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Post-natal ontogeny of the mandible and ventral cranium in *Marmota* species (Rodentia, Sciuridae): allometry and phylogeny

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Abstract Post-natal ontogenetic variation of the marmot mandible and ventral cranium is investigated in two species of the subgenus *Petromarmota* (*M. caligata*, *M. flaviventris*) and four species of the subgenus *Marmota* (*M. caudata*, *M. himalayana*, *M. marmota*, *M. monax*). Relationships between size and shape are analysed using geometric morphometric techniques. Sexual dimorphism is negligible, allometry explains the main changes in shape during growth, and males and females manifest similar allometric trajectories. Anatomical regions affected by size-related shape variation are similar in different species, but allometric trajectories are divergent. The largest modifications of the mandible and ventral cranium occur in regions directly involved in the mechanics of mastication. Relative to other anatomical regions, the size of areas of muscle insertion increases, while the size of sense organs, nerves and teeth generally decreases. Epigenetic factors, developmental constraints and size variation were found to be the major contributors in producing the observed allometric patterns. A phylogenetic signal was not evident in the comparison of allometric trajectories, but traits that allow discrimination of the Palearctic marmots from the Nearctic species of *Petromarmota* are present early in development and are conserved during post-natal ontogeny.

Keywords Mandible/ventral cranium · Sexual dimorphism · Allometric trajectories · Masticatory muscles/epigenetics/constraints · Phylogenetic signal

Introduction

Allometry refers to the pattern of covariation among several morphological traits or between measures of size and shape (Klingenberg 1998). The study of allometry originally focused on the covariation among measurements in ontogeny and evolution using the equation of simple allometry $y = bx^k$ (y , x trait measurements; b value of y for $x = 0$; k allometric coefficient) proposed by Huxley (1924, 1932a, b, cited in Klingenberg 1998) or its extension to multiple measurements. In this model, y is said to show positive allometry with respect to x when $k > 1$ (i.e., y 'grows faster' than x) or negative allometry when $k < 1$ (i.e., ' y grows slower than x '). In the absence of allometry ($k = 1$), the two traits are isometric and their ratio is constant although their absolute value may vary. In 1966, Gould reviewed the subject of allometry and separated its definition from specific mathematical relationships among variables. Later, Mosimann (1970) defined allometry as the association between size and shape, and isometry as the absence of size-related variation. Thus, the separation of size and shape components of form is fundamental for the study of allometry following the Gould–Mosimann approach.

In the late 1980s and early 1990s the development of Procrustes superimposition methods for Cartesian co-ordinates of anatomical landmarks (see [Material and methods](#)) provided scientists with an effective tool for an efficient separation of size and shape components of morphological variation. The new field of geometric morphometrics (Adams et al. 2004) immediately found very fruitful applications in the study of animal allometry. For instance, Collard and O'Higgins (2001) and O'Higgins and Collard (2002) investigated homoplasy in the evolution of long faces in baboons and mandrills, Ponce de León and Zollikofer (2001) compared

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developmental, growth and allometric trajectories of *Homo sapiens* and *Homo neanderthalensis*, Zelditch et al. (2000) analysed angles between vectors of ontogenetic allometric coefficients describing piranha body form, and Larson (2004) compared scaling patterns in *B. americanus* with those of *R. sylvatica* to address the question of whether general allometric patterns of chondrocranial growth might exist in larval anurans. In all these studies highly significant allometries were found and these are of potential importance in influencing the direction of evolutionary change. This is because natural selection may be particularly effective on traits whose correlated modifications follow the preferential direction set by an allometric trajectory (Gould 2002).

Sciurids are an interesting taxon to study the role of allometry in the evolution of animal morphology. During the radiation of this family (Mercer and Roth 2003; Herron et al. 2004) pronounced changes in size occurred independently in several lineages (twice only in the marmotine clade, with *Cynomys* and *Marmota* remarkably larger than most of their close relatives in the polyphyletic genus *Spermophilus*). Furthermore, sciurids are considered to be inclined to convergence of skeletal characters in species of similar size (Hafner 1984; Roth 1996; Velhagen and Roth 1997). Hafner (1984) found sciurid phenetic clusters reflecting either size (small-, medium-, large species) or ecological similarities (diggers and climbers, and, among climbers, desert/scrub foragers, terrestrial/arboreal foragers, adept climbers) in his morphometric analysis of cranial and post-cranial bones, while Roth (1996) presented a cladogram based on “qualitative characters of the cranium,” that is, “what one might have expected had we performed our analysis on just a single character: size.”

Swiderski (2003) recently exemplified the usefulness of the geometric morphometric method in the analysis of allometric patterns in the sciurid family. A geometric morphometric analysis of the mandible morphology of the fox squirrel, *Sciurus niger*, indicated that no more than 50% of shape variation is correlated with size while traditional morphometric analysis on the same sample suggested that almost all ontogenetic variation is explained by allometry. The different outcome is mainly due to the inadequacies of traditional morphometric approaches in separating size and shape components of form and points to possible flaws in empirical evidence about the role of allometry as an evolutionary constraint.

Ball and Roth (1995), and Thorington and Darrow (1996) emphasised the importance of morphological studies on sciurid jaw and cranial anatomy, given the significant role of features of these anatomical regions in subfamilial classification, and their potential value as a basis for phylogenetic analyses. Their analyses of jaw muscles of New World and Old World squirrels showed that shared dietary adaptations between species are not necessarily reflected in masticatory function. Thus the Old World, hard-fruit eating species have a more powerful stroke of the incisor bite (Thorington and Darrow 1996) but this does not hold for the New World species

(Ball and Roth 1995). Velaghen and Roth (1997) examined evolutionary allometries in the mandible of New World squirrels (including the marmot species, *M. monax* [Linneus 1758]) showing that “the scaling of the mandible among the New World tree squirrels is generally isometric.” The mandibular proportions of the Old World squirrels were found to be very similar to those of the New World ones, while the terrestrial squirrels (Marmotini) displayed greater differences from their sciurid relatives. However, no comparison of ontogenetic stages was performed to investigate how the morphologies of adults relate to growth, ontogenetic allometry and development.

The large increase in size that occurred during the evolution of *Marmota* and the divergent morphology of the marmotine mandible point to the need and potential interest of investigating the role of allometry in the evolution of this clade. Indeed, marmots are a peculiar group being the largest true hibernating mammals (Barash 1989; Armitage 2000). Their remarkable adaptations for surviving in the cold (for instance, reproductive skipping and degrees of sociality correlated to environmental harshness) attracted curiosity well before marmots became the subject of scientific research. Thus, in the Alps they were extensively hunted because their fat was believed to have extraordinary curative properties.

Compared to the extensive literature on eco-ethology of marmots (Barash 1974; Arnold 1990; Blumstein and Armitage 1998, 1999; Armitage 1999; Bibikov 1999) their morphology has been the subject of few studies and the studies that have been carried out very rarely involve more than one species (exceptions are Hoffmann et al. 1979 and Polly 2003). Recently the first geometric morphometric studies describing the comparative morphology of the adult mandible and cranium of a wide range of marmot species were reported by Cardini (2003, 2004), Cardini and O’Higgins (2004) and Cardini et al. (in press). Also, the ontogeny of marmot skeletal characters was recently investigated in a study on the post-natal ontogeny of the mandible of *M. flaviventris* (Audubon and Bachman 1841) by Cardini and Tongiorgi (2003). Conspicuous morphological changes during growth were found that increase robusticity. The majority of the shape variation between age classes was shown to be due to allometric scaling. Three explanations were suggested for the shape differences among age classes: (1) after the first few weeks of life, rapid shape changes are observed in the juvenile mandible which may be partly accounted for by the shift from a liquid (milk) to a solid (plants) diet, (2) allometric scaling might preserve mechanical function as size increases and, (3) after sexual maturity, agonistic behaviour between individuals may promote mandibular remodeling aimed at increasing the power of incisor bite, incisors being the main weapons in intraspecific conflicts and predator defence.

