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Marmot evolution and global change in the past 10 million years

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Introduction

Ground squirrels of the genus *Marmota* are known for their ability to tolerate bitterly cold climates, which they in part accomplish with their exceptional ability to hibernate for as much as eight months a year (Armitage *et al.*, 2003). Most of the 15 living species are associated with montane habitats, and those that are not, like the North American woodchuck (*Marmota monax*) and the eastern European and central Asian bobak (*M. bobak*) inhabit regions with strongly seasonal climates and often bitterly cold winters (Armitage, 2000) (Figure 9.1). All marmots construct burrows, which can be more than one meter deep even in comparatively mild climates and as much as seven meters deep in the harsh climates of the Himalayas (Barash, 1989). During the cold phases of the last half of the Quaternary the fossil record demonstrates many marmots inhabited periglacial environments (Zimina and Gerasimov, 1973; Kalthoff, 1999). For these reasons, marmots are sometimes considered to be a quintessentially Quaternary clade, specialists on the cold variable climates that are unique to the past 2.6 million years of Earth's history. The world in which they originated, however, was very different; a warmer one in which there were no tundra biomes, no glacial–interglacial cycles, and no permanent ice cover in the Northern Hemisphere. In this chapter, we review the fossil and phylogenetic history of marmots, the palaeoenvironments in which they originated, and their relationship to glacial–interglacial cycles to better understand the contexts in which the specializations of this unique clade of rodents arose.

The Quaternary, the current geological period, is defined by the onset of permanent ice sheets in the Northern Hemisphere 2.58 million years ago and is by far the coldest period since the extinction of the last non-avian dinosaurs 65 million years ago (Zachos *et al.*, 2001; Gibbard *et al.*, 2010). Its more than 50 glacial–interglacial cycles are part of the erratic decline in global mean temperature since the warm mid-Miocene climatic optimum 15–17 Ma, driven by combination of relatively low atmospheric CO_2, the ocean–atmosphere dynamics created by the current configuration of continents, and astronomically induced changes in insolation (Figure 9.2). The waxing and waning of ice sheets, rises and falls in sea level, and changes in temperature gradients have

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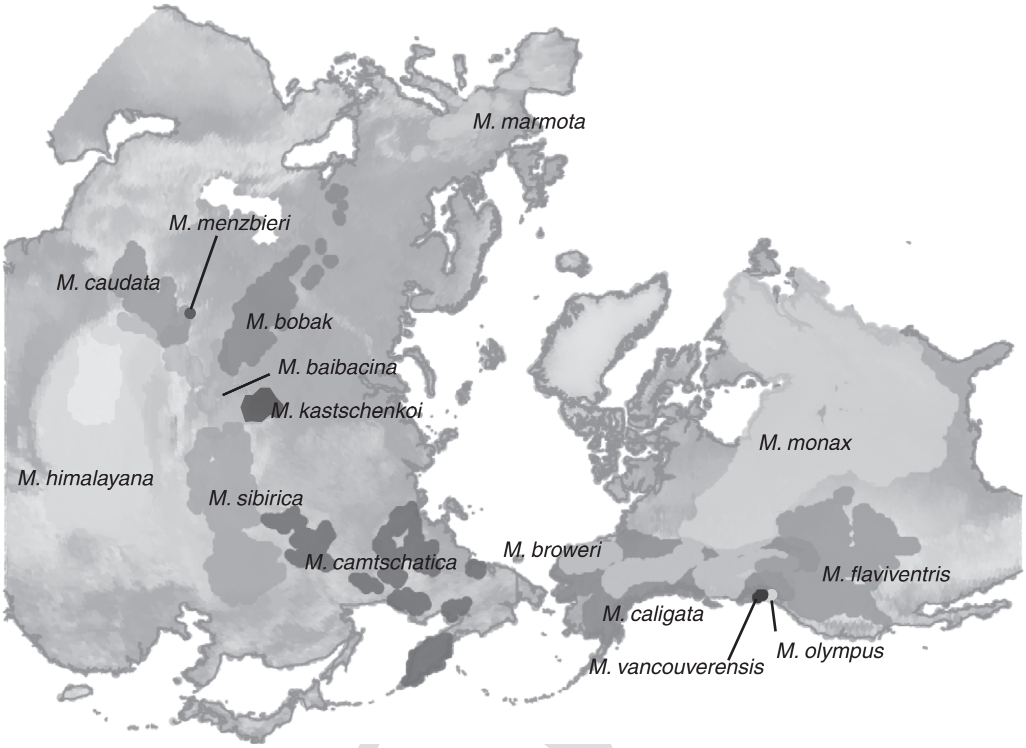

Figure 9.1 Map of the geographic ranges of the living marmot species. A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.

iteratively impacted ocean currents, airflow patterns, precipitation patterns, cloud cover and albedo for more than two million years.

Despite the magnitude of change during the Quaternary, its effect on vertebrate evolution is contested. At mid- and high-latitudes climate cycles have reorganized plant communities (Jackson and Overpeck, 2000), caused turnover in mammalian communities (Blois and Hadly, 2009), created allopatric vicariant events (Mercer and Roth, 2003; Rödder *et al.*, 2013), repeatedly restructured the genetics of species (Stewart, 2009; Hewitt, 2011), shifted the geographic ranges of species (Graham *et al.*, 1996; Lyons, 2003; Lawing and Polly, 2011; Rödder *et al.*, 2013), and generated new biomes like tundra and mammoth steppe (Guthrie, 2001; Graham, 2011). Species that were extant at the beginning of the Quaternary are now extinct, and most modern species had not yet arisen (Lister, 2004). Despite the biological impact of these events, it is clear that organisms have responded more through geographic sorting than evolutionary adaptation (Kahlke, 1992; Graham *et al.* 1996; Lawing and Polly, 2011). Palaeontological data show that the average longevity of species is much longer than individual glacial–interglacial cycles and nearly as long as the Quaternary itself (Barnosky, 2005) and molecular data indicate that many living sister-species diverged prior to the beginning of the Quaternary (Klicka and Zink, 1997; Zink *et al.*, 2004), collectively suggesting that

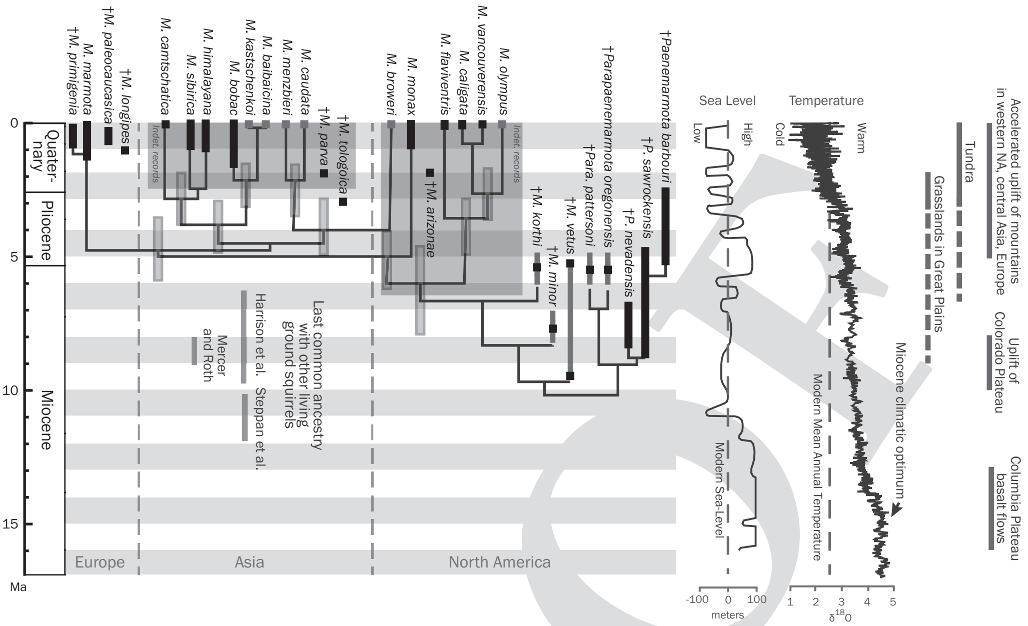

Figure 9.2 Phylogeny, fossil record, and geological history of marmots. Fossil record (thick black lines) of living and extinct marmots is shown superimposed on a phylogenetic tree. Grey uncertainty bars on fossil occurrences show the range of credible ages of key individual fossils. Grey boxes around the North American and Asian clades show the range of indeterminate fossil crown group marmots. Daggers indicate extinct species. Major environmental and geological events are shown at the right. Three molecular clock estimates of the split between *Marmota* and other ground squirrels are shown. ($\delta^{18}O$, delta oxygen-18, is the stable isotope proxy for temperature.)

the climatic events have not been a primary driver of speciation. Note that last common ancestry between living sister-species is different from the origin of those species because the closest relatives of living species may be extinct.

