Mandible and molar morphometrics suggest adaptive divergence between *Apodemus* species in the Alps

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Abstract:
Three *Apodemus* species occur in the Alps: the Alpine specialist *A. alpicola*, the generalist A. *sylvaticus*, and *A. flavicollis*. Based on molecular phylogeny, these species are closely related, with A. *alpicola* and *A. flavicollis* being sister species. The three species are extremely difficult to identify based on morphological characters, thus constituting cryptic species. The present study addressed the relationship between their habitat preferences and the morphological differentiation of their masticatory apparatus, on the small geographical scale of the Massif des Écrins in the French Alps. A geometric morphometric analysis of mandible and molar shape was implemented, complemented by an analysis of biomechanical ratios describing mandible functioning.

Regarding the habitats, *A. flavicollis* appeared as restricted to humid forest lowlands, while *A. alpicola* occupies a wide range of high-altitude habitats; *A. sylvaticus* appears as a generalist species which habitat largely overlaps those of the two other species. From a morphological point of view, *A. alpicola* appeared well differentiated from both, *A. sylvaticus* and *A. flavicollis*, regarding molar shape, mandible size and shape. This morphological divergence presumably involves an adaptive response to a diet enriched in invertebrate preys, requiring an elongated incisor, but not so powerful chewing. In contrast, the two forest dwellers *A. sylvaticus* and *A. flavicollis* appeared extremely close in their morphology, hindering any robust identification based on molar or mandible morphology.

Intraspecific variation of mandible morphology along the altitudinal gradient is also documented for both, the highly generalist *A. sylvaticus*, and the high-altitude specialist *A. alpicola*, suggesting ability to adjust to local resources on a short-time scale. Given the current global warming, deeply affecting Alpine environments, this ability to respond to changing resources may be crucial for the mid-term survival of the Alpine specialist *A. alpicola*.

Keywords: geometric morphometrics, biomechanics, masticatory apparatus, *Apodemus alpicola, Apodemus sylvaticus, Apodemus flavicollis*.

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Morphometrics of Alpine *Apodemus*

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Keywords. – *Apodemus alpicola; Apodemus flavicollis; Apodemus sylvaticus*; geometric morphometrics; masticatory apparatus; biomechanics.

Introduction

Among the widespread and abundant rodents in Europe, the long-tailed wood mouse *A. sylvaticus* and the yellow-necked mouse *A. flavicollis* are generalist rodents that occur in sympatry in much of their ranges (Michaux, 2005). The development of genetic methods for their identification (Michaux et al., 2001) allowed to clarify their relationships, and to recognize that morphological identifications were very difficult between these two cryptic species. Genetic methods however confirmed the validity of another closely related species, the Alpine field mouse *A. alpicola* (Storch and Lütt, 1989; Vogel et al., 1991). This species is restricted to the Alps, with specialized habitat preferences in high altitudes compared to the generalist wood and yellow-neck mouse (Reutter et al., 2003).

These three species can be regarded as cryptic species (Ancillotto et al., 2017). Their close morphological similarity, despite their divergence since ~2 million years (Michaux et al., 2002; Suzuki et al., 2008), suggests the occurrence of stabilizing selection limiting the morphological divergence. However, diet differences have been described between the Alpine field mouse and its two relatives, the wood mouse and the yellow-necked mouse (Reutter et al., 2005), with an important component of invertebrates in the diet of the Alpine field mouse. Ecological differences in diet should promote morphological divergence in structures related to food processing such as mandible (Renaud et al., 2007) and molar teeth (Gómez Cano et al., 2013; Renaud et al., 2005).

In rodents, incisors and molars are separated by a diastema and do not occlude at the same time (Cox et al., 2012), with biting at the incisors and chewing at the molars. Different masticatory muscles are involved, the temporal muscle being mainly involved during incision while the masseter muscles are involved in chewing. Mandible shape can thus vary adaptively as a response to diet. At a broad phylogenetic scale, faunivorous taxa tend to display elongated mandibles favoring captures of preys at the incisors, while herbivorous taxa exhibit massive mandibles with expanded angular regions, allowing for the insertion of powerful masseteric muscles (Michaux et al., 2007). Similar trends can be observed between populations of a species, with a biomechanical optimization for incisor biting favored in mice displaying a shift towards a predatory behavior (Renaud et al., 2018). Since the mandible is submitted to bone remodeling as a response to muscular loading, non-heritable plastic responses to diet differences can modulate mandibular growth (Dubied et al., 2025). This environmentally-driven plasticity can lead to functional changes that increase biomechanical efficiency of food processing in the face of an increased solicitation and can thus be considered as adaptive (Anderson et al., 2014). In natural rodent populations, heritable and non-heritable changes in mandible morphology cannot be distinguished and both processes can contribute to the adjustment to local resources at different time scales.