The pattern of ontogenetic shape change that emerged from the study of the mandible of *M. flaviventris* has not yet been verified in other marmot species and in different skeletal structures. Indeed, *M. flaviventris* may

be a peculiar species being the smallest living marmot and belonging to a lineage (the subgenus *Petromarmota*) that includes only four species, all inhabiting the Rocky Mountains (Steppan et al. 1999). In fact, the genus *Marmota* consists of 14 species, of which the vast majority belong to the mainly Palearctic subgenus *Marmota* (Steppan et al. 1999; to avoid confusion between *Marmota* as a genus and *Marmota* as a subgenus, the latter will here be indicated with *Marmota*_{SG}). None of them, to our knowledge, except *M. flaviventris*, has been the subject of previous ontogenetic studies of mandibular or skull morphology. Ontogenetic allometry, in particular, is interesting because it provides a possible mechanism to explain the development of sexual dimorphism (when present), the development and evolution of interspecific differences, and may provide insights into functional–morphological integration and adaptation to diverse habitats.

This study therefore aims to develop a deeper understanding of the role of ontogenetic allometry in shaping the mandible and ventral cranium in four *Marmota*_{SG} species (*M. caudata* [Geoffroy 1844], *M. himalayana* [Hodgson 1841], *M. marmota* [Linneus 1758], *M. monax*) and two *Petromarmota* representatives (*M. caligata* [Eschscholtz 1829], *M. flaviventris*). Our study is aimed at answering the following questions:

1. If allometry is significant, do male and female mandibles and ventral crania share a common allometric trajectory in all species such that any sexual dimorphism in shape is reached thorough extension/truncation of a common allometry?
2. Does ontogenetic allometry play a significant role in modelling the mandible and ventral cranium of marmots?
3. Do different marmot species share common allometries of the mandible and ventral cranium that are extended or truncated to generate interspecific differences?
4. If allometry is significant, is the ‘degree of allometry’ (i.e., the proportion of the total shape change during post-natal ontogeny that is size-related) similar in the mandible and ventral cranium in each taxon and is it correlated between species to any variable in the set of eco-morphological data available for this study?
5. To what extent are morphological changes in the ventral cranium of each species associated with those found in the mandible, and what is the anatomical nature and relationship of these?

Materials and methods

Specimens, dental measurements, digital images, landmarks

Marmot left hemimandibles (labial side) and ventral crania are photographed in a standardised way (Cardini and Tongiorgi 2003; Cardini and O’Higgins 2004) and

landmarked using TPSdig (Rohlf 2004). The form (size and shape) of the photographic projections of hemimandibles and ventral crania is represented by configurations of landmark coordinates (i.e., a set of topographically corresponding anatomical landmarks — Marcus et al. 2000). Only the left side of the ventral cranium is examined to avoid redundancy in the shape variables and to avoid the confounding issue of asymmetry. Landmark definitions are given in Tables 1 and 2 and illustrated in Fig. 1.

Sciurid hemimandibles are particularly suitable for two-dimensional geometric morphometric analyses because they are fairly flat (Velhagen and Roth 1997). To mitigate against errors introduced by a two-dimensional study of a highly three-dimensional structure, such as the cranium, measurement errors and photographic distortions are minimised by choosing almost co-planar landmarks and by taking pictures at a distance (1 m) more than ten times the length of a skull.

In *M. flaviventris* five age classes can be estimated by using the relationship between age and premolar wear described by Van Vuren and Salsbury (1992). This relies on changes in the distances between the paraconid and protoconid cusps of the lower left premolar as they wear. These are measured with digital calipers to the nearest 0.1 mm. The precision of the caliper measurements is tested as described in Cardini and Tongiorgi (2003). No similar technique is available for evaluating the age of the other marmot species. However, an approximate discrimination between the young and the adults in the other marmot species is carried out through analyses of mandibular size and shape and dental measurements (Cardini 2003). For this reason the analysis focuses on the issue of ontogenetic allometry rather than on differences in shape among age classes (with the exception of *M. flaviventris*).

After removing damaged specimens and a few outliers, 363 specimens of different age classes remained (Table 3, Appendix).

Table 1 Landmarks on the labial side of the hemimandible

No.	Definition
1	Upper extreme anterior part of the incisor alveolus
2	Anterior top of the mandibular symphysis
3	Anterior extremity of the maxillary toothrow (premolar alveolus)
4	Intersection of the dental ridge with the dorsal portion of the masseteric ridge (base of the coronoid process)
5	Tip of the coronoid process
6–7	Anterior and posterior tip of the condyle
8	Posterior extremity of the angular process
9	Mental foramen

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

Table 2 Ventral cranium landmarks, and corresponding anatomical regions

No.	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 foramen lacerum 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

Geometric morphometrics and statistical analyses

Patterns of variation in the configurations of landmarks are analysed in the present study using techniques from geometric morphometrics. Geometric morphometrics is a group of analytical methods that preserves complete information about the relative spatial configuration of landmarks throughout an analysis and utilises the properties of Kendall’s shape space (Slice 2001). The shape spaces and associated statistics of these methods are well understood (Dryden and Mardia 1998) and yield highly visual and readily interpretable results.

The landmarks are registered using generalised Procrustes analysis (GPA), which minimises the sum of squared distances between homologous landmarks by translating, rotating and scaling them to best fit. This registration method does not introduce bias into the distribution of specimens whose landmarks vary independently and according to random error (Rohlf 1999)

and produces consistently accurate estimates of the mean shape when compared to other available methods (Rohlf 2003). Scaling is according to centroid size (CS, i.e., the square root of the sum of squared Euclidean distances from each landmark to the centroid, which is the mean of landmark coordinates). Centroid size is used in this study as an expression of the overall scale of the landmark configuration, and thus of the structures under study and to examine ontogenetic allometry.

As a result all analyses of shape are carried out on data sets from which centroid size has been partitioned. Information about the centroid size of the individual specimens prior to GPA is retained for the purpose of studying size/shape relationships.

The registering of landmark coordinates through GPA results in each specimen being represented as a single point in a non-Euclidean shape space (Slice 2001) that is projected into a linear tangent space to Kendall’s (1984) shape space (Dryden and Mardia 1998), and statistical analyses carried out within that space using standard multivariate methods. This approach is satisfactory when variations are small (see O’Higgins 2000), as in these data. In the present study the level of distortion arising from projecting from the non-Euclidean shape space to the tangent space is examined by comparing the Procrustes distances (PRD; approximately, the square root of the sum of squared distances between corresponding landmarks of a pair of specimens) in the shape space with the Euclidean distances in the tangent space using Tps-Small (Rohlf 2004).

Geometric morphometric analyses are performed using computer programs from the ‘TPS’ (Thin Plate Spline) series, written by Rohlf (2004), and the programs Morphue (Slice 1999) and Morphologika (O’Higgins and Jones 1999). Two block partial least squares (PLS) analysis (Rohlf and Corti 2000) is employed to explore shape covariation between the mandible and the ventral cranium.

The relationship between shape and centroid size (i.e., allometry) within and between species is examined through multivariate regression of the shape variables onto log-transformed centroid size (Rohlf et al. 1996; Monteiro 1999). Log-transformed size always led to a slightly larger proportion of explained shape variance. Tests for common slopes and for homogeneity of the intercept (Rohlf 2004) are performed to compare the allometric trajectories between sexes of each species and among species (with pooled sexes). Additionally, angles are computed pairwise between allometric vectors and the resulting interspecific dissimilarity relationships (angles) between the allometric trajectories are summarised with an UPGMA (unweighted pair-group method using averages) phenogram.