Marmots have clearly adjusted to the peculiarities of Quaternary climate cycles, but their tolerance of harsh, cold environments may be coincidental. A tectonic argument has recently been made that marmots radiated in response to a series of mountain building events in the late Cenozoic of western North America, northeastern and south central Asia, and southern Europe (Nikol'skii and Rumiantsev, 2012). In this scenario, marmots would have originated as lowland specialists similar to other living ground squirrels, dispersed in the Miocene through lowlands of western North America and Eurasia, and subsequently colonized rising mountain chains to produce the living diversity of marmots via allopatry and local environmental specialization. Elevation, topography and tectonic processes are known to influence speciation because they create genetic barriers, new habitats and environmental gradients, and they can drive changes in sea level and intercontinental connections (Mercer and Roth, 2003; Guralnick, 2007; Waltari and Guralnick, 2009; Badgley, 2010). Topography and climate combine to be strong predictors of species density in the present and the past (Badgley and Fox, 2000; Badgley and Finarelli, 2013) and episodes of tectonic uplift are known to be associated with regional increases in species diversity (Barnosky and Carrasco, 2002; Kohn and Fremd, 2008).

The extent to which Quaternary climate cycles, tectonics, or both have influenced marmot evolution can be assessed by examining the timing and context of their origination and radiation. In this chapter we critically evaluate evidence from molecular phylogenetics, palaeontology, geology, species distribution modelling and morphometrics to do just that. When did crown group and stem group *Marmota* originate and when did they radiate? In what environment did the ancestor of living marmots live and how did that environment compare to its closest antecedents? How have the climatic and orogenic histories of the past 10 million coincided with marmot evolution? Are marmots climatically or environmentally specialized compared to one another or to their closest non-marmot relatives? In what context did their large body size evolve? How have glacial–interglacial cycles affected their geographic distributions? In this review we synthesize data from new and published sources. The phylogenetic, morphometric, fossil occurrence and some of the climatic data are synthesized from previously published sources (including our own previous work). Marmot species distribution models for the last glacial maximum are original to this paper. We first describe the data and methods behind our new analyses, after which we evaluate these questions.

Data and methods

Data

Digital geographic range data for living North American marmot species came from Patterson *et al.* (2005), which are updated versions of Hall's (1981) maps, and Eurasian species from IUCN (2012). Modern vegetation cover data are from Matthews (1983), which is a global distribution of 32 vegetation types that classifies both natural cover and cultivated land. Biome and ecoregion data come from Bailey (1989), whose classification is based on a combination of topography, climate, vegetation, and soils. Elevation data are from TerrainBase (Hastings and Dunbar, 1998).

Modern climate data are from Hijmans *et al.* (2005) WorldClim data set, which consists of the 1950–2000 averages of 19 bioclimatic variables representing annual and seasonal averages and extremes of temperature, precipitation, variability, and seasonality (Nix, 1986). Reconstructed climate data for the Last Glacial Maximum (LGM; 21 ka) are from Braconnot *et al.* (2007), a global circulation climate model (GCM) generated by the Palaeoclimate Modelling Intercomparison Project (PMIP) using the MIROC3.2 model. We transformed the model's climatic variables into the same 19 bioclimatic variables (Lawing and Polly, 2011). We chose not to use LGM climate reconstructions based on the CCSM model (Braconnot *et al.*, 2007) because the MIROC3.2 data are more congruent with fossil marmot occurrences during the last glacial phase based on our own evaluations. MIROC3.2 was also found to be more congruent with fossil occurrences in other studies (Guralnick and Pearman, 2009; McGuire and Davis, 2013).

All modern geographic data were resampled using an equidistant sampling grid with 50 km spacing (Polly, 2010). This sampling density approximates the geographic mixing of an average fossil assemblage and is thus appropriate for making comparisons with the palaeontological record (Fortelius *et al.*, 2002). The sampling grid and some of the resampled climatic and environmental data are available at http://mypage.iu.edu/~pdpolly/Data.html.

Tooth size data consisting of maximum mesiodistal lengths of the upper fourth premolar (P4) and lower third molar (m3) and skull length data were collected by PDP from the modern marmot samples described by Polly (2003).

Fossil occurrences of marmots were obtained from the published literature, the NOW Database (http://www.helsinki.fi/science/now/), and the combined FaunMap and MioMap Databases (http://www.ucmp.berkeley.edu/neomap/). The online database records were checked against the published literature for accuracy in taxonomy, location, and age (about 25% of the records were updated in one or more of these categories). Additional records were added for critical periods and regions (Maul, 1990; Kalthoff, 1999; Paunovic and Rabeder, 2000; Tleuberdina and Forsten, 2001; Baryshnikov, 2002; Tesakov *et al.*, 2007; Cuenca-Bescós *et al.*, 2010; Petronio *et al.*, 2011).

The global sea-level curve and oxygen isotope (global mean annual temperature) curves in Figure 9.2 are from Haq *et al.* (1987; in Miller *et al.* 2005) and Zachos *et al.* (2001) respectively. The phylogenetic tree of living marmots in Figure 9.2 is from Steppan *et al.* (2011). Divergence times and error bars in that tree were based on molecular clock data calibrated using *M. minor.* The phylogenetic tree for fossil taxa is after Voorhies (1988), Kelly (2000) and Goodwin (2007).

Climatic habitat modelling

Climatic habitat models show the geographic areas with climate that is compatible with the modern geographic range of a species. We used habitat models to evaluate whether climate is a limiting factor for modern marmots and to estimate the geographic ranges of marmot species at the time of the last glacial maximum (LGM) 21 000 years ago. First, climate envelopes were estimated by finding the maximum and minimum values of each climate variable in the modern geographic range of each species. These values define a rectilinear (or BIOCLIM) envelope in the multivariate climate space that serves as a descriptor of the range of climate that each species is known to tolerate (Nix, 1986; Hijmans and Graham, 2006). Then the geographic areas were found where the climate falls within the envelope, thus modelling the area in which climate is compatible with the observed tolerances of the species.

We did not use GARP (Anderson *et al.*, 2003) or MaxEnt (Phillips *et al.*, 2006) because these methods intentionally overparameterize to improve the modeling of actual geographic distributions. While more precise, these methods are not transferrable to the geological past because their models utilize correlations between climate variables that have demonstrably changed over time, thus compromising the accuracy of these methods in contexts other than the present (Nogués-Bravo, 2009; Lawing and Polly, 2011; Svenning *et al.*, 2011). In practice, choice of method makes little difference at continental scales for ranges; for example, the modelled distributions of the spotted hyena, *Crocuta crocuta*, produced by Varela *et al.* (2010) and Polly and Eronen (2011) are nearly identical despite substantial differences in data and methods.

Climate envelope size

Climate envelope size is measured as the volume of the multidimensional climate space occupied by a species standardized by the number of climate variables used in its construction. First, each variable was standardized to a scale of 0 to 1, defined by the minimum and maximum values for the entire continent. Precipitation variables are highly skewed so we took their natural logarithm before standardizing. The full climate envelope volume was calculated for each species as the product of its range on each of the 19 bioclimate variables. Because volume increases with the number of variables, we standardized by taking its 19th root. The resulting value thus represents the proportion of the continent's climate occupied by the species. For example, an envelope size of 0.5 means that the range of each climate variable space occupied by the species is, on average, about half the range of found on the entire continent.

Body mass estimation for fossil species

Body mass was estimated for fossil species using regression of log mass on log third molar length in modern species. Molar length was first cubed to scale linearly with body mass, which is a volumetric variable (LaBarbera, 1989). The midpoint between immergent (before hibernation) and emergent (after hibernation) body masses as reported by Armitage and Blumstein (2002) were used because body mass varies considerably over an individual marmot's lifetime because of hibernation. Our body mass regression was $\log(\text{mass}) = 0.4419 * \log(\text{m3 length}^3) + 6.0664$. Note that our body mass estimates are coarse because of the inherent seasonal variability in marmot body mass and because the correlation between tooth size and body mass is low ($R = 0.44$). We keep this uncertainty in mind in drawing our conclusions.

Abbreviations

We use the following abbreviations on this chapter: LGM, last glacial maximum (18 000 – 21 000 years ago); Ma, megannum (million years); MAT, mean annual temperature.

