strong genetic relationships with *M. caligata*. The hypothesis of accelerated morphological evolution during genetic bottlenecks in the recent evolutionary history of *M. vancouverensis* is strengthened by the VC analysis. This outcome, together with findings on the mandible (Cardini, 2003) and behavioural observations (Barash, 1989; Blumstein, 1999, 2003), stresses the usefulness of complementing genetic analyses with morphological and ethological studies for assessing population uniqueness and carefully planning conservation strategies.

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APPENDIX

Museum catalogue number and locality of collection for the adult specimens*

sp. and ssp [†]	Museum	Catalogue number	Locality ^{‡,§}	ssp.	Museum	Catalogue number	Locality
<i>Marmota baibacina</i>							
<i>centralis</i>	BMNHL	12.4.1.41	Alatau	?	ZIN	63933	Altaj
<i>centralis</i>	BMNHL	12.4.1.39	Alatau	?	ZIN	63931	Altaj
<i>centralis</i>	BMNHL	14.5.10.74	Central Asia	?	ZIN	63930	Altaj
<i>centralis</i>	BMNHL	14.5.10.73	Central Asia	?	ZIN	50165	East Kazakhstan
<i>centralis</i>	BMNHL	8.3.2.74	Thian Shan	?	ZIN	84028	East Kazakhstan
?	BMNHL	92.1.1.15	Thian Shan	?	ZIN	50165	East Kazakhstan
?	BMNHL	98.12.15.1	North-west Mongolia	?	ZIN	84029	East Kazakhstan
?	USNM	175424	Altaj	?	ZIN	46147	East Kazakhstan
?	ZIN	63932	Altaj	?	ZIN		
<i>M. bobak</i>							
	BMNHL	594a	Russia		ZIN	50292	South-central Europe; Russia
	ZIN	44227	North-central Kazakhstan		ZIN	50283	South-central Europe; Russia
	ZIN	44236	North-central Kazakhstan		ZIN	50296	South-central Europe; Russia
	ZIN	44218	North-central Kazakhstan		ZIN	50297	South-central Europe; Russia
	ZIN	44212	North-central Kazakhstan		ZIN	50293	South-central Europe; Russia
	ZIN	44208	North-central Kazakhstan		ZIN	50285	South-central Europe; Russia
	ZIN	44229	North-central Kazakhstan		ZIN	50287	South-central Europe; Russia
	ZIN	11987 oc	South-central Europe; Russia		ZIN	50289	South-central Europe; Russia
	ZIN	50300	South-central Europe; Russia		ZIN	15459 oc	South-east Europe; Russia
<i>M. broweri</i>	USNM	290276	Alaska		USNM	583155	Alaska
<i>M. caligata</i>							
<i>caligata</i>	USNM	74996	Alaska	<i>nivaria</i>	USNM	72235	Montana
<i>caligata</i>	USNM	96533	Alaska	<i>nivaria</i>	USNM	72223	Montana
<i>caligata</i>	USNM	96207	Alaska	<i>okanagana</i>	USNM	81913	Alberta
<i>caligata</i>	USNM	98154	Alaska	<i>okanagana</i>	USNM	66695	British Columbia
<i>caligata</i>	USNM	271698	Alaska	<i>okanagana</i>	USNM	66696	British Columbia
<i>caligata</i>	USNM	271699	Alaska	<i>okanagana</i>	USNM	66697	British Columbia
<i>caligata</i>	USNM	271701	Alaska	<i>okanagana</i>	USNM	66698	British Columbia
<i>caligata</i>	USNM	48580	Alaska	<i>okanagana</i>	USNM	67076	British Columbia
<i>caligata</i>	USNM	96206	Alaska	<i>oxytona</i>	USNM	174503	Alberta
<i>caligata</i>	USNM	146449	Alaska	<i>oxytona</i>	USNM	174502	Alberta
<i>caligata</i>	USNM	135161	Yukon	<i>oxytona</i>	USNM	53595	British Columbia