In all species, principal components analyses (PCA) of both the ventral cranial and the mandibular shape variables are employed to investigate intraspecific (GPA superimposition one species at a time) and interspecific

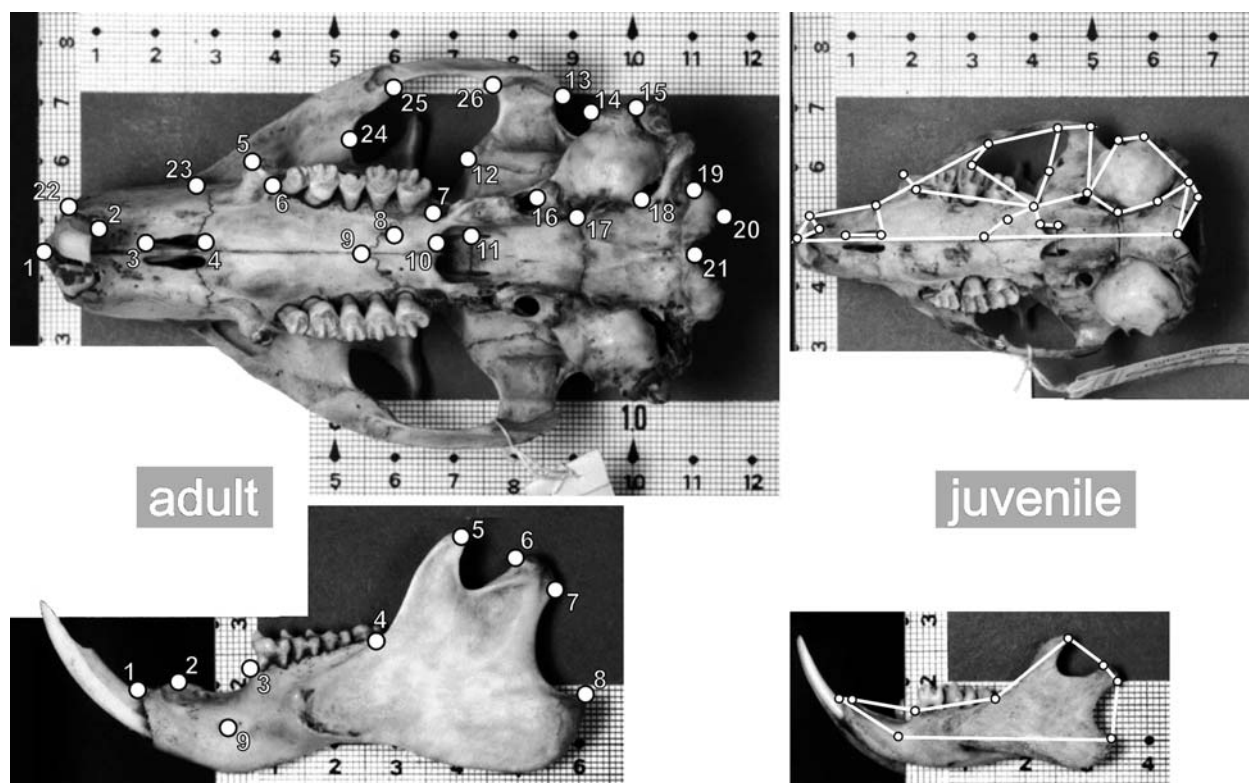


Fig. 1 The landmark configuration is shown on the adult mandible and ventral cranium, while the wireframe used for 'stylised' drawings of both structures is shown on a juvenile specimen. The

millimetre paper in the background provides information on the scale factor and shows that no photographic distortions are present. Landmark definitions are given in Tables 1 and 2

Table 3 Sample size

Species	Structure	Females	Males	Total
<i>M. caligata</i>	Hm	32	23	59
	vc	34	26	64
<i>M. caudata</i>	hm	24	18	45
	vc	21	17	47
<i>M. flaviventris</i>	hm	39	30	72
	vc	43	34	80
<i>M. himalayana</i>	hm	18	26	55
	vc	16	22	52
<i>M. marmota</i>	hm	13	14	67
	vc	9	8	37
<i>M. monax</i>	hm	31	20	65
	vc	34	25	73

Total includes specimens of unknown sex

(specimens of all species simultaneously GPA superimposed) marmot phenetic relationships. Additionally for *M. flaviventris*, the UPGMA is applied to perform a cluster analysis of the matrix of Procrustes distances between the ventral cranial and mandibular mean shapes in each age class, and the significance of size and shape differences is tested using analyses of variances. SPSS 9.0.1 (1999), Statistica 4.5 (1993), NTSYS-pc 2.10z (Rohlf 2002) and TpsRegr 1.28 (Rohlf 2004) were used for these statistical analyses.

Results

Ontogeny and sexual dimorphism

Sexual dimorphism in the allometric trajectories of the mandible and ventral cranium is rarely detected in the regressions of shape onto size for each marmot species (Table 4). The slopes of female and male regression line are similar for both structures in all marmots except *M. caligata* (where the slope for the ventral cranium is significantly different, $P = 0.03$). The intercepts of the allometric trajectories are alike for males and females with *M. caligata* again presenting the only major exception (significance of difference in mandibular intercept, $P = 4.03 \times 10^{-5}$); the mandible and the ventral cranium of *M. flaviventris* also manifest significantly different intercepts between sexes ($P \approx 0.05$). Indeed, the *M. caligata* mandible seems to represent the only example of highly significant sexual dimorphism in allometries, but the regression model that fits different regression lines for males and females (separate intercepts) only negligibly (4.0%) increases the percentage of shape variation explained by size compared to the regression performed with pooled sexes (same regression line). Congruently, inspection of the deformation grids for the mandibular shapes predicted by the regression model (results not shown) indicates that the only difference between males

Table 4 Multivariate regressions of mandibular and ventral cranial shape onto their centroid size: tests for allometry (1, slope; 2, intercept)

Species	Test for sexual dimorphism in allometry						Test for allometry with pooled sample (males and females)					
	Struc-ture	Test for	Wilks' λ^a	F_s	df	P^b	Wilks' λ	F_s	df	P	% size-related shape variation	P (F_{Goodall}^c)
M. caligata	hm	1	0.701	1.157	14, 38	0.345	0.107	26.239	14, 44	8.7×10^{-17}	43.6	< 0.0001
		2	0.362	4.910	14, 39	4.03×10^{-5}						
	vc	1	0.0539	3.291	48, 9	0.0300	0.0134	23.052	48, 15	2.70×10^{-8}	37.6	< 0.0001
		2	0.101	1.854	48, 10	0.147						
M. caudata	hm	1	0.747	0.604	14, 25	0.836	0.291	5.228	14, 30	7.3×10^{-5}	13.2	< 0.0001
		2	0.518	1.725	14, 26	0.111						
	vc	1		n small ^d				n small			16.5	< 0.0001
		2										
M. flaviventris	hm	1	0.740	1.301	14, 52	0.239	0.149	23.308	14, 57	1.50×10^{-18}	30.0	< 0.0001
		2	0.666	1.897	14, 53	0.0480						
	vc	1	0.294	1.299	48, 26	0.239	0.0141	45.247	48, 31	3.60×10^{-19}	31.3	< 0.0001
		2	0.225	1.941	48, 27	0.0335						
M. himalayana	hm	1	0.599	1.290	14, 27	0.276	0.0975	26.442	14, 40	7.80×10^{-16}	43.9	< 0.0001
		2	0.787	0.541	14, 28	0.887						
	vc	1		n small			0.00459	13.550	48, 3	0.0262	40.6	< 0.0001
		2										
M. marmota	hm	1	0.507	0.696	14, 10	0.740	0.146	21.650	14, 52	7.40×10^{-17}	21.9	< 0.0001
		2	0.363	1.379	14, 11	0.300						
	vc	1		n small				n small			24.5	< 0.0001
		2										
M. monax	hm	1	0.774	0.709	14, 34	0.750	0.514	3.379	14, 50	0.00075	7.3	< 0.0001
		2	0.724	0.953	14, 35	0.517						
	vc	1	0.0768	2.254	48, 9	0.0959	0.0930	4.877	48, 24	4.5×10^{-5}	14.5	< 0.0001
		2	0.175	0.983	48, 10	0.557						

^aWilks' λ statistic is based on a comparison of the residual (deviation from the fitted regression) variance-covariance matrix and total (residuals plus predictions based on the regression) variance-covariance matrix (Rohlf 2004).