Origin and radiation of marmots

Fossil and molecular evidence both agree that crown group *Marmota* originated in western North America in the late Miocene, between six and eight million years ago (Figure 9.2). Here we review the current phylogenetic status of the living species and

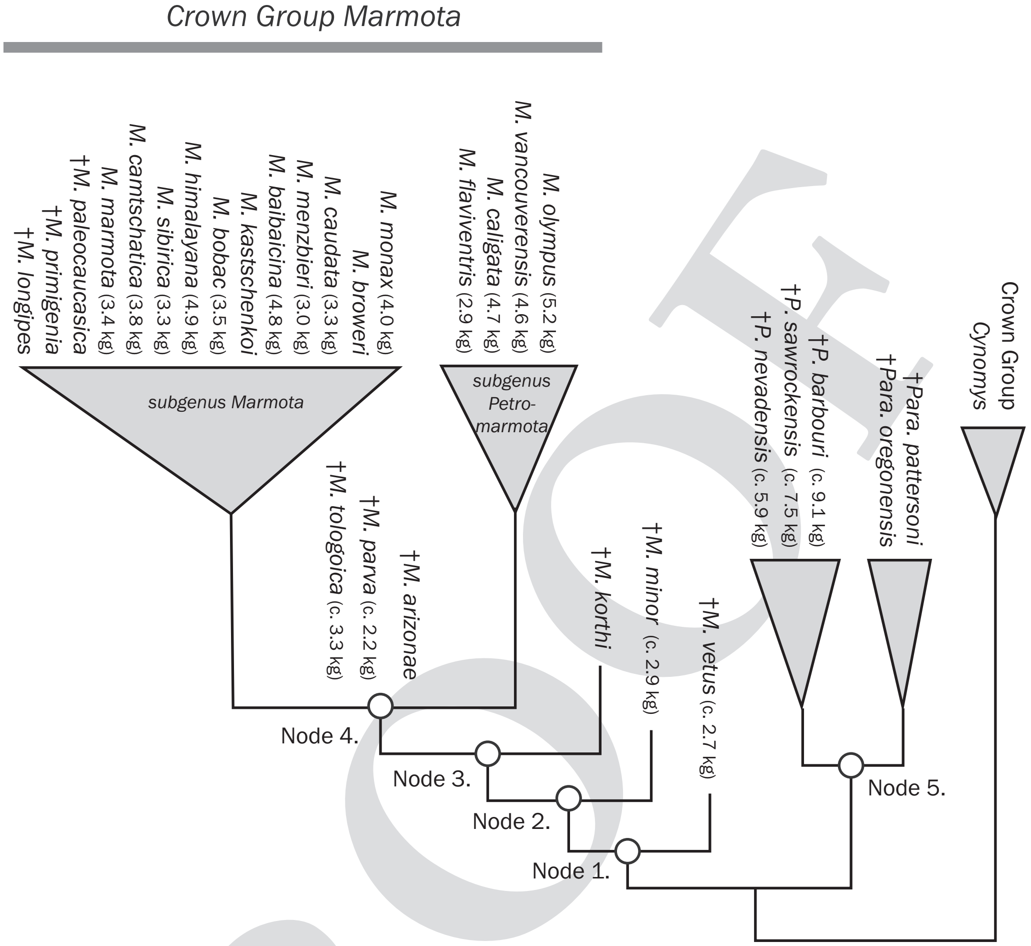

Figure 9.3 Phylogenetic relationships, body masses, and putative morphological synapomorphies of marmots. **Node 1.** *Marmota*: mesial and distolingual cingula confluent on P3; M3 metaloph reduced or absent; p4 protolophid complete, attached low; enlarged p4 relative to lower molars; reduction of distal margin of m3; m1–2 mesiodistally compressed (Goodwin, 2007). **Node 2.** Unnamed: p4 longer than m1–2; metalophids on m1–3 partially reduced; distal m3 further reduced (Kelly, 2000). **Node 3.** Unnamed: increased body size; m1–2 metalophids clearly defined (Kelly, 2000). **Node 4.** Crown group *Marmota*: metalophids on m1-3 further reduced; cheek teeth higher crowned; m1-2 further compressed mesiodistally (Kelly, 2000). **Node 5.** *Paenemarmota* + *Parapaenemarmota*: very large body size; weak masseteric crest on mandible; deep longitudinal striations on lower incisors; root of incisors extend mesial to m3; p4 narrower at mesial end than distal end; high p4 and m1 metalophid connecting protoconid and metaconid; deep fold around lateral margin of talonid basin; rugose floor of talonid basin (Voorhies, 1988; Martin, 1998). Body masses are from Table 9.1. Daggers indicate extinct species.

critically review the fossil record of marmots. We look at the history of both the crown group, which is the last common ancestor of living marmots and all of its descendants, and the stem group, which is the extinct taxa that lie outside the crown group but are more closely related to it than to other living taxa (Jefferies, 1979) (Figure 9.3).

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Molecular, morphological and palaeontological data all agree that marmots are members of a ground squirrel clade, specifically the spermophiline group (formerly *Spermophilus sensu lato*, ground squirrels). Molecular phylogenetic analyses all find *Marmota* to be monophyletic, but they differ about which taxa are more closely related (Harrison *et al*., 2003; Mercer and Roth, 2003; Steppan *et al*., 2011). Mercer and Roth (2003), using nuclear IRBP and mitochondrial 12S and 16S for an analysis of squirrel relationships, found that *Cynomys* (prairie dogs) was more closely related to marmots than was *Callospermophilus* (golden-mantled ground squirrels), but these authors were unable to study all spermophilines, including some that are likely to be the closest living relatives of marmots. Harrison *et al*. (2003) sampled additional ground squirrels and found marmots sister to North American *Callospermophilus* and *Otospermophilus* (rock squirrels). The only genus with an ancestral home in Asia is *Spermophilus sensu stricto* (Helgen *et al*., 2009), and unless it is sister to *Marmota*, then the molecular phylogenetics unambiguously supports the stem-lineage ancestor of the marmots having been North American. Molecular clock dating estimates for the last common ancestor of marmots and their closest living relatives range from 7 Ma (Mercer and Roth, 2003) to 10 Ma (Harrison *et al*., 2003) and approximately 11 Ma (Steppan *et al*., 2011). These dates are in good agreement with the fossil record, contra exaggerated claims by Thomas and Martin (1993) that the fossil record placed the divergence at nearly 30 Ma.

The phylogeny of living marmots has been analyzed using several molecular sequences and markers, predominantly mitochondrial (Kruckenhauser *et al*., 1999; Steppan *et al*., 1999; Brandler and Lyapunova, 2009; Brandler *et al*., 2010; Steppan *et al*., 2011). From these, it appears that marmots originated in North America, and that there was at least one dispersal to Eurasia and possibly a dispersal of a derived Eurasian lineage back to North America (*M. broweri*). The mitochondrial tree (cyt b/ND3/ND4) from the most complete of these phylogenies (Steppan *et al*., 2011) is reproduced in Figure 9.2. Molecular clock estimates suggest that the marmot crown group originated around 6 Ma, that dispersal to Eurasia occurred at 6–3 Ma, and that most species divergences occurred prior to the beginning of the Quaternary 2.58 Ma. As discussed below, these dates are generally in good agreement with the marmot fossil record.

Nevertheless, the biogeographic reconstruction of a return dispersal from Eurasia leading to *M. broweri* should be viewed with caution. It is based on a single locus, and the limited nuclear data (Brandler *et al*., 2010; Steppan *et al*., 2011) weakly support a geographically simpler scenario; a single dispersal to Eurasia with no back dispersal, wherein North American and Eurasian species form monophyletic groups that are sister to each other. More nuclear data are needed to resolve this uncertainty. The nuclear and mitochondrial data do agree on several points: a montane western North American clade of *M. caligata*, *M. flaviventris*, *M. olympus*, and *M. vancouverensis*, a Eurasian clade (which may or may not include the North American species *M. broweri* or *M. monax*), and a Eurasian *bobak* group.

The marmot fossil record, which is a comparatively good one, is in broad agreement with the molecular evidence. Marmots have been widespread and common in the North American fossil record for the past five million years and in Eurasia for the past

2.5 million years, but were rare before then. Their rarity prior to 5.0 and 2.5 Ma is not due to a poor fossil record – both continents are rich with other small to medium sized fossil rodents (Janis *et al.*, 2010; Wang *et al.*, 2013) – but because they were neither diverse nor common.

Extinct members of the marmot stem group shared many features with living marmots, but some were very different in their body sizes and habitats. Stem group marmots can be divided into those more closely related to the crown group (which are normally classified as part of the genus *Marmota*) and those belonging to a completely extinct clade of exceptionally large ground squirrels, referred to here as the *Paenemarmota* clade (Figure 9.3). The *Paenemarmota* clade originated in the Late Miocene around 9 Ma and persisted through the end of the Pliocene about 2.5 Ma and inhabited areas that today are devoid of marmots, including the Great Plains, southern Arizona, and northern Mexico (Repenning, 1962; Voorhies, 1988). Only a few members lived in the more mountainous areas of the west, notably *Parapaenemarmota* (Kelly, 2000; Goodwin, 2009). As described below, the palaeoenvironments of these regions were considerably different from today. The smallest members of the clade were as large as the largest living marmots (*c.* 5.9 kg), and *Paenemarmota barbouri*, was a true giant of at least 9 kg by our estimates (Table 9.1; Figure 9.3), maybe even 16 kg (Goodwin and Bullock, 2012).