APPENDIX Continued

sp. and ssp [†]	Museum	Catalogue number	Locality ^{‡,§}	ssp.	Museum	Catalogue number	Locality
<i>caligata</i>	USNM	135163	Yukon	<i>oxytona</i>	USNM	170741	British Columbia
<i>cascadensis</i>	USNM	88005	British Columbia	<i>oxytona</i>	USNM	101299	British Columbia
<i>cascadensis</i>	USNM	88006	British Columbia	<i>oxytona</i>	USNM	101300	British Columbia
<i>cascadensis</i>	USNM	42638	Washington	<i>oxytona</i>	USNM	202790	British Columbia
<i>cascadensis</i>	USNM	42793	Washington	<i>oxytona</i>	USNM	226148	British Columbia
<i>cascadensis</i>	USNM	90132	Washington	<i>oxytona</i>	USNM	170682	British Columbia
<i>cascadensis</i>	USNM	226719	Washington	<i>oxytona</i>	USNM	256660	British Columbia
<i>cascadensis</i>	USNM	233212	Washington	<i>sheldoni</i>	USNM	137319	Alaska
<i>cascadensis</i>	USNM	90134	Washington	<i>vigilis</i>	USNM	97952	Alaska
<i>nivaria</i>	USNM	221012	Alberta	<i>vigilis</i>	USNM	97953	Alaska
<i>nivaria</i>	USNM	114833	Idaho	<i>vigilis</i>	USNM	235255	Alaska
<i>nivaria</i>	USNM	72222	Montana	<i>vigilis</i>	USNM	235257	Alaska
<i>nivaria</i>	USNM	72225	Montana				
<i>M. camtschatica</i>							
<i>bunpei</i>	BMNH	1937.6.12.10 (15084)	Jakutia	?	ZIN	41505	Jakutia
?	BMNH	58.11.18.3	Kamtschatka	?	ZIN	41449	Jakutia
?	BMNH	1.11.22.8	Kamtschatka	?	ZIN	41531	Jakutia
?	ZIN	57873	East Transbaikal Region	?	ZIN	41550	Jakutia
?	ZIN	57874	East Transbaikal Region	?	ZIN	41475	Jakutia
?	ZIN	57872	East Transbaikal Region	?	ZIN	41502	Jakutia
?	ZIN	57880	East Transbaikal Region	?	ZIN	41503	Jakutia
?	ZIN	57879	East Transbaikal Region	?	ZIN	41514	Jakutia
?	ZIN	57877	East Transbaikal Region	?	ZIN	13561 oc	Jakutia
?	ZIN	57885	East Transbaikal Region	?	ZIN	78913	Kamtschatka
?	ZIN	78912	East Transbaikal Region	?	ZIN		
<i>M. caudata</i>							
<i>aurea</i>	USNM	62114	Pamir	?	USNM	173378	Kashmir (North India)
<i>aurea</i>	USNM	62118	Pamir	?	USNM	173380	Kashmir (North India)
?	USNM	62112	Kashmir (North India)	?	USNM	173381	Kashmir (North India)
?	USNM	173376	Kashmir (North India)	?	USNM	173382	Kashmir (North India)
?	USNM	173377	Kashmir (North India)	?	USNM	173383	Kashmir (North India)
<i>M. caudata</i>							
?	USNM	35500	Kashmir (North India)	?	BMNH	5.10.8.2	Kashmir (North India)
?	USNM	173384	Kashmir (North India)	?	BMNH	8.7.6.27	Kashmir (North India)