^bSignificant values, in this and other Tables, are in italics

^cThe Goodall's F is a test that assesses (using Procrustes distances) the significance of the ratio of squared distance between predictions and mean to squared distance from the specimens to their predictions. This is analogous to the testing of the ratio of explained variance to unexplained variance in regression (Rohlf 2004)

^dSample size too small for multivariate tests

and females in their allometry consists of relative backward displacement of the mental foramen in males compared to females and allometric variation is similar in both sexes (49.6% for males and 44.9% for females). On the whole, these small differences do not strongly mitigate against using a pooled sex slope for subsequent analyses comparing species. Further, this pooling is justified by the results of interspecific comparisons of mandibular allometric trajectories using only males or only females of *M. caligata* in which no appreciable differences in results is found.

Age classes can be estimated only for *M. flaviventris*. Results of analyses of variances (sex $\times$ species) for size and shape of the ventral cranium are substantially similar to those obtained by Cardini and Tongiorgi (2003) on the mandible and are briefly summarised in this section.

Size

Sexual dimorphism in size is significant and male mandibles and crania are on average respectively 6.0 and 7.2% bigger than those of females. Growth proceeds

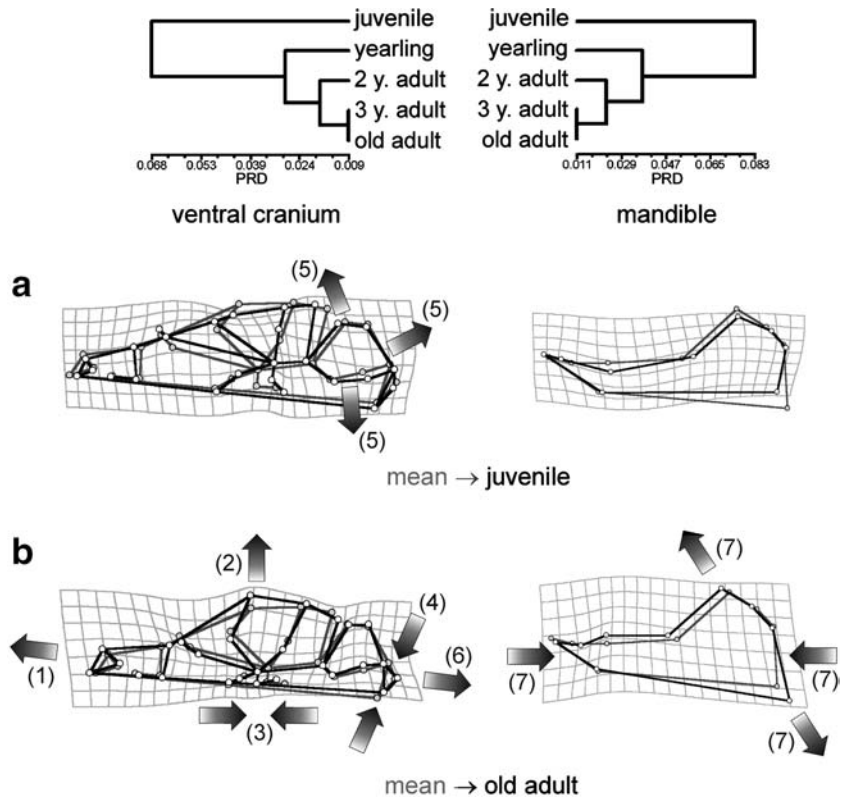
quickly before sexual maturity but it goes on in the adults at least until they are 4 years old.

Shape

The comparison of cranial shape among *M. flaviventris* age groups perfectly mirrors what is found in the mandible if the juvenile group is excluded (as in Cardini and Tongiorgi 2003). Thus, sexual dimorphism in shape is negligible ($P > 0.05$ in MANOVA), and shape differences among age classes are related to size variation ($P > 0.05$ when size-related shape changes are removed in a MANCOVA with size as covariate). The rate of shape change becomes progressively smaller as individuals grow older (compare phenogram branch lengths at different ages in Fig. 2a).

Mean shapes of all age classes are computed with pooled sexes and superimposed on the overall mean. TPS deformation grids between the overall mean and the means of both juveniles and adults are used to illustrate shape changes during post-natal ontogeny in *M. flaviventris*.

Fig. 2 Comparisons of average shapes for the five age classes of *M. flaviventris*. Ventral cranium on the left and mandible on the right. **a** UPGMA phenograms. **b** TPS transformation from the average shape of all age classes to that of either a juvenile (individual in its first year of life; magnification $\times 1.6$) or an old adult (4 or more years old; magnification $\times 3.0$); *arrows* help to detect prominent shape changes during growth; *numbers* refer to descriptions of shape changes given in the text



Relative elongation of the snout and enlargement of the zygomatic arch (Fig. 2b1–2) are the most evident ones and imply that they grow faster than other regions. The regions of the palate (palatine and presphenoid) and foramen magnum (Fig. 2b3–4) are relatively ‘contracted’ in the adults. Also the tympanic bulla is characterised by a relative reduction of its size during post-natal ontogeny (larger in juveniles, Fig. 2b5). The apparent backward displacement of the basioccipital (Fig. 2b6) is due to the concomitant elongation of the cranial base and reduction in the curvature of the cranial vault. The condyles become bigger and the foramen magnum shifts from a slightly downward-facing orientation to being almost perpendicular to the ventral surface of the cranium.

Intraspecific allometry: amount of size-related shape variation and patterns of shape changes

Shape variation in the mandible and the ventral cranium is significantly correlated with size in all species (Table 4), and a large proportion (upto 43.9%) of total shape change during marmot post-natal development is explained by ontogenetic scaling.

Size-related shape variation is very similar in all species, as suggested by deformation grids for largest specimens of each ontogenetic series (Fig. 3). The allometric shape changes in the mandible and the ventral cranium closely resemble those observed between the average shapes of *M. flaviventris* juveniles and adults (compare Fig. 3 with Fig. 2b). During