The extinct taxa most closely related to crown group marmots – *Marmota vetus*, *M. minor*, and *M. korthi* – were comparatively small animals *c.* 2.5–3.0 kg (Table 9.1; Figure 9.3). By comparison, the smallest living marmot, *M. flaviventris*, has a midpoint mass (the midpoint between average immergent and emergent body mass) of about 2.9 kg (Armitage and Blumstein, 2002; Table 9.2). The geologically oldest member of this clade, *M. vetus*, may have originated by 10 Ma, with the caveat that its type specimen is from an imprecisely specified group of geological formations whose ages span the range 12–5 Ma, leaving open the possibility that its first occurrence was 6 Ma (Marsh, 1871; Black, 1963; Tedford *et al.*, 2004). *Marmota vetus* was a Late Miocene contemporary of *Paenemarmota* on the wooded grasslands of the Great Plains of Nebraska. The remaining stem group taxa closest to living marmots are all from high elevation sites in western North America (Kellogg, 1910; Black, 1963; Kelly, 2000).

Fossils belonging to the crown group are known from about 6 Ma to the present in North America, but were comparatively rare until about 3 Ma. Most of these have not been studied thoroughly enough to be assigned to particular species and are represented in Figure 9.2 by dark grey boxes. The crown group spread rapidly across western North America as far south as the margins of the rising Colorado Plateau in central Arizona and north to Cape Deceit along what would have been the southern foothills of the western Brooks Range in Alaska by 3 Ma.

The oldest Eurasian marmot fossils occur around 3 Ma (Figure 9.2). The earliest are *M. tologoica* from the Baikal region (Erbaeva, 2003), *M. parva* from the Linxia Basin in Gansu, China (Qiu *et al.*, 2004), and an unreferred marmot from Shanxi, China (Wang *et al.*, 2013). The palaeoenvironments at these locations were also quite different then than today, as described below.

Table 9.1 Mean dental measurements and midpoint body mass for living and fossil marmots. Tooth lengths are in mm, body masses are in kg. The sources for tooth measurements are reported. Body masses for living species are from Armitage and Blumstein (2002) and masses of extinct species were estimated from lower m3.

Species	N	P4 Len	m3 Len	Mass	Source
Living species					
M. baibacina	4	4.96	5.69	4.8	Our data
M. broweri	8	4.73	5.14		Our data
M. caligata	63	5.05	5.42	4.7	Our data
M. caudata	31	5.30	5.78	3.3	Our data
M. flaviventris	143	4.72	4.77	2.9	Our data
M. himalayana	31	5.36	6.02	4.9	Our data
M. marmota	29	5.01	5.04	3.4	Our data
M. menzbieri	1	4.43	4.99	3.0	Our data
M. monax	187	4.45	5.24	4.0	Our data
M. olympus	5	5.17	5.14	5.2	Our data
M. sibirica	30	4.95	5.33	3.3	Our data
M. vancouverensis	9	5.01	5.04	4.6	Our data
Extinct species					
M. korthi	2	4.29	—	—	Kelly, 2000
M. minor	1	4.20	4.20	2.9	Black, 1963
M. parva	1	2.90	3.40	2.2	Qiu *et al.*, 2004
M. tologoica	2	4.70	4.65	3.3	Erbaeva, 2003
M. vetus	1	—	4.00	2.7	Black, 1963
P. barbouri	10	—	10.00	9.1	Voorhies, 1988
P. nevadensis	2	—	7.20	5.9	Repenning, 1962
P. sawrockensis	3	—	8.63	7.5	Voorhies, 1988

An Asian occurrence of *Marmota* from the Middle Miocene of the Zaisan Basin, Kazakhstan has been reported in the literature (Shevyreva, 1968). The fossils, which are from the Akzhal and Sarybulak Formations, were referred to *M. vetus* but were never described or illustrated. At 12 Ma (Tleuberdina and Forsten, 2001), they are older than the oldest stem group marmots in North America and predate all the molecular estimates of the divergence between *Marmota* and its nearest living relatives (Figure 9.2). The age and geography of this material makes it likely that these fossils are either part of the early stem group radiation of ground squirrels or are from younger geological units in Zaisan. Until it can be shown that they have synapomorphies uniting them with marmots and that they are truly found in the Akzhal and Sarybulak Formations, we will not consider them to be relevant to the origin of marmots.

Combining the fossil and molecular data thus brackets the origin of crown group marmots in western North America between 5 and 8 Ma and the dispersal to Eurasia between 3 and 6 Ma. Fossils confirm that crown group marmots were unquestionably distributed from North America to the Urals by 3 Ma. The series of low stands in sea

Table 9.2 Climate and environment for living marmot species. Forest cover is the proportion of the geographic range with vegetation classified as wooded or forested and mountain domain is the proportion of each range classified in a mountain ecoregion domain. MAT, mean annual temperature; prop, proportion of total range; Climate envelope size is roughly the proportion of the continental climate envelope occupied by each species (see text for explanation).

Species	Forest cover (prop)	Mountain domain (prop)	Median elevation (m)	Median MAT (°C)	Median precipitation (cm)	Climate envelope size
M. baibacina	0.25	0.65	1220	1.0	60	0.26
M. bobak	0.03	0.01	255	3.1	40	0.20
M. broweri	0.13	0.54	520	−11.1	40	0.16
M. caligata	0.61	0.82	975	−3.6	69	0.47
M. camtschatica	0.48	0.85	760	−10.3	75	0.39
M. caudata	0.00	0.92	3163	1.8	78	0.46
M. flaviventris	0.30	0.36	1516	6.5	54	0.43
M. himalayana	0.07	0.71	4244	0.2	82	0.55
M. marmota	0.88	0.87	1301	5.6	138	0.22
M. menzbieri	—	—	1375	4.0	104	—
M. monax	0.79	0.16	342	1.3	99	0.43
M. olympus	—	—	1301	5.0	437	—
M. sibirica	0.24	0.43	1220	−1.0	79	0.28
M. vancouverensis	—	—	510	7.4	348	—
Marmot median	0.25	0.65	1220	1.5	79	0.39
Eurasian median	0.53	0.33	102	6.9	481	1.00
North American median	0.52	0.22	405	1.2	529	1.00

level after 5 Ma would have provided several opportunities for dispersal during this window (Figure 9.2; Mercer and Roth, 2003). Marmot fossils become increasingly common after 3 Ma, indicating that they had become frequent and abundant in mammalian communities. Prior to 3 Ma, marmot fossils were rare despite good fossil records in both Eurasia and North America, suggesting that early marmots were either confined to high-elevation environments (which have poor fossil records compared to low-elevation environments) or were genuinely rare.

Climate, environment and habitats of living marmots

Living marmots typically prefer habitats where grass forage, well-drained slopes and substrates that permit burrowing are available, often ones with seasonally low temperatures and winter snow (Armitage, 2000, 2013). They are most commonly found at high elevations near or above the timberline or at lower elevations in forest openings. Hibernation, which may last for up to 7.2 months, protects them against seasonal food shortages caused by cold, snow cover or drought (Armitage, 2000).

Marmots reproduce soon after emerging from hibernation in order for the reproductive females and young to gain as much weight as possible before their active cycle ends.

For purposes of comparison, we summarized marmot environments using the climatic and environmental parameters that characterize their modern geographic ranges (Table 9.2). The summaries describe the climate and environment of the entire species range, not the specific local microhabitats favored by marmots. The summaries should thus be viewed as the regional climatic and environmental boundaries (or envelopes) inside which marmot microhabitats are embedded. Because of the coarseness of the fossil and palaeoclimatic records, these summaries provide an appropriately coarse basis for making comparisons between the habitats of living marmots and the regional palaeoenvironments of their fossil forebears.

Based on these summaries, modern marmot ranges are selectively more mountainous, less forested and colder than average for their continents. Ignoring the tiny ranges of *M. vancouverensis, M. olympus* and *M. menzbieri*, about 65% of the range of marmot species (median value) falls within mountain. Only four out of 15 species have less than 50% of their ranges in mountain ecosystems. By comparison, only about 33% of Eurasia and 22% of the North American continent is mountain domain, thus indicating that marmot ranges are preferentially in mountains. Only two species have ranges that are dominantly non-mountainous (*M. bobak and M. monax*). Eight species have median elevations of more than 1000 m, whereas the two low elevation species have median elevations less than 500 m. By comparison, the median elevation of Eurasia is 102 m and North America is 405 m, indicating that marmots selectively inhabit higher elevations. Only *M. marmota* and *M. monax* are widely distributed in forested regions (median forested part of species ranges is 84%); the median distribution of marmots in forested areas is 25%, which suggests that marmots flourish in non-forested domains (about 52% of the two continents fall in forested domains). Living marmots are associated with cold, seasonal climates found at high latitudes and elevations (Armitage, 2013). Four of the species have ranges whose median mean annual temperature is below freezing, and ten have at least part of their range in areas that cold (Table 9.2).