Regarding molar shape, herbivorous taxa tend to display broad teeth allowing for a large occlusal surface, compared to faunivorous ones displaying elongated molars (Gómez Cano et al., 2013). A similar trend has been observed between populations within *A. sylvaticus* (Renaud et al., 2015a; Renaud and Michaux, 2003). In such murine rodents, plastic changes are not involved in molar shape variation, since once erupted, only wear is affecting molar geometry.

A divergence of these feeding structures is thus be expected in the *A. alpicola* compared to its two related species, as an adaptive response to its divergent diet. Furthermore, if generalist species adjust their diet as a function of the local availability, functionally-relevant traits related to the exploitation of food resources should vary according with altitude, that largely determines the type of habitat and hence of food available in these Alpine areas.

To test for this hypothesis, a morphometric study was conducted on a set of *Apodemus* mice from the French Alps, including *A. alpicola*, *A. flavicollis* and *A. sylvaticus*, focusing on the morphology of the first upper molar and of the mandible. Predictions were as follows. (1) A differentiation in mandible shape is expected between *A. alpicola* and the two other species *A. flavicollis* and *A. sylvaticus.* An elongation of the mandible, with an optimization for incisor biting, is expected to characterize *A. alpicola*, since such feature is associated with an increasing proportion of animal prey in the diet (Renaud et al., 2018). Long incisors, adapted to seize prey, are also expected (Renaud et al., 2019). (2) Since mandible shape can vary even on very short time-scales, due to plastic variations in response to mastication (Anderson et al., 2014), differences are expected to occur depending on the local environment, especially in the most generalist species *A. sylvaticus*. (3) Over longer time-scales, adaptive evolution of the molar morphology is expected as well. Murine rodents feeding on animal preys such as invertebrates display slender first upper molar than omnivorous and herbivorous taxa (Gómez Cano et al., 2013); such a trend could be ongoing in *A. alpicola*.

Material

Wood mice of the genus *Apodemus* were trapped in a series of localities from the Massif des Écrins in the French Alps (Fig. 1) in years 2003, 2007 and 2008 between April and August (Table 1). Sympatric species in a given locality were trapped at the same time. Specimens were manually cleaned and identified using a by-then standard approach, based on PCR amplification complemented for some of them by the sequencing of the mitochondrial cytochrome *b* gene (Michaux et al., 2002; Michaux et al., 2001). All skulls and tissues are stored at the CBGP collections (CBGP - Small Mammal Collection”, https://doi.org/10.15454/WWNUPO).

A first run of morphometric analyses identified 16 specimens for which recurrent inconsistencies with the genetic identification occurred (see Supplementary Figures 1 and 2). For these animals, the cytochrome *b* was sequenced in order to check for the identifications. Previous identifications were validated in six cases; reattribution to another species occurred in two cases. In the remaining eight cases, the identification could not be validated, either due to poor quality of the sequences, or to poor match with either of the species, possibly due to the occurrence of nuclear copies of the cyt-*b*, obscuring the phylogenetic relationships. These eight specimens were discarded of the final morphometric analysis, leading to a sampling including 40 *A. alpicola*, 13 *A. flavicollis* and 64 *A. sylvaticus* (Table 1). For each trapping spot, habitat data were recorded, as presence / absence of the following items in the landscape: 1) altitude meadows; 2) bocages hedges; 3) grasslands; 4) forest edges; 5) rock walls and screes; 6) riparian forests; 7) wetlands; 8) forests; 9) mixed forests; 10) coniferous trees; 11) mountain pine; 12) fir forest; 13) larch; 14) deciduous forests; 15) ash; 16) alder; 17) aspen. Note that the modalities were sometimes partly redundant, with for instance mountain pine, fir forest and larch being part of coniferous forests. This coding was used to consider if the type of forest, or some specific tree species, were important for a given *Apodemus* species.