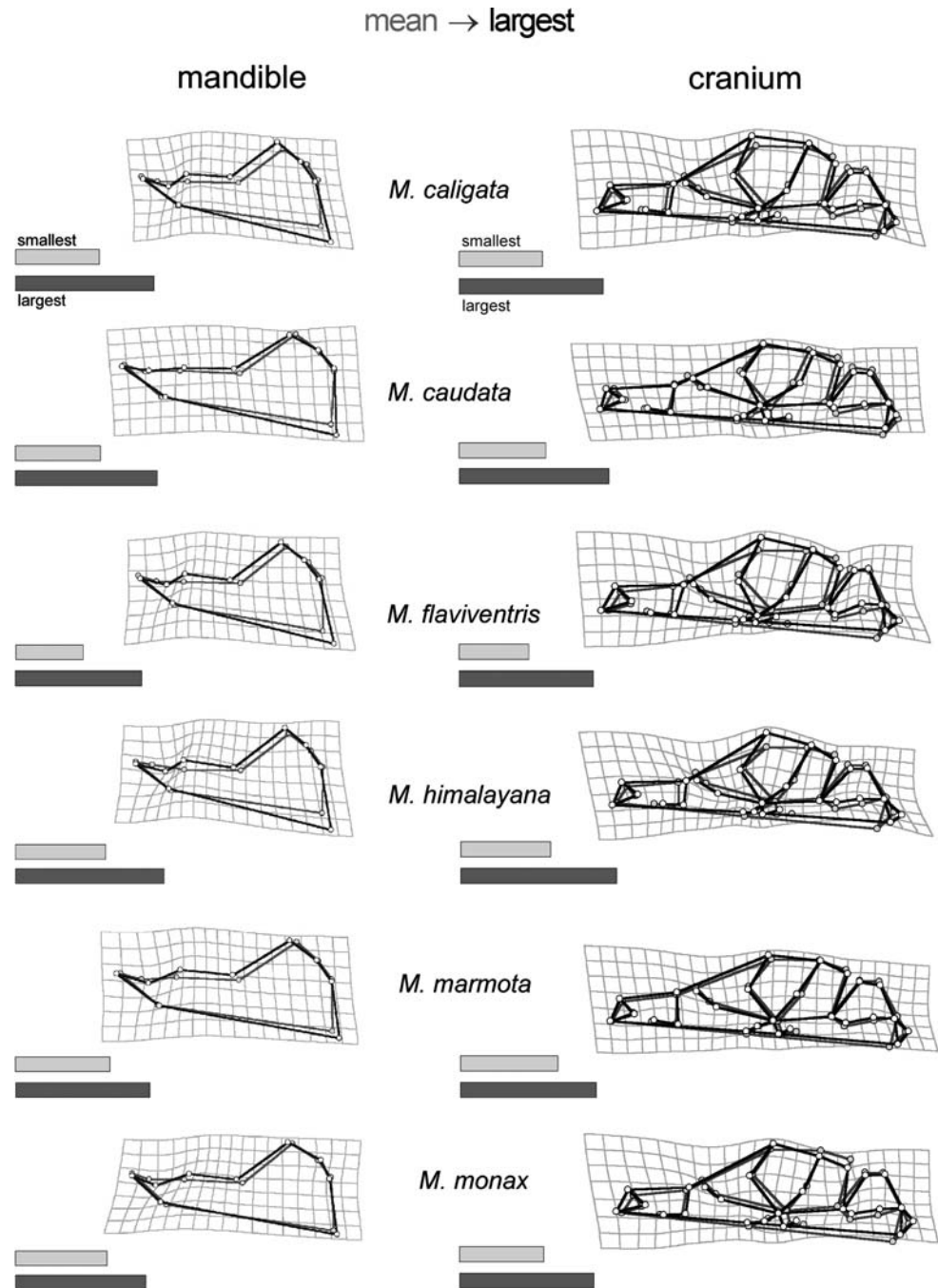
post-natal ontogeny the mandible becomes relatively deeper and shorter (Fig. 2b7), the angular process is longer and the curvature of the diastema (landmarks 2–3) is more pronounced. The zygomatic arch enlarges and the snout becomes longer, relative reduction of size occurs in the palate, foramen magnum and tympanic bulla.

Interspecific allometry: comparison of trajectories

Allometric trajectories show significant interspecific differences both in the mandible and ventral cranium (test for common slope for the mandible: $\lambda_{\text{Wilks}} = 0.575$, $F_{70, 1613.3} = 2.841$, $P = 3.2 \times 10^{-13}$; and ventral cranium: $\lambda_{\text{Wilks}} = 0.120$, $F_{240, 1469.1} = 3.250$, $P = 7.6 \times 10^{-43}$). The angles of allometric trajectories are compared in Fig. 4 through a UPGMA cluster analysis of the matrix of pairwise angles between vectors. The phenogram topology is fairly similar in the two structures with the exception of *M. monax* whose mandibular allometric trajectory is strongly divergent.

The specimens of all six species are projected onto the first two principal components (PC) of the shape variables for the mandible and the ventral cranium (Fig. 5). Smaller and younger specimens tend to be to the right of plots and larger and older ones to the left since PC1 scores decrease with size in both datasets. Large overlaps are visible among different species for the mandible. A better separation is achieved with the ventral cranium. For this structure, PC1 summarises most allometric changes in post-natal ontogeny while

Fig 3 Shapes (magnification $\times 3.0$) predicted by the multivariate regression of shape onto size for largest mandible (left) and cranium (right) of each species sample; the lines next to the deformation grids are proportional to the centroid size of the smallest (light grey) and largest (dark grey) specimen in each group



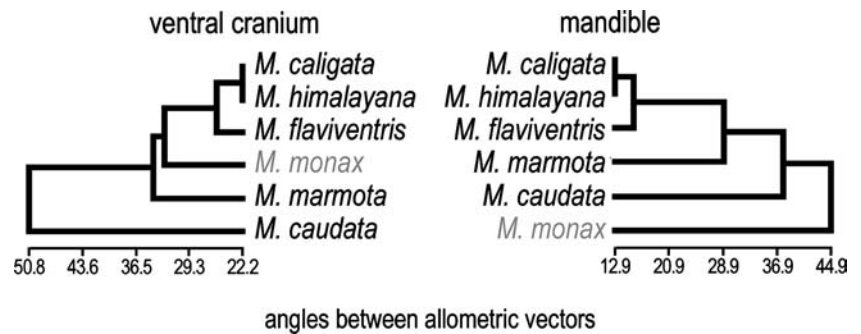
PC2 suggests differences of possible phylogenetic and zoogeographic relevance. The shape of the ventral cranium is slender and elongated in Palearctic species of the subgenus *Marmota* (*M. caudata*, *M. himalayana* and *M. marmota*) but enlarged in the Nearctic *M. monax*. *Petromarmota* species (*M. caligata* and *M. flaviventris*) have somewhat an intermediate shape between those of Palearctic and Nearctic representatives of the subgenus *Marmota*. This pattern seems to already be present in young marmots as suggested by the precocious separation of groups for which several

juveniles are available (*M. himalayana*, *Petromarmota* species, *M. monax*).

Degree of allometry: comparison in the mandible and ventral cranium and correlation with eco-morphological variables

Amounts of size-related shape variation during marmot post-natal ontogeny are similar in the mandible and ventral cranium. Indeed, a very high correlation between

Fig 4 Comparison of angles between allometric trajectories for the ventral cranium and mandible (UPGMA cluster analysis on the matrix of pairwise angles)



the degree of allometry of the two structures is found ($r = 0.99$).

Bivariate correlations between the degree of allometry and eco-morphological variables (from the present study and the literature — Table 5) are sought. *M. caudata* and *M. marmota* are excluded from this part of the analysis because results for their uneven samples have a strong influence on correlations (see Discussion). The degree of allometry is highly correlated ($r > 0.98$, $P < 0.05$) with the ages of dispersion and first reproduction. Correlation with growth (range of size variation in the samples during post-natal ontogeny) is high but not significant. Also correlations with other eco-morphological variables are not significant.

Mandible-ventral cranium covariation

In all marmot species the first PLS vector is the only one with $P < 0.01$ in the permutation test; hence, it summarises the vast majority of significant information about the covariation (from 97.0% in *M. caligata* to 56.6% in *M. monax*) of the mandible and ventral cranium (Table 6). Examination of the shape variation (deformation grids) along the first PLS vector (Fig. 6) indicates that the morphological traits whose shape consistently varies in the same ‘direction’ in the mandible and ventral cranium are essentially the same as those affected by allometry. In fact, given its high correlation with size ($0.72 \leq r \leq 0.94$, with only the *M. monax* mandible $r = 0.49$), one can interpret the first PLS vector as expressing the covariation between the two structures during growth. The PLS plots of the mandible and the ventral cranium are thus very similar to those already presented in the section on allometry (Figs. 3,4). The graphical output of the PLS analysis is exemplified by *M. caligata* (Fig. 6). During ontogeny, the areas of insertion of the masseters are characterised by the concomitant relative increase of their surface in both structures, the snout becomes relatively elongated, the diastema curvature increases in the mandible, the palate shrinks relative to the remaining ventral cranium, the mandibular horizontal ramus become relatively deeper, while the tympanic bulla and occipital foramen remain relatively small.