The climatic ranges of living marmots can be placed in a global context by measuring the sizes of their climate envelopes as proportions of the global terrestrial climate envelope (Table 9.2). These numbers indicate how much of the available range of temperature, precipitation, and seasonality in modern terrestrial climates is utilized by marmots. Most species use less than a third of global climate, and only *M. himalayana* more than half. In contrast, widespread temperate species like coyote (*Canis latrans*), white-tailed deer (*Odocoileus virginianus*) and fox squirrel (*Sciurus niger*) have envelope sizes of 0.74, 0.68 and 0.43, respectively. Arctic specialists Arctic fox (*Vulpes lagopus*) and musk-ox (*Ovibos moschatus*) have envelope sizes of 0.46 and 0.37. The climatic range of living marmot species is thus more is restricted, on average, than many other mammals.

Marmots are also climatically differentiated from other ground squirrels. Figure 9.4 compares the distributions of mean annual temperature and annual precipitation for all living species of *Cynomys* and *Spermophilus* with all *Marmota*. While there is extensive overlap, marmots on average are found in climates that are colder by $8 - 10°C$ and

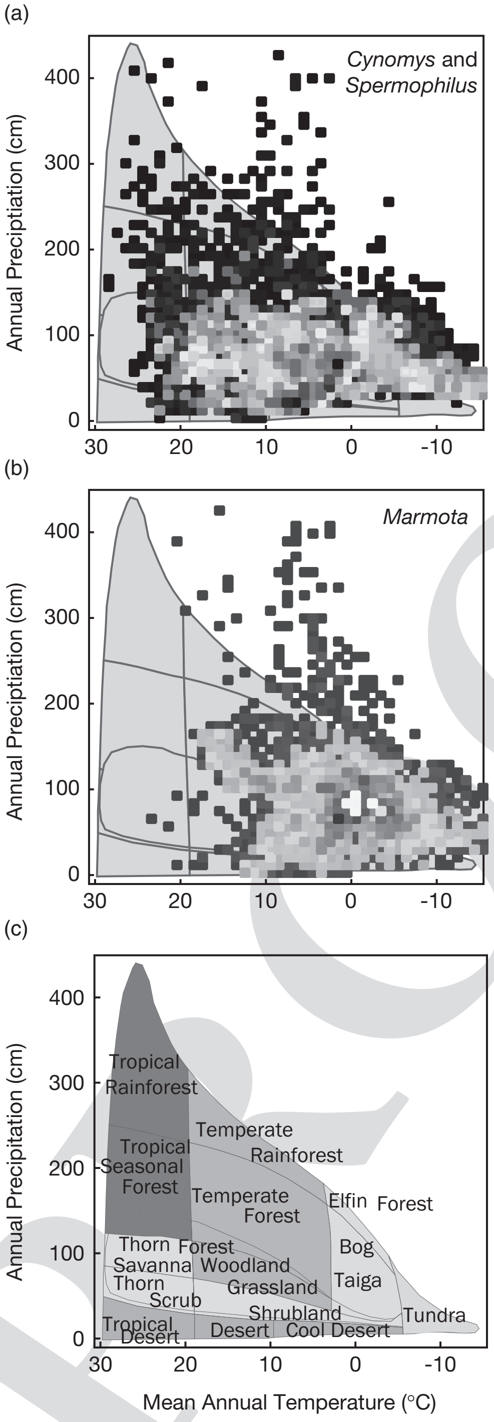

Figure 9.4 Distribution of marmots and other ground squirrels in climate space as defined by mean annual temperature (°C) and precipitation (cm). **(a)** Density histogram showing the distribution of all species of *Cynomys* and *Spermophilus*. Light colours indicate higher density. **(b)** Density histogram of *Marmota*. **(c)** Biome classification of Whittaker (1975) based on the same climate variables. A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.

wetter by 50 cm than other ground squirrels. Individual comparisons indicate that *M. bobak* and *M. flaviventris* live in climates most similar to *Cynomys* and *Spermophilus*.

The climatic habitats of individual marmot species are loosely correlated with their phylogeny, which suggests that closely related species occupy similar climates. Davis (2005) found that the distance between marmot species in climate space was correlated with phylogenetic distance based on mtDNA sequence data. Marmot body size and habitat are also loosely correlated with climate. About 10% of body size variance and about 10% of vegetative habitat variance in Eurasian species can be accounted for by climate (Caumul and Polly, 2005).

Despite the climatic specializations of marmots, climate in the strict sense is unlikely to be a limiting factor on their geographic ranges. Seasonal nutritional shortages, snow cover, and the availability of herbaceous forage have been shown to be important factors in marmot distributions and patterns of hibernation (Armitage, 2000, 2007, 2013). Our analyses confirm that realized marmot ranges are smaller than their potential range in terms of climate envelopes. Geographic areas that fall within marmot climate envelopes (habitat models) were up to 15 times larger than the ranges actually inhabited by marmots (Table 9.3). If marmots were limited strictly by their climate tolerances, then the size of their real ranges should be about the same as the habitat models (Zimmermann *et al*., 2010; Svenning *et al*., 2011). Seasonality, which is thought to be an important feature of marmot habitats (Armitage, 2013), is included in our climate data: while strong seasonality is a feature of marmot habitats, our data show that not all seasonal climates are home to marmots. Factors such as forage and patterns of snow cover are also likely to be important (Armitage, 2013), as are topography, soil type, interactions with predators, and competitive interactions among marmots.

Our data suggest that, unlike climate in the strict sense, terrain and inter-marmot relationships are likely to be limiting factors for marmots. The range of *Marmota caligata*, for example, is confined to the mountainous areas of the North American northwest, but its climatic range extends across the Canadian Shield in areas inhabited by *M. monax* (Figure 9.5). The restriction of *M. caligata* to the mountains could be mediated by either competition with woodchuck or terrain, but not by climate. Adaptations to terrain are the most likely cause because *M. caligata* and *M. marmota* have overlapping distributions in the Rockies, where they are separated by elevation. Differences in terrain are associated with differences in forage, landscapes, snow cover and availability of south-facing slopes on which snow melts early in the season (Armitage 2000, 2013). Terrain more clearly defines the ranges of *M. camtschatica, M. caudata*, and *M. marmota*, which have climatic envelopes that are compatible with extensive lowland areas in western Siberia, Anatolia, and northern Europe respectively and where no competing marmots live. Note, however, that the fossil record shows that *M. marmota* lived on the Northern European Plain during glacial periods, presumably extirpated from the mountainous Alps by glacial ice (Kalthoff, 1999). We thus cautiously suggest that the interaction between terrain, climate, vegetation, and substrate, better explains the current ranges of marmots than does climate by itself.

Table 9.3 Past and present range sizes for living marmot species. Modern range sizes, sizes of modern climatic habitat models (the geographic area that falls within the climate envelope of each species) and last glacial maximum (LGM) climatic habitat models are reported, along with the proportional size of the modern habitat model to the real range and the proportional size of the LGM habitat model to the modern model.

Species	Modern range (km²)	Modern habitat model (km²)	Model / real	LGM habitat model (km²)	LGM / Modern model
M. baibacina	620 000	4 215 000	680%	1 212 500	29%
M. bobak	790 000	1 730 000	219%	7500	0%
M. broweri	217 500	655 000	301%	772 500	118%
M. caligata	2 535 000	11 282 500	445%	7 157 500	63%
M. camtschatica	1 015 000	15 580 000	1535%	11 082 500	71%
M. caudata	545 000	2 547 500	467%	3 825 000	150%
M. flaviventris	1 715 000	2 980 000	174%	1 907 500	64%
M. himalayana	2 410 000	4 825 000	200%	3 387 500	70%
M. marmota	205 000	962 500	470%	812 500	84%
M. menzbieri	2500	2500	100%	0	0%
M. monax	7 585 000	15 457 500	204%	1 610 000	10%
M. olympus	5000	2500	50%	0	0%
M. sibirica	1 522 500	2 715 000	178%	2 042 500	75%
M. vancouverensis	7500	2500	33%	0	0%

Marmot origins: North American climate and environment 10–5 Ma

Marmots split from other living ground squirrels in North America in the Late Miocene, 10–8 Ma. The *Paenemarmota* clade predominantly inhabited the Great Plains, as did the oldest close relative of crown group marmots, *M. vetus*. Other close relatives and the earliest members of the crown group lived in the western parts of the continent. The crown group originated in high altitude regions of western North America between 7–5 Ma. The climate, vegetation and topography was considerably different in the Late Miocene than today and was undergoing profound transformations. Here we review the palaeoclimatic and palaeoenvironmental context of marmot origins.