?	USNM	173385	Kashmir (North India)	?	BMNHL	89.3.9.7	Pamir
?	USNM	173386	Kashmir (North India)	?	BMNHL	92.1.1.7	Pamir
?	USNM	298212	North Pakistan	?	BMNHL	9.4.3.112	Turkestan (East Uzbekistan)
?	USNM	327143	North Pakistan	?	BMNHL	76.3.9.3	?
?	USNM	353196	North Pakistan	?	BMNHL	8.10.3.16	?
?	USNM	353197	North Pakistan	?	ZIN	40555	Pamir
?	USNM	353199	North Pakistan	?	ZIN	40553	Pamir
?	USNM	353198	W Pakistan	?	ZIN	27912	Pamir-Alai
?	BMNHL	10.12.2.25	East Uzbekistan or West Pamir	?	ZIN	51537	Pamir-Alai
?	BMNHL	69.493	East Pakistan	?	ZIN	22535	Pamir-Alai
?	BMNHL	88.3.20.25	Kashmir (North India)				
<i>M. flaviventris</i>							
<i>avara</i>	USNM	94343	British Columbia	<i>luteola</i>	USNM	186520	Wyoming
<i>avara</i>	USNM	99759	British Columbia	<i>nosophora</i>	USNM	575170	Colorado
<i>avara</i>	USNM	99760	British Columbia	<i>nosophora</i>	USNM	156923	Idaho
<i>avara</i>	USNM	221898	Idaho	<i>nosophora</i>	USNM	168477	Montana
<i>avara</i>	USNM	221896	Nevada	<i>nosophora</i>	USNM	233382	Montana
<i>avara</i>	USNM	79365	Oregon	<i>nosophora</i>	USNM	291192	Montana
<i>avara</i>	USNM	212471	Oregon	<i>nosophora</i>	USNM	243663	Utah
<i>avara</i>	USNM	242645	Oregon	<i>nosophora</i>	USNM	243664	Utah
<i>avara</i>	USNM	234960	Washington	<i>nosophora</i>	USNM	147183	Wyoming
<i>dacota</i>	USNM	168884	South Dakota	<i>nosophora</i>	USNM	168799	Wyoming
<i>dacota</i>	USNM	191366	South Dakota	<i>nosophora</i>	USNM	180918	Wyoming
<i>dacota</i>	USNM	191367	South Dakota	<i>nosophora</i>	USNM	168494	?
<i>dacota</i>	USNM	65920	Wyoming	<i>obscura</i>	USNM	128750	New Mexico
<i>engelhardtii</i>	USNM	157828	Utah	<i>obscura</i>	USNM	128753	New Mexico
<i>engelhardtii</i>	USNM	243665	Utah	<i>obscura</i>	USNM	128754	New Mexico
<i>engelhardtii</i>	USNM	244551	Utah	<i>obscura</i>	USNM	228271	New Mexico
<i>engelhardtii</i>	USNM	244552	Utah	<i>obscura</i>	USNM	228273	New Mexico
<i>engelhardtii</i>	USNM	158500	Utah	<i>obscura</i>	USNM	135505	New Mexico
<i>flaviventris</i>	USNM	100532	California	<i>parvula</i>	USNM	93688	Nevada
<i>flaviventris</i>	USNM	100533	California	<i>parvula</i>	USNM	93689	Nevada
<i>flaviventris</i>	USNM	88243	California	<i>parvula</i>	USNM	93690	Nevada
<i>flaviventris</i>	USNM	23951	Nevada	<i>sierrae</i>	USNM	108792	California
<i>flaviventris</i>	USNM	80360	Oregon	<i>sierrae</i>	USNM	42112	California
<i>flaviventris</i>	USNM	211232	Oregon	<i>sierrae</i>	USNM	42368	California