Discussion

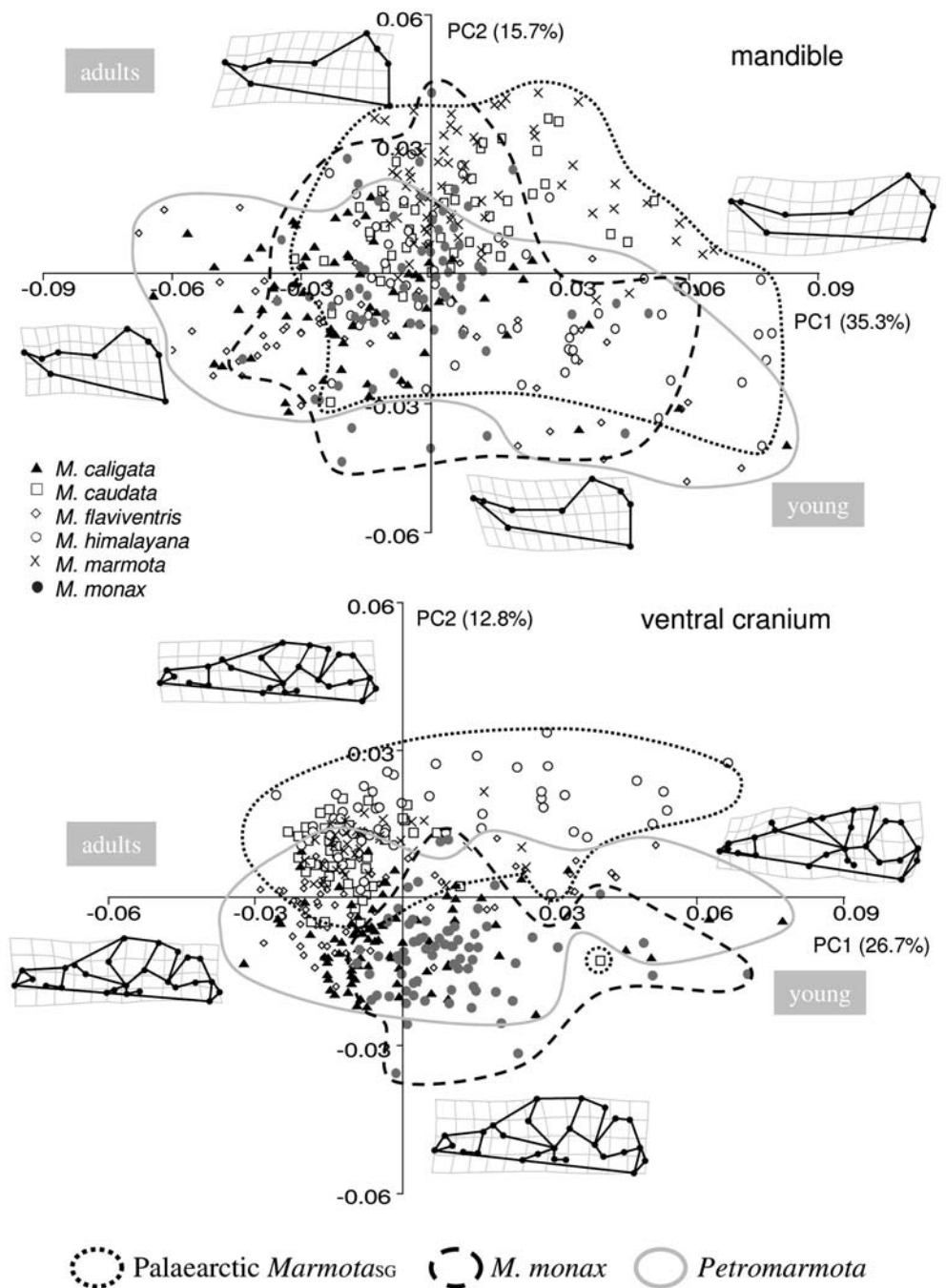
Ontogeny and sexual dimorphism

Results from the analysis of the ventral cranium post-natal ontogeny in *M. flaviventris* corroborates previous finding on the mandible by Cardini and Tongiorgi (2003). Most cranial traits that differ between age classes can be explained by allometry. Sexual dimorphism is generally not pronounced in marmots. However, differences in size between males and females are significant, which implies that males progress further along the common allometric trajectory. However, on average, *M. flaviventris* males are only 3% larger than females and the effect of this small size difference on shape is either negligible or too modest to be detected in natural population samples (Voss et al. 1990). This reasoning probably has general validity in the genus *Marmota*. Sexual dimorphism in size is found in all adult marmots (Cardini 2003; Cardini and O’Higgins 2004) and males and females share a common allometric trajectory in each of the species included in the analysis; however, as with *M. flaviventris*, the extension of the common trajectory in males produces negligible sexual dimorphism in adult shape, and this is congruent with the consistent but small differences in size between sexes.

Intra- and interspecific allometry: amount of size-related shape variation, patterns of shape changes and comparison of trajectories

The proportions of size-related shape change in the post-natal ontogeny of the marmot mandible and ventral cranium vary from less than 10% in *M. monax* to almost 50% in *M. caligata* and *M. himalayana*. However, the patterns of shape change predicted for the extreme points of the allometric trajectories are similar and mirror those seen in the deformation grids of juvenile and adult average shapes of *M. flaviventris*. This observation suggests that in all marmot species allometry is an important aspect of post-natal ontogeny and, as with *M. flaviventris*, most shape differences among age classes are likely to be size-related adjustments.

Fig 5 Principal components analysis of mandibular and ventral cranial shape of the six marmot species. Plot of the first two PCs (percentage of shape variance summarised by each PC is given in parentheses). Deformation grids for extreme points along each axis are shown (deformations magnified $\times 1.5$)



If significant allometry is found in all analysed species, what is the nature of the changes that modify the spatial and functional relationships of the anatomical regions of the mandible and ventral cranium? Allometric shape variations help to maintain functions that would be lost if growth proceeded geometrically (Emerson and Bramble 1993). This is why isometry is generally unexpected in studies of ontogenetic series.

Allometric modifications may also be related to constraints that compel different anatomical regions to grow at different rates. For instance, a relative

reduction in size is found in relation to the premolar–molar tooth row, around the foramina (palatine foramina and foramen magnum) and in the tympanic bulla. This is likely because the dentition and nervous system complete their development relatively early. Likewise a relative increase in size of the otic capsule is common during mammalian skull ontogeny (Novacek 1993), although an early developed ear can also be seen as a pre-adaptation in a group where acoustic communication is important and predator presence is signalled with alarm calls.

Table 5 Average values for life history variables

species	behaviour			body (gr.)			
	S	D	R	L	WE	WI	WL
<i>M. caligata</i>	2	2	3	510	3283	6187	2904
<i>M. caudata</i>	3	3	3	473	2631	3923	1292
<i>M. flaviventris</i>	1	1	2	416	2422	3431	1009
<i>M. himalayana</i>	3	2 ¹	3 ¹	535	3445	6420	2975
<i>M. marmota</i>	3	2	3	550	2825	5000	2175
<i>M. monax</i>	0	0	1	484	3356	4718	1362

S degree of sociality: 0 solitary, 1 female kin group, 2 restricted family, 3 extended family (Armitage 2000); D age of dispersion (years), and R age of first reproduction (Rymalov personal communication; Blumstein and Armitage 1998, 1999; Armitage 1999; Armitage 2000). Mean values for body variables (Armitage personal communication): L body length (mm); WI weight at immergence (g); WE weight at emergence; WL weight loss during hibernation

^a*Marmota himalayana* has been poorly studied but its behavioural ecology is generally considered to be similar to that of other large species of the same subgenus. Being the largest marmot, together with *M. olympus*, and living at high altitude on the Himalayas, dispersion at 2 years of age and first reproduction at 3 years are very likely

Table 6 PLS analysis of shape covariation between the mandible and the ventral cranium

	Pair of vectors ^a	Cumulative % of covariation	Permutation test ^b
<i>M. caligata</i>	1	97.0	0.1
<i>M. caudata</i>	1	63.3	0.4
<i>M. flaviventris</i>	1	91.9	0.1
<i>M. himalayana</i>	1	96.7	0.1
<i>M. marmota</i>	1	84.4	0.1
<i>M. monax</i>	1	56.6	0.5