The Great Plains at 10–8 Ma would have had low relief with braided stream complexes carrying coarse sediments eastward away from the Rocky Mountains and their predecessors (McMillan *et al.*, 2002). Prior to 12 Ma, the Great Plains supported a woodland vegetation with no clear modern analogue whose exceptionally high primary productivity supported more herbivore species than a similar biome would today (Janis *et al.*, 2002, 2004; Fox and Koch, 2003). By 8–6 Ma, during the time of *Marmota vetus* and *Paenemarmota sawrockensis*, a vegetative turnover from C_3 to C_4 plants was underway, producing what were probably the first truly extensive open tall grassland habitats of the Cenozoic (Janis *et al.*, 2004; Edwards *et al.*, 2010). This vegetative transition was associated with an increase in precipitation seasonality. Stable isotope data indicate that

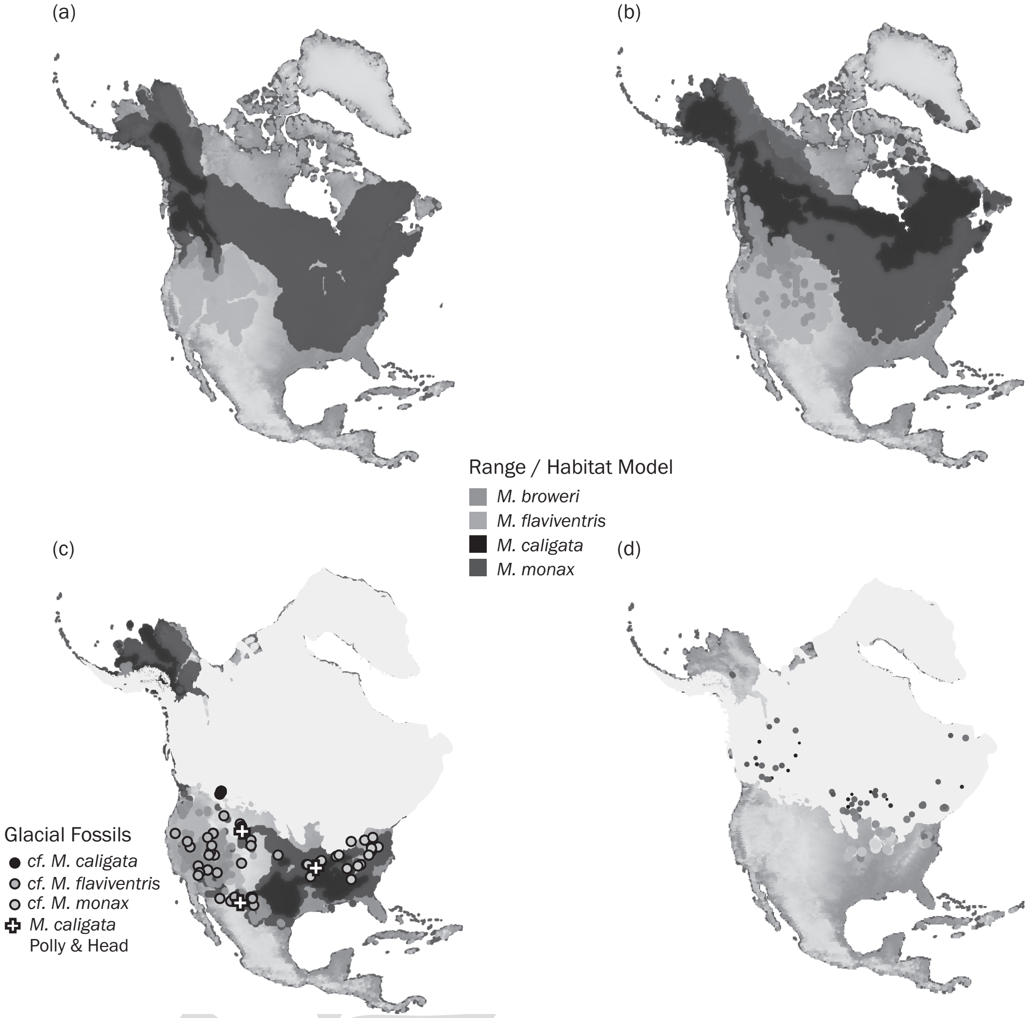

Figure 9.5 Past and present distributions of *Marmota broweri* (purple), *M. caligata* (red), *M. flaviventris* (yellow), and *M. monax* (blue). (**a**) Modern ranges. (**b**) Climatic habitat models for the present day. Each model shows regions that fall within the climate envelope of the modern species. (**c**) Last glacial maximum (LGM) climatic habitat models. Actual fossil occurrences from the Wisconsinan period are shown as black-rimmed points (see text for discussion). Ice cover at LGM is superimposed. (**d**) Geographic variation in size of in modern *M. monax* superimposed on glacial ice. Relative size is indicated by the radius of the point and its colour (dark is small). Points are scaled linearly by skull length proportional to the range between shortest and longest. A sharp size boundary runs roughly along the former ice margin, marking the transition from *M. m. canadensis* to the north and larger subspecies to the south. A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.

there was virtually no seasonality prior to 13 Ma, followed by increasing aridity punctuated with seasonal wet periods by 7 Ma (Fox, 2000). The wet season shrank from about 28 to 41 weeks of the year at 9 Ma to only 11–24 weeks by 7 Ma. These stem group marmots lived in communities with other ground squirrels, extinct borophagine canids, a hyaena, large browsing camels, browsing and grazing horses, and early rattlesnakes. This transitional grassy woodland with increasingly seasonal aridity was the ancestral environment of stem group marmots. By the time the crown group originated farther west between 7–5 Ma, C_4 vegetation had became the dominant forage on the Great Plains (Edwards *et al.*, 2010) and browsing ungulates had almost completely replaced by grazers in Great Plains ecosystems by 4.5 Ma (Janis *et al.*, 2004). The vegetative transition on the Great Plains was also accompanied by increasing incidence of wildfires, which would have made burrowing a life-saving strategy (Edwards *et al.*, 2010). By 5 Ma, the only marmot that remained in these now-open Great Plains ecosystems was the giant *Paenemarmota barbouri*, which had a body mass of 10 kg or more. Even though living marmots sometimes consume C_4 grasses, their diets consist largely of C_3 herbaceous plants (Armitage, 2000).

The crown group originated 7–5 Ma in mountainous areas of western North America in habitats that were atypical for earlier members of the stem group. Western North America was undergoing remarkable topographic transformations, including geologically rapid continental extension and uplift that stretched open the Great Basin and lifted mountain chains along the Pacific Coast (Dickinson, 1979; Horton *et al.*, 2004). The continent was stretched more than 100 km east to west by a two-phase process that was culminating by the Late Miocene (Surpless *et al.*, 2002). Stable isotope data suggest that uplift of the ranges close to the coast, such as the central Cascades, slowed between 15.4 and 7.2 Ma, after which they began rising again, sharply so after 3 Ma (Kohn *et al.*, 2002). Plant fossils indicate that the elevation of western Nevada had been higher than 3000 m at 16–15 Ma, dropping to present elevations of about 1000–2100 m by 10 Ma (Wolfe *et al.*, 1997). Thus, the landscapes inhabited by the earliest crown group marmots would have been a mosaic of newly exhumed mountainsides with deeply dissected stream valleys. Abundant scree slopes, rocky fields and thickly sedimented valley floors would have been created along the coast by rapid uplift and incision and farther inland by extension, faulting and down-drop of crustal blocks to form the basin and range topography of today's Great Basin.

The changing topography enhanced rain shadow effects and increased the precipitation gradient that differentiates the moist Pacific Coast from arid inland basins. The coastal ranges have been high enough to cast some rain shadow for at least 16 Ma (Crowley *et al.*, 2008), but their effect on the precipitation gradient became more dramatic by 7 Ma. In lowlands there was a shift toward greater aridity with wet seasons with annual precipitation of 500–850 mm before 7.2 Ma, dropping to 200–600 mm by 7 Ma (Retallack *et al.*, 2002). Precipitation seasonality increased through the same sequence.