APPENDIX Continued

sp. and ssp [†]	Museum	Catalogue number	Locality‡:§	ssp.	Museum	Catalogue number	Locality
<i>fortirostris</i>	USNM	41345	California	<i>sierrae</i>	USNM	41914	California
<i>luteola</i>	USNM	139082	Colorado	<i>sierrae</i>	USNM	41198	California
<i>luteola</i>	USNM	498417	Colorado	<i>sierrae</i>	USNM	42858	California
<i>luteola</i>	USNM	25523	Wyoming	<i>sierrae</i>	USNM	42859	California
<i>luteola</i>	USNM	25524	Wyoming	<i>warreni</i>	USNM	202937	Colorado
<i>luteola</i>	USNM	25527	Wyoming				
<i>M. himalayana</i>							
<i>himalayana</i>	USNM	62122	Chinese Turkestan	?	USNM	576183	Kunlun Shan (China)
<i>himalayana</i>	USNM	84099	Kashmir (North India)	?	USNM	576184	Kunlun Shan (China)
<i>himalayana</i>	USNM	84100	Kashmir (North India)	?	USNM	573031	Kunlun Shan (China)
<i>himalayana</i>	USNM	84101	Kashmir (North India)	?	USNM	573037	Chinese Turkestan
<i>himalayana</i>	USNM	84103	Kashmir (North India)	?	BMNHL	96.11.4.9	Sichuan (Central China)
<i>himalayana</i>	USNM	84104	Kashmir (North India)	?	BMNHL	23.9.1.41	Tibet
<i>himalayana</i>	USNM	198638	Kashmir (North India)	?	BMNHL	5.12.5.2	Tibet
<i>himalayana</i>	USNM	259439	Sikkim (North India)	?	BMNHL	5.12.5.3	Tibet
<i>robusta</i>	USNM	144038	China	?	BMNHL	23.9.1.38	Tibet
<i>robusta</i>	USNM	144039	China	?	BMNHL	23.9.1.39	Tibet
<i>robusta</i>	USNM	240674	Kansu (North-West China)	?	BMNHL	23.9.1.40	Tibet
<i>robusta</i>	USNM	240675	Kansu (North-west China)	?	BMNHL	22.9.1.82	Yunnan, Mekong-Yangtze (South China)
<i>robusta</i>	USNM	240677	Kansu (North-west China)	?	BMNHL	11.2.1.94	Kansu (North-west China)
<i>robusta</i>	USNM	102576	Tibet	?	BMNHL	8.2.29.1	?
<i>robusta</i>	USNM	255958	Tibet	?	BMNHL	8.7.6.30	?
<i>robusta</i>	USNM	255960	Tibet	?			
<i>M. marmota</i>							
<i>marmota</i>	BMNHL	8.8.10.64	French Alps	<i>marmota</i>	BMNHL	2.8.4.30	Swiss Alps
<i>marmota</i>	BMNHL	8.8.10.145	French Alps	<i>marmota</i>	BMNHL	2.8.4.32	Swiss Alps
<i>marmota</i>	BMNHL	7.1.1.195	Swiss Alps	<i>marmota</i>	BMNHL	2.8.4.33	Swiss Alps
<i>marmota</i>	BMNHL	2.8.4.31	Swiss Alps	<i>marmota</i>	DBA UMR	Not in catalogue	Appennini
<i>marmota</i>	DBA UMR	Not in catalogue	Appennini	<i>marmota</i>	SC	175(I)	Swiss Alps
<i>marmota</i>	DBA UMR	Not in catalogue	Appennini	<i>marmota</i>	SC	178	Swiss Alps
<i>marmota</i>	DBA UMR	Not in catalogue	Appennini	<i>marmota</i>	SC	159 (I)	Swiss Alps