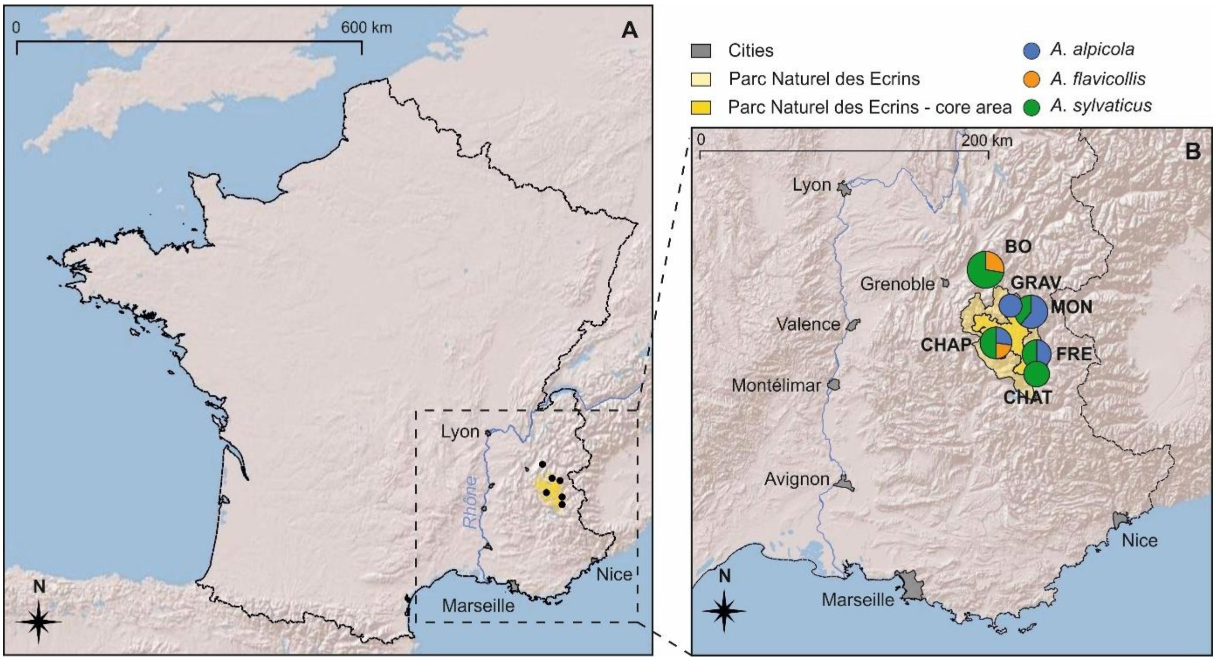

Figure 1. Location of the studied localities. A) Situation of the studied area within Western Europe (France). B) Area of the Massif des Écrins in the French Alps, with the localities of trapping and their composition regarding the three *Apodemus* species.

Species	Locality	Code	meanLat	meanLong	Date	minAlt	maxAlt	N_Md	N_UM1
alpicola	La Chapelle-en-Valgaudémar	ALP_CHAP	44.79	6.20	07/2007	1030	1450	6	5
	Freissinières	ALP_FRE	44.74	6.51	06/2007	1200	2050	8	8
	La Grave	ALP_GRAV	45.04	6.29	06/2005 + 06/2008	1360	1390	12	12
	Le Monêtier-les-Bains	ALP_MON	45.00	6.46	04/2007	1580	1940	14	14
flavicollis	Le Bourg d'Oisans	FL_BO	45.04	6.06	08/2007	730	730	8	7
	La Chapelle-en-Valgaudémar	FL_CHAP	44.82	6.14	07/2003 + 07/2007	1000	1030	5	5
sylvaticus	Le Bourg d'Oisans	SY_BO	45.49	6.08	08/2007	730	1220	21	19
	La Chapelle-en-Valgaudémar	SY_CHAP	44.82	6.14	07/2007	990	1030	11	10
	Châteauroux-les-Alpes	SY_CHAT	44.62	6.52	04/2008	850	1660	15	15
	Freissinières	SY_FRE	44.74	6.52	06/2007	1130	1480	8	9
	Le Monêtier-les-Bains	SY_MON	45.01	6.47	04/2007	1500	1940	9	9

Table 1. Sampling of the study. Each locality was covered by several trapping spots; mean latitude (meanLat) and longitude (meanLong) are provided as well as the altitudinal range covered (minAlt: minimum altitude, maxAlt: maximum altitude). Date: date of trapping. N_Md: number of mandibles; N_UM1: number of first upper molars included in the final morphometric analysis.

Methods

Data collection

Mandibles and tooth rows were photographed using a Leica MZ 9.5 binocular. The hemi-mandible was placed flat on its lingual side. Based on former morphometric studies of the mouse mandible (Klingenberg, 2009) and its incisor (Renaud et al., 2019), nineteen landmarks were defined on the labial side (Fig. 2) and positioned using TPSdig2 (Rohlf, 2010). Sixteen of them described the overall shape of the mandibular bone. Three additional landmarks were located on the teeth: at the tip of the incisor, the basis of the incisor bevel, and on the anterior cup of the first lower molar.

First upper molars (UM1) were manually orientated so that the occlusal surface matched at best the horizontal plane. The shape of UM1 was described using 64 points sampled at equal curvilinear distance along the two-dimensional outline of the occlusal surface using the Optimas software. An outline-based method was chosen, because reliable landmarks are difficult to position on murine-like molars [e.g. (Renaud et al., 1996; Renaud and Michaux, 2007)]. The top of the cusps is abraded by wear and cannot be used to assess the position of the cusps, and landmarks bracketing the cusps on the outline are difficult to position, given the smooth undulations delineating the cusps along the outline. The starting point was tentatively positioned at the anterior-most part of the tooth.

For mandibles and molars, the right side was usually considered, but left mandibles or teeth were occasionally pictured when the right one was damaged. This concerned 12 mandibles (10 % of the total sample) and three molars (3 % of the data). The pictures were then mirrored and measured as right ones.