Vegetation in the west was transformed during this period, with increasing differentiation between upland and lowland vegetation. Prior to 8 Ma the west was dominated by coniferous forests at high elevations, cool deciduous forests at mid elevations, and warm temperate evergreen forests in the lowlands (Graham, 2011; Retallack, 2004). By 7.3–7.2 Ma the lowlands were vegetated with tall grasslands and seasonally waterlogged riparian meadows followed by semi-arid scrub similar by 7.2 Ma (Retallack *et al.*, 2002). At 6 Ma the mean annual temperature was about 11°C in the valleys, similar to northern Mexico today (Wolfe *et al.*, 1997; Retallack, 2004). At 7 Ma, high latitude winter temperatures were about 15°C warmer than today and tundra was only just starting to be established at high latitudes (Graham, 2011). Alpine tundra communities were probably rare or non-existent at the mid-latitudes where crown group marmots originated.

The origin of crown group marmots thus involved a transition from ancestrally low-elevation, non-seasonal environments to high-elevation ones with seasonal precipitation but relatively warm temperatures. *Marmota minor* and *M. korthi*, the closest fossil relatives of the crown group, both lived in these warm, increasingly dry upland environments with other burrowing rodents, browsing camels, horses, and antilocaprids, extinct browsing chalicotheres, and mastodon (Kellogg, 1910; Kelly, 2000). The closest modern climatic analogue of these environments is in the Sierra Madre Occidental mountains of Mexico, which are covered with mixed oak–pine vegetation above 1 km up to the peaks at 3.5 km. The highest peaks of the Sierra Madre are above the tree line and snow is, at most, seasonal. Whether there would have been seasonal snow cover in the habitats of the first crown group marmots is impossible to know, but the prolonged deep snows of their modern habitats would not have existed.

The predominantly C_3 diet of marmots seems to be an ancestral condition from which they have not departed. Their historical biogeography suggests that they fared better at high elevations, where C_4 plants have remained rare, than they did on the Great Plains and other low elevation areas from which they disappeared in the Late Miocene and Pliocene as C_4 grasslands expanded. Whether their specialization on harshly seasonal environments that are not easily tolerated by other mammals arose as a trade-off in the milieu of C_4 expansion is beyond the scope of our data, but it is a hypothesis that could be explored with detailed comparative analysis of diets in living and fossil marmots, geochemical analysis of the soils and sediments from which fossil marmots have been recovered, and better resolution of the phylogenetic relationships of stem-group marmots.

After their origination, crown group marmots expanded northward into what is today British Columbia and Alaska by 3 Ma. Their spread into this region is closely associated with the uplift of new mountainous terrains, decline in mean annual temperatures, and more increase in seasonality. Prior to 5 Ma, southern Alaska had a flat topography with mean elevation of 0.2 km and south flowing rivers. The rugged Alaska and St Elias ranges of southern Alaska had mean elevations of 3 km by 2.5 Ma (summarized by White *et al.*, 1997). The first marmot fossils in Alaska occur around 3 Ma. By that time, high latitudes and high elevations had become colder with frigid winters that were colder than 7 Ma but still warmer than today. Boreal forests and tundra were present in Alaska and northwestern Canada by 2.3 Ma (White *et al.*, 1997).

Expansion: Eurasian climate and environment 5–2 Ma

The first Asian fossil marmots are found about 3.2 Ma, just before the Bering Strait opened at 3 Ma (Fyles *et al.*, 1991). Although molecular clock estimates suggest that dispersal to Asia could have occurred as early as 5 Ma (Steppan *et al.*, 2011), there is as yet no fossil evidence to confirm their presence prior to 3.2 Ma. Uplift of the Tibetan Plateau had been intensifying since about 7 Ma, creating many of the high elevation landscapes now associated with China and Central Asia (Wang *et al.*, 2008). Uplift events at 3.6 – 2.6 Ma were associated with increased monsoonal climates to the south and drier climates to the north of the rising Himalaya and Tibetan Plateau (Rae *et al.*, 1998; Zisheng *et al.*, 2001). The oldest substantiated fossil occurrence is *M. tologoica* from Transbaikalia (Erbaeva, 2003). At the time, that region was covered in a mosaic vegetation of steppes, meadows and mixed forests of oak, holly, elm, pines, spruce and birches (Alexeeva and Erbaeva, 2005; Erbaeva *et al.*, 2012). Another early Asian marmot, *M. parva* lived about 2 Ma on the Chinese Loess Plateau (Qiu *et al.*, 2004), which is a region in northern China and southern Siberia that after 8 Ma started receiving heavy accumulations of wind-blown dust from the rising and increasingly arid Tibetan Plateau. The Loess Plateau generally became drier after 3 Ma, transforming the vegetation from warm, moist cypress forests to a drier forest–grassland environment of spruce and herbs by the time of *M. parva* (Wu *et al.*, 2007). *Marmota parva* is the smallest crown group marmot, with an estimated body mass around 2.18 kg (Table 9.1). The environments of the first Asian marmots were thus broadly similar to the environments of the first crown group marmots in North America, milder and less harsh than their environments later in the Quaternary.

By 1 Ma, the cooling and drying of the early Quaternary further transformed the Asian climate and replaced the Transbaikalian mixed woodlands with open steppe in the lowlands and spruce and pine dominated forest in the uplands and river valleys. Glacial cycles between 1 and 0.75 Ma were marked by the first evidence of permafrost in the region (Alexeeva and Erbaeva, 2000). By 0.5 Ma the modern species *M. sibirica* and *M. camtschatica* occurred in the region (Erbaeva, 2003), which was by then dominated by dry steppes, scrublands, and deserts in the lowlands and alpine and taiga forest in the uplands (Alexeeva and Erbaeva, 2005). The transformation of Asian marmot environments during the Quaternary thus also broadly paralleled the events in North America.

In Europe, the first marmot fossils are found about 1.25 Ma. Mean annual temperatures in Europe had been steady around 15°C prior to 5 Ma then had declined sharply to about 10°C by 2.5 Ma (Mosbrugger *et al.*, 2005). The flora of this pre-marmot period had been open grassland habitats dominated by large mammals, including hyaenids, horses, rhinos, giraffids, and gomphothere elephants at 10 Ma, replaced by moist woodlands by 5 Ma (Eronen *et al.*, 2009). Seasonality increased sharply after 5 Ma toward an annual temperature range of as much as 23°C by the end of the Pliocene based on evidence from plants (Mosbrugger *et al.*, 2005), and it was in this climatic context that marmots spread into Europe.

Quaternary glacial–interglacial cycles and marmot distributions

For the past 2.5 Ma, the climate of the Northern Hemisphere has been increasingly dominated by glacial–interglacial cycles that each last about 100 million years. We used fossil occurrences and climate-based range reconstructions for the last glacial maximum (LGM) to assesses how the individual glacial–interglacial cycles have impacted the environments and geographic distributions of marmots. The LGM data provide a snapshot of marmots during glacial phases, and modern data provide a snapshot from interglacial phases. The response of marmots to glacial–interglacial cycles is of special interest for forecasting how they might respond to anthropogenic climate change (Guralnick, 2007; Guralnick and Pearman, 2009; Waltari and Guralnick, 2009). So far, marmots have been demonstrably moved upslope by changes in vegetation, rainfall and snow cover during the late twentieth century (Armitage, 2013).

Our data suggest that marmot ranges, on average, contracted during glacial phases (Table 9.3), contra previous interpretations based on extralimital fossil occurrences that glacial ranges were larger. Our interpretation is based on a combination of fossil occurrences and climatic habitat models in which the modern climate envelopes were projected onto an LGM palaeoclimate model. Fossil occurrences, which are plentiful in North America, are broadly consistent with our LGM models (Figure 9.5; see further discussion below). In Table 9.3 the column labelled 'LGM/Modern' reports the size of the modelled LGM range as a percentage of the modelled modern range. We compared the LGM habitat models to the modern habitat models instead of the real ranges because climate envelopes are known to over-predict ranges, thus we make the working assumption that our LGM models are similarly over predicted. Note, however, that most of the LGM habitat models are larger than the real modern distributions. With that caveat, we found that on average, marmot geographic distributions were only 74% as large as they are today. Only *M. broweri* and *M. caudata* had larger ranges during glacial cycles. Thus we conclude that most marmot ranges probably did not expand during cold glacial cycles and are more likely to have contracted.

The conclusion that marmot ranges were smaller during glacial cycles is surprising because Pleistocene marmot fossils are frequently found outside their modern ranges. Examples of such extralimital occurrences include *M. marmota* on the northern European plain (Kalthoff, 1999), *M. sibirica* and *M. camtschatica* in the Transbaikal (Erbaeva, 2003), and *M. flaviventris* in southern Arizona and New Mexico (Harris, 1990). However, extralimital occurrences do not imply range expansions if marmots were also extirpated from other parts of their ranges by ice or unfavorable environments. Fossil occurrences and our LGM habitat models suggest this was indeed the case. For example, *M. monax* and *M. caligata* were extirpated from large parts of their modern range by ice sheets, which resulted in LGM ranges that were both translocated and smaller (Figure 9.5).