<i>marmota</i>	DBA UMR	Not in catalogue	Appennini	<i>marmota</i>	USNM	14336	Swiss Alps
<i>marmota</i>	MSNM Ma	4532	Italian Alps	<i>marmota</i>	USNM	115219	Swiss Alps
<i>marmota</i>	MSNM Ma	6085	Italian Alps	<i>marmota</i>	USNM	115220	Swiss Alps
<i>marmota</i>	PNGP	Not in catalogue	Italian Alps	<i>marmota</i>	USNM	115221	Swiss Alps
<i>marmota</i>	PNGP	Not in catalogue	Italian Alps	<i>marmota</i>	USNM	115222	Swiss Alps
<i>marmota</i>	SC	173	Swiss Alps				
<i>M. menzbieri</i>	ZIN	45476	East Uzbekistan		ZIN	57912	North-west Tagikistan
	ZIN	45474	East Uzbekistan		ZIN	45472	Uzbekistan
	ZIN	65848	East Uzbekistan		ZIN	31703	Kirghizistan
	ZIN	31704	Kirghizistan				
<i>M. monax</i>	USNM	72186	Minnesota	<i>prebolorum</i>	USNM	78355	Massachusetts
<i>canadensis</i>	USNM	72187	Minnesota	<i>prebolorum</i>	USNM	78358	Massachusetts
<i>canadensis</i>	USNM	243949	New Scotland	<i>prebolorum</i>	USNM	96140	Massachusetts
<i>canadensis</i>	USNM	191345	North Dakota	<i>prebolorum</i>	USNM	23033	New Hampshire
<i>ignava</i>	USNM	291554	Labrador	<i>rufescens</i>	USNM	35361	Minnesota
<i>monax</i>	USNM	77924	District of Columbia	<i>rufescens</i>	USNM	43560	Minnesota
<i>monax</i>	USNM	244482	Illinois	<i>rufescens</i>	USNM	186521	Minnesota
<i>monax</i>	USNM	337132	Indiana	<i>rufescens</i>	USNM	67692	New York
<i>monax</i>	USNM	347752	Indiana	<i>rufescens</i>	USNM	67693	New York
<i>monax</i>	USNM	53920	Missouri	<i>rufescens</i>	USNM	228524	North Dakota
<i>monax</i>	USNM	96574	Pennsylvania	<i>rufescens</i>	USNM	25184	Ontario
<i>monax</i>	USNM	396279	Pennsylvania	<i>rufescens</i>	USNM	174594	Ontario
<i>monax</i>	USNM	259345	Virginia	<i>rufescens</i>	USNM	227256	Wisconsin
<i>monax</i>	USNM	283359	Virginia	<i>rufescens</i>	USNM	228929	Wisconsin
<i>monax</i>	USNM	207198	Alabama	<i>rufescens</i>	USNM	233345	Wisconsin
<i>monax</i>	USNM	236424	Arkansas	<i>rufescens</i>	USNM	233348	Wisconsin
<i>monax</i>	USNM	58695	North Carolina	<i>rufescens</i>	USNM	234703	Wisconsin
<i>monax</i>	USNM	249883	North Carolina	<i>rufescens</i>	USNM	243073	Wisconsin
<i>ochracea</i>	USNM	77142	British Columbia	<i>rufescens</i>	MSNM Ma	4550	?
<i>ochracea</i>	USNM	77143	British Columbia	?	BMNHL	19.7.7.2552	Canada
<i>ochracea</i>	USNM	202785	British Columbia	?	BMNHL	36.11.6.31	Labrador
<i>petrensis</i>	USNM	291786	British Columbia	?	BMNHL	36.11.6.30	Labrador
<i>petrensis</i>	USNM	101295	British Columbia	?	BMNHL	36.11.6.34	Labrador
<i>petrensis</i>	USNM	203532	British Columbia	?	BMNHL	6.1.6.6	West Virginia
<i>prebolorum</i>	USNM	78357	Massachusetts	?	BMNHL	592.c	?