^aOnly the first vector whose proportion of explained covariation is at least 50% is shown

^bA permutation test with 1,000 permutations (observed value included) to test for the covariation of shapes (tested one vector at a time); values indicate the proportion of time (expressed as percentage) random values equalled or exceeded the observed value

The relatively short snout of the young (positive allometry) is part of another trend of early neurocranial and late facial expansion found in most mammals (Laghenbach and Van Eijden 2001). If this is also adaptive for suckling, it has not been investigated. On the other hand, a relationship between diet and morphology can be suggested for the extensive form of modifications that occur in the first year of life. In *M. flaviventris*, and presumably in all other species, this is the period in which the largest changes in size and shape occur during an individual life. Rapid growth is needed to increase the survival chances of juveniles during hibernation. Extensive bone remodelling is partly correlated with size changes but also with the rapid shift from a liquid (milk) to a solid (plants) diet after weaning (Laghenbach and Van Eijden 2001;

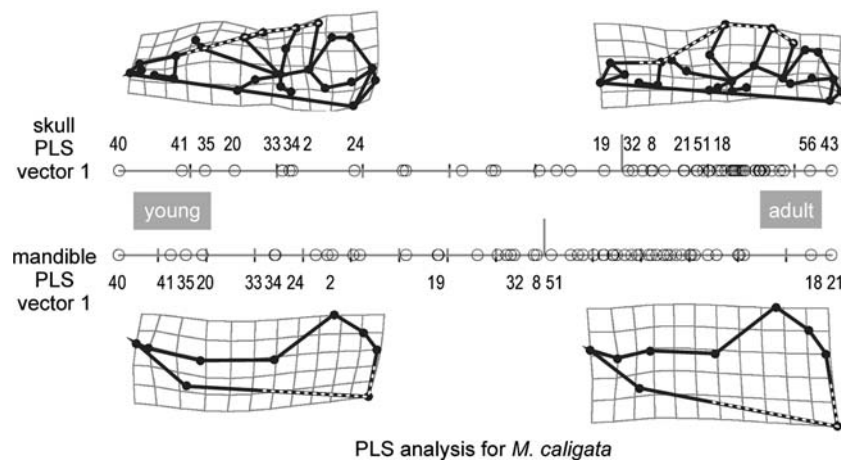


Fig 6 Partial least squares analysis of mandibular and ventral cranial shape in *M. caligata*. The first vector of covariation for each structure and the shape predicted by PLS for extreme specimens along this vector are shown (dotted lines are regions of insertion of masseters). The numbers above the partial least squares vectors

identify the same specimens (those at the extremes or by the origin of each vector were chosen as examples) for the mandible and the ventral cranium: similar relative positions indicate a high covariation in the two structures

Cardini and Tongiorgi 2003). Relative enlargement of the surface of insertion of the masticatory muscles provides growing marmots with more efficient chewing for food processing and more powerful bites for defence and intraspecific competition (Cardini and Tongiorgi 2003).

Thus, ontogenetic scaling has an important role in all of the marmots that have been studied, but the proportion of size-related shape variation is quite variable. *M. monax* has a low degree of allometry. Shape changes predicted by ontogenetic scaling are less conspicuous than in the other species (e.g., less pronounced elongation of the angular process — Fig. 3). Absolute ontogenetic size variation is also the smallest among the marmots that have been studied. *M. monax* has some unique eco-ethological traits for the genus *marmota*: it is a solitary species, also lives in forests and commonly starts reproduction after the first hibernation. All other species are social, restricted to habitats with alpine or steppe meadows and never mate until they are 2 years old or older. The cranial morphology of *M. monax* is also rather distinctive (Cardini and O'Higgins 2004) and interspecific divergence seems to begin early in the ontogeny (see PCA scatterplot in Fig. 5).

In this study, two other species are found, which have a low degree of allometry: *M. caudata* and *M. marmota*. Sampling error is large in *M. caudata*. Young specimens are uncommon and the only small juvenile in the sample may have strongly affected the outcome of the regression of shape onto size. Particular caution needs to be exercised with regard to this species. The sample of *M. marmota* might not be representative of the variation in the wild. This is suggested by the fact that the sample contains juveniles that are larger than in all other species, despite it not being the largest marmot in the study. In addition, most of the specimens for which the mandible was analysed are from the same population. Again, results for this species should be regarded as provisional until verified on larger samples.

Different species have different allometric trajectories (both for the mandible and ventral cranium). The exclusion of *M. caudata* and *M. marmota* from the comparison of allometric trajectories does not substantially change its outcome (the significance of differences between species remains $P < 0.0001$). This result also holds, with very few exceptions, if trajectories are compared pairwise between species (results not shown). The contribution of divergent allometries to the production of phylogenetically informative interspecific differences is, nevertheless, unclear, since no evident similarity between trajectories of members of the same subgenus (with the possible exception of *M. caligata* showing some similarities with *M. flaviventris* but also with *M. himalayana*) is found that may help to explain clusters of Palaearctic *Marmota*_{SG} versus *Petromarmota* species observed in interspecific comparisons of the adults (Cardini 2003; Cardini and O'Higgins 2004).

Degree of allometry: comparison in the mandible and ventral cranium and correlation with eco-morphological variables

The degree of allometry is about the same in both structures in each species.

That the mandible and ventral cranium show a similar degree of allometry is not surprising, given the strong functional and developmental correlation of the two structures. Why the degree of allometry is so variable between different species is, however, less clear.

If results for *M. caudata* and *M. marmota* are not considered, a pattern emerges, which indicates a possible link with life history traits. The degree of allometry increases with the age of first reproduction (and with that of dispersion, which occur 1 year before). Dispersion and reproduction are delayed in those species, which live in the harshest environments (Armitage 2000), where winters are longer and hibernation lasts for most of the year. The time span for reaching sexual maturity (considering only active seasons) is approximately 7–8 months for *M. monax*, 9 for *M. flaviventris*, more than 12 for *M. caligata* and *M. himalayana* (Armitage, personal communication). The degree of allometry correlates, thus, with the actual time necessary for an individual to become adult. Why is this so? Adult size matters to some extent. Larger species tend to have a larger degree of allometry. However, the correlation with the age of first reproduction is the highest, and this life history trait is only partially correlated to adult size. It may be speculated that, since muscles insert on regions that show extensive allometric changes, a prolonged bone remodelling by muscles might be involved in producing allometric modifications whose extent is roughly proportional to the length of pre-adult life (the period when muscle development is more intense).

Mandible-ventral cranium covariation

Correlated shape changes during the ontogeny of the mandible and ventral cranium are not unexpected (as mentioned in the previous section).

Covariation is particularly evident in the areas of insertion of masticatory muscles. Muscles generate forces that epigenetically contribute to remodelling the rodent mandible (Atchley et al. 1992; Herring 1993) and cranium (Lightfoot and German 1998). Correlated shape changes are thus linked, to some extent, to muscle development, which, although partially genetically regulated, may be influenced by environmental factors like diet (Miller and German 1999) and agonistic behaviour. Phenotypic variation that does not reflect genetic differences might be found in these regions. However, diagnostic characters of phenetic groups congruent with phylogeny discovered by Cardini (2003) and Cardini and O'Higgins (2004) involve the areas of insertion of the masseters. Thus, despite the preceding argument, a strong phylogenetic signal, which appears precociously,

at least in the ventral cranium (see PCA plot), seems to be present in the angular process of the mandible and in the zygomatic arch, and it is not masked by size-related adjustment and epigenetic factors influencing the development of those same regions.

Conclusions

Allometry accounts for the main shape changes in the mandible and ventral cranium during marmot post-natal ontogeny. Allometric shape changes may have a dual 'role': preserving function during size increase (size adjustments of shape) and, through changes of allometric trajectories, contributing to the appearance of new morphological traits. Allometry also occurs when developmental constraints do not allow a uniform growth of all anatomical regions.