The geographic responses of individual marmot species vary considerably in ways that may help explain features of their modern geographic and phenotypic variation (Figure 9.5). The LGM habitat models and fossils suggest that *M. broweri* remained confined to the same area that it occupies today, but was split into two populations in the Brooks Range by ice and unsuitable climates. Such a split is generally consistent with the molecular phylogeography of living populations (Gunderson *et al.* 2009). Habitat models of both *M. monax* and *M. caligata* suggest that their ranges were split by the LGM ice sheet into a northern distribution in Beringia and southern distribution south of the glacial margin. No Beringian fossils have heretofore been referred to either of those species, but a glacial allopatric split may explain the curious distribution of body size in living *M. monax*. Populations of *M. monax canadensis* are substantially smaller than southern populations and there is a sharp line between small and large body size roughly along the southern margin of the glacial ice (Figure 9.5d). This pattern could be explained by the expansion of small-bodied populations from Beringia in post-glacial times to meet the larger southern forms in the region of the Great Lakes, a hypothesis that could easily be tested with molecular phylogeography. Habitat models suggest that the range of *M. flaviventris* was broadly contiguous with its current range, but shifted southwestward. The modern distributions of *M. vancouverensis* and *M. olympus* are too small to make meaningful LGM reconstructions, but they were likely to have been confined to small refugia along the Pacific Coast within or close to their modern ranges. *Marmota vancouverensis* is thought to be an island isolate that has speciated allopatrically from *M. caligata* (Steppan *et al.*, 1999; Cardini *et al.*, 2007, 2009). This scenario is supported by our LGM habitat models, which split the range of *M. caligata* into three areas, one in Alaska, one south of the glacial margins, and one on the coast at the southern end of Vancouver Island. If correct, then glacial vicariance may better explain the origin of *M. vancouverensis* than island isolation.

The LGM distribution of *M. caligata* is of special interest because ice cover and habitat models suggest that it was impacted more than any other marmot species (Figure 9.5c) and extirpated from almost all of its modern range during glacial phases. Most of its suitable climate was found south of the glacial margins in what is today in the Great Plains and Midwest (Figure 9.5c). Attention should therefore be given to the glacial fossil occurrences south of the ice, most of which have heretofore been referred to *M. flaviventris* or *M. monax*. However, Late Quaternary fossil mammals have often arbitrarily been referred to the geographically nearest living species (Bell *et al.*, 2010). Several fossil samples previously referred to *M. flaviventris* or *M. monax* were linked with *M. caligata* in a maximum likelihood analysis of a large morphometric data set (Polly and Head, 2004). That analysis placed *M. caligata* at Moonshiner Cave in Idaho in the early Holocene, Bear Park Cave in Idaho during the early Holocene, at Papago Springs in Arizona during that last glacial, and Schliepers Pit in Illinois in the early Holocene (Figure 9.5c). These occurrences are consistent with our habitat model reconstruction. The identity of marmot fossils deserves closer scrutiny, ideally with ancient DNA studies.

Two marmot species, *M. bobak* and *M. monax*, live in lowland habitats that are atypical of the clade. Their preference for low elevations appears to be derived because the last common ancestor of the crown group lived in high elevations, as have most other crown group taxa. Indeed, the oldest *M. monax* fossils are from a high elevation early to mid Pleistocene cave in Colorado (Polly, 2003). The ranges of these two species also share some common features with the habitats of the ancestors of the crown group, notably their extension into comparatively warm climates like the southern margin of the distribution of *M. monax* in northern Mississippi and Alabama. While these two species are not associated with scree slopes, which appears to be an important habitat feature of marmots since their crown-group origin, they are distributed largely in association with deep soils that originated from glacial till, glacial outwash and river floodplains, which provide them with the unconsolidated substrates needed to construct their burrows and hibernacula.

Evolution of body size in marmots

Marmots are the largest living sciurids (Barash, 1989; Armitage and Blumstein, 2002; Goodwin, 2009). The origin of their large body size has a complicated history, however, because the oldest members of the crown group were considerably smaller than their stem group relatives *Paenemarmota* (Figure 9.3; Table 9.1). In fact, current understanding of the phylogenetic relationships of stem group marmots suggests that body size at the base of the stem group was small; *M. vetus*, the oldest taxon, was about 2.9 kg, similar to many non-marmot ground squirrels.

The *Paenemarmota* stem group evolved extremely large body sizes. Even the smallest members of that clade were as large as the largest living marmots. The largest was *P. barbouri*, whose body mass has been estimated at 9.5–9.8 kg based on femur dimensions and 14.4–16.2 kg on basis of premolar size, *P. sawrockensis* estimated at 10.0–12.4 kg based on premolar size (Goodwin and Bullock, 2012). Our estimate of 9.1 kg thus seems to be conservative.

At 2–3 kg, the earliest members of the crown group were a little smaller than living marmots (cf. *M. flaviventris*). Even though the fossil record of pre-Quaternary marmots is sparse, crown group marmots appear to have maintained a comparatively small body size until 3 – 2 Ma when global climatic deterioration and the increasing amplitude of glacial–interglacial cycles would have created harsh environments at high elevations and northerly latitudes.

Small ancestral body size succeeded by larger body size later in the crown group's history appears to be consistent with the physiology, growth and hibernation of living marmots. Large body size, or more specifically fast growth rate, has been argued to be an adaptation to harsh, seasonal climates (Barash, 1989; Armitage and Blumstein, 2002; Armitage, 2007). Small ancestral body size is therefore consistent with the comparatively mild climates of the Late Miocene and Pliocene; and the larger size of later marmots is consistent with the harsher, colder, more seasonal climates of the Quaternary. Better understanding of the relationships of stem group marmots will improve our understanding of the climatic, environmental and ecological contexts of size evolution.

Ecomorphological specialization in marmots

Skeletal and dental differentiation between marmot species is small and only loosely correlated with diet and habitat. All marmots live in burrows in unconsolidated soil or scree and have mixed diets of forbs, bulbs, fruits and sometimes dry or woody plants with only proportional differences in food preference (Barash, 1989; Caumul and Polly, 2005). Species and subspecies differ enough that unidentified marmot skulls can be referred morphometrically with 80%–100% accuracy (Polly and Head, 2004; Cardini *et al.*, 2009), but their the variation in their skulls, mandibles and teeth is so weakly correlated with diet, habitat, and phylogenetic relationship that only about 10%–25% of shape variance explained by these factors (Cardini and Tongiorgi, 2003; Caumul and Polly, 2005). Intraspecific and intraspecific differentiation in these structures is thus more likely due to chance, sexual selection or factors other than to adaptation local environments and climates. The Vancouver Island marmot, for example, is the most phenotypically but least genetically differentiated species (Cardini, 2003; Polly, 2003; Cardini *et al.*, 2007, 2009; Nagorsen and Cardini, 2009).

Despite their weak intraspecific specializations, marmot morphology strongly differs from other squirrels. Mandible and skull shape differentiates marmots from their closest ground squirrel relatives and from sciurids as a whole (Swiderski *et al*, 2000; Cardini, 2003; Michaux *et al.*, 2008; Casanovas-Vilar and van Dam, 2013; Lv *et al.*, 2013). The specialized mandible morphology of marmots is functionally associated with their highly herbivorous diets through the proportions of the moment arms of the muscles of mastication (Velhagen and Roth, 1997; Zelditch *et al.*, 2009; Swiderski and Zelditch, 2010; Casanovas-Vilar and van Dam, 2013). Marmots are also distinctive from other sciurids in their dental proportions, probably also associated with their leafy diets (Goodwin, 2009).

Summary

Crown group marmots originated in environments different from their modern habitats in all respects except topographic relief. Fossil and molecular evidence agrees that the crown group originated in western North America at 7–5 Ma. Late Miocene temperatures were milder than today, but were becoming more seasonally arid and cooler. The founders of the crown group were small animals, much smaller than their Great Plains ancestors and about the size of the smallest living marmots. The first members of the crown group were themselves strongly differentiated from their own ancestors, which were large-bodied animals that inhabited wooded, grass-covered, low-relief landscapes that have no modern analogue. The origin of living marmots thus involved a reduction in body size and an ecological transition to forested high-relief, high-elevation landscapes, with seasonally arid environments. Their origin was not associated with harshly cold or snow-covered environments; those came later. Whether hibernation originated independently after the origin of the crown group as Quaternary climates grew colder, or arose earlier as a response to seasonal aridity is impossible to determine. Marmots having originated in warm, seasonal, rocky environments of the Late Miocene were able to specialize on the even harsher high-elevation and high latitude environments that were created with the onset of Quaternary climates. Our findings partially support the tectonic model of marmot origins proposed by Nikol'skii and Rumiantsev (2012), except insofar as marmots originated as specialists on high elevation, high-relief topography, not as lowland specialists.

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