APPENDIX Continued

sp. and ssp. [†]	Museum	Catalogue number	Locality ^{‡,§}	ssp.	Museum	Catalogue number	Locality
<i>prebolorum</i>	USNM	78356	Massachusetts	?	BMNHL	592.d (51.8.16.19)	?
<i>prebolorum</i>	USNM	78360	Massachusetts	?	BMNHL	1989.337	?
<i>prebolorum</i>	USNM	78354	Massachusetts	?	BMNHL	1991.119	?
<i>M. olympus</i>							
	USNM	66950	Washington, Olympic P.		USNM	241659	Washington, Olympic P.
	USNM	67611	Washington, Olympic P.		USNM	241947	Washington, Olympic P.
	USNM	67612	Washington, Olympic P.		USNM	241948	Washington, Olympic P.
	USNM	92768	Washington, Olympic P.		USNM	241659	Washington, Olympic P.
	USNM	241657	Washington, Olympic P.		USNM	242102	Washington, Olympic P.
	USNM	241658	Washington, Olympic P.		USNM	242103	Washington, Olympic P.
<i>M. sibirica</i>							
	BMNHL	95.2.21.4	Amurland (South-central Siberia)		ZIN	78666	Tuva (South-central Siberia)
	USNM	175602	Mongolia		ZIN	78680	Tuva (South-central Siberia)
	USNM	259440	Mongolia		ZIN	78682	Tuva (South-central Siberia)
	USNM	268752	Mongolia		ZIN	78689	Tuva (South-central Siberia)
	ZIN	81139	Tuva (South-central Siberia)		ZIN	78687	Tuva (South-central Siberia)
	ZIN	81137	Tuva (South-central Siberia)		ZIN	78690	Tuva (South-central Siberia)
	ZIN	78671	Tuva (South-central Siberia)		ZIN	78679	Tuva (South-central Siberia)
	ZIN	78663	Tuva (South-central Siberia)		ZIN	78686	Tuva (South-central Siberia)
	ZIN	78670	Tuva (South-central Siberia)		ZIN	78684	Tuva (South-central Siberia)
<i>M. vancouverensis</i>							
	MVZ	12091	Vancouver Island		MVZ	12100	Vancouver Island
	MVZ	12092	Vancouver Island		MVZ	12098	Vancouver Island
	MVZ	12090	Vancouver Island		MVZ	12093	Vancouver Island
	MVZ	12095	Vancouver Island				
<i>Spermophilus beldingi</i>							
	BMNHL	38.4.1.39	California		BMNHL	98.12.27.1 (88754)	California
	BMNHL	2.4.1.137	California		BMNHL	29.11.7.32	California
<i>S. citellus</i>							
<i>gravojerici</i>	BMNHL	31.11.11.35	Greece	<i>karamani</i>	BMNHL	47.1105	Yugoslavia
<i>gravojerici</i>	BMNHL	31.11.11.37	Greece	<i>karamani</i>	BMNHL	47.1110	Yugoslavia
<i>gravojerici</i>	BMNHL	31.11.11.39	Greece				

<i>S. richardsoni</i>	BMNHL 1938.4.1.53 BMNHL 1938.4.1.45	North Dakota North Dakota	BMNHL 1938.4.1.46	North Dakota
<i>S. undulatus</i> ¶	BMNHL 98.2.6.1	Altaj	BMNHL 12.4.1.21	Siberia
<i>S. variegatus</i> <i>grammurus</i>	BMNHL 92.11.1.10	Colorado	BMNHL 55.275	Messico
<i>Cynomys leucurus</i>	BMNHL 40.829	Wyoming		
<i>C. ludovicianus</i>	BMNHL 60.513 BMNHL 67.7.8.34 (1433.b)	Kansas ?	BMNHL 77.436 BMNHL 1433.a	? ?
<i>Tamias** sibiricus</i>	USNM 200614 USNM 200617	Jakutia Jakutia	USNM 257369	East Siberia
<i>Tamias striatus</i>	USNM 36950 USNM 47413	Tennessee Tennessee	USNM 306058	Virginia
<i>Sciurus vulgaris</i> <i>infuscatus</i> ?	BMNHL 27.7.1.1 BMNHL 47.1115	Spain Yugoslavia	BMNHL 34.11.26.12	Yugoslavia

*Abbreviations: BMNHL, British Museum of Natural History (London, UK); MVZ, Museum of Vertebrate Zoology (Berkeley, California, USA); USNM, National Museum of Natural History (Washington DC, USA); ZIN, Zoological Institutes of the Russian Academy of Sciences (St. Petersburg, Russia); ZIN 'catalogue number' oc, ZIN osteological collection; MSNM Ma, Museo di Storia Naturale di Milano (Italy); PNGP, National Park Gran Paradiso (Torino, Italy); SC, collection of Dino Scaravelli; DBA UMR, Department of Animal Biology, University of Modena and Reggio Emilia. †?, subspecies unknown. ‡?, locality unknown. §Geographical position of mountain ranges: Alatau: Kazakhstan, Kirghizistan, Uzbekistan; Altaj: Mongolia, south Siberia; Thian Shan: Kirghizistan, China; Alai: Kirghizistan; Pamir: Tagikistan. ¶*Spermophilus undulatus* (Pallas, 1778) is a senior synonym of *S. eversmanni* (Hoffmann *et al.*, 1993) which is the species name in the BMNHL collection. **The specimens were classified as *Eutamias sibiricus* in the USNM collection, but *Eutamias* is considered a subgenus of *Tamias* by Hoffmann *et al.* (1993).