Correlated shape changes in the mandible and ventral cranium also occur and follow a strong allometric pattern. The development of masticatory muscles plays a role in this concerted remodelling, which produces roughly similar shape features in the post-natal ontogeny of all studied marmots. Although speculative, the findings suggest a relationship between the amount of size-related shape variation in post-natal ontogeny and the length of time during which bone remodelling mediated by muscles is most effective. Epigenetic factors may, thus, contribute to allometries making the phylogenetic signal in allometric trajectories difficult to detect.

The interplay of epigenetic factors and developmental constraints in producing allometric changes during ontogeny may indeed reflect morpho-functional relationships with a long evolutionary history. In a larval anuran (*Bufo americanus*), Larson (2004) found that "measurements associated with the oral region, braincase, and otic capsule tend to scale with negative allometry, whereas those associated with the posterior palatoquadrate and insertion sites for the major jaw and buccal muscles scale with isometry or positive allometry." These findings on the ontogeny of the chondrocranium in a basal tetrapod lineage are quite reminiscent of the findings in a mammal taxon.

If allometry does not contribute to the production of adult shape differences of phylogenetic relevance, mandibular and cranial traits that allow discrimination of the two main marmot clades must develop early and be conserved during post-natal ontogeny.

The allometric patterns suggested by the comparison of the four largest samples available for this study are not always congruent with those of *M. caudata* and *M. marmota*, whose samples are smaller and dishomogeneous. A comparison of ontogenetic trajectories including other marmot species and outgroup taxa is desirable to support the findings and investigate evolutionary allometries in the marmotine clade.

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Appendix

Abbreviations USNM, National Museum of Natural History (Washington, USA); BMNHL, British Museum of Natural History (London, UK); ZIN, Zoological Institutes of the Russian Academy of Sciences (St. Petersburg, Russia); PNGP, National Park Gran Paradiso (Torino, Italy); SC, collection of Dino Scaravelli; DBA UMR, Department of Animal Biology, University of Modena and Reggio Emilia.

M. caligata USNM 42636, 42638, 42793, 48580, 53595, 66696, 66697, 66698, 68716, 72222, 72223, 72225, 72226, 72227, 72235, 74995, 74996, 74998, 76233, 81913, 88005, 88006, 90132, 90134, 96206, 96207, 96533, 97952, 97953, 98154, 101296, 101298, 101300, 114833, 127594, 135161, 135163, 137319, 146449, 170741, 174501, 174502, 174503, 202533, 202790, 221012, 226148, 226719, 230108, 233212, 235255, 235257, 235258, 271698, 271699, 271701; only mandible: BMNHL 593.a or 45.7.4.9, 593.c (or 62.12.12.7), USNM 67073; only skull: BMNHL 1398.b, 2.3.7.5, USNM 66695, 67076, 101299, 170682, 210830, 256660.

M. caudata BNHML, 10.12.2.25, 5.10.8.2, 69.493, 76.3.9.3, 8.10.3.16, 8.7.6.27, 88.3.20.25, 9.4.3.112, 92.1.1.7, USNM 35497, 35498, 35500, 62112, 62114, 62116, 62117, 62118, 173377, 173380, 173381, 173382, 173383, 173384, 298212, 327143, 353196, 353197, 353199; only mandible: BMNHL 1937.6.12.7, 77.11.23.3, 91.5.16.2, 97.10.3.54, USNM 35499, 62115,

353200; only skull: BMNHL 89.3.9.7 (or 1963a), 9.4.3.111, ZIN 22535, 27912, 2805 or 15318, 29355, 32666, 40549, 40551, 40553, 40555, 51537, USNM 62113, 62119, 173376, 173378, 173385, 173386, 353198.

M. flaviventris BMNHL 40.823, USNM 23951, 25523, 25524, 25527, 30143, 41419, 41914, 42080, 42112, 42122, 42368, 65920, 74057, 74373, 79365, 80360, 88243, 89312, 93688, 93689, 93690, 93708, 99759, 99760, 100532, 100533, 108792, 128750, 128753, 128754, 133505, 139082, 147183, 156923, 157828, 158033, 158500, 158980, 168477, 168799, 168883, 168884, 170148, 177297, 180918, 186520, 191366, 191367, 191369, 204891, 208268, 211232, 212471, 221896, 221898, 228271, 228273, 229842, 233382, 234960, 242645, 243663, 243664, 243665, 244551, 244552, 274340, 291192, 575170; only mandible: USNM 72565, 89311; only skull: USNM 41198, 41345, 42858, 42859, 93709, 94343, 168494, 202937, 215215, 498417.

M. himalayana BMNHL 11.2.1.94, 11.2.1.95, 12.3.18.2, 22.9.1.82, 22.9.1.83, 22.9.1.85, 23.9.1.38, 23.9.1.40, 23.9.1.41, 36.4.12.6, 5.12.5.2, 5.12.5.3, 8.2.29.1, 8.7.6.30, 96.11.4.2, 96.11.4.9, USNM 62121, 62122, 84099, 84100, 84101, 84102, 84104, 102576, 144038, 144039, 144040, 144041, 144042, 144043, 198638, 240674, 240675, 240676, 240677, 255960, 259438, 259439, 573031, 573032, 573033, 573035, 573036, 573037, 576183, 576184; only mandible: BMNHL 11.10.3.5, 25.10.2.4, 26.10.12.1, 8.7.6.20, 91.10.7.98, 99.3.1.13, USNM 198637, 255959, 255961, 255962; only skull: BMNHL 23.9.1.39, 92.1.1.4, USNM 84103, 255958, 255963, 395249, 573034.

M. marmota BMNHL 1087.a, 19.7.7.2363, 19.7.7.2859, 2.8.4.30, 2.8.4.31, 2.8.4.32, 2.8.4.33, 59.9.6.36 (or 1087.c), 7.1.1.131, 7.1.1.195, 7.4.19.1, 8.8.10.145, 8.8.10.63, 8.8.10.65, USNM 14336, 115219, 115220, 115221, 115222, MSNM Ma 4532, 6085, 6103, DBA UMR three specimens not in catalogue, SC 160, 173, 178, 182, 159(II), 175(I); only mandible: BMNHL 1087.b, 55.12.24.124, MSNM Ma 4501, 4799, 6084, 6104, PNGP 1 specimen not in catalogue, SC 6, 12, 15, 17, 32, 39, 40, 45, 158, 161, 164, 165, 166, 167, 168, 171, 149, 159(I), 21B, 25B, 26B, 29B, 2B (A1/2), 34B, 35B, 36B, 38B, A1/1 or B41, A7; only skull: BMNHL 8.8.10.64, PNGP 2 specimens not in catalogue, USNM 153386, DBA UMR 2 specimens not in catalogue, SC 175(II).

M. monax BMNHL 19.7.7.2552, 1989.337, 1991.119, 36.11.6.30, 36.11.6.31, 36.11.6.34, 36.11.6.35, 592.b, 592.c, 592.d (or 51.8.16.19, 592.e, 6.1.6.6, MSNM Ma 4550, USNM 23033, 25184, 35361, 43560, 53920, 67692, 67693, 68717, 71074, 72186, 72187, 77142, 77143, 77924,

78354, 78355, 78356, 78357, 78358, 96140, 96574, 101295, 174594, 177740, 186521, 191345, 202785, 203532, 227255, 227256, 228929, 233345, 234703, 236424, 242724, 243073, 243949, 244482, 247013, 259345, 283359, 291554, 291786, 291787, 337132, 347745, 347746, 347752, 396279, 564087; only mandible: BMNHL 592.a (or 43.9.14.9), 36.11.6.32, USNM 243607, 293895; only skull: USNM 58695, 78360, 81901, 170740, 202786, 207198, 228524, 233348, 245442, 249883, 564086.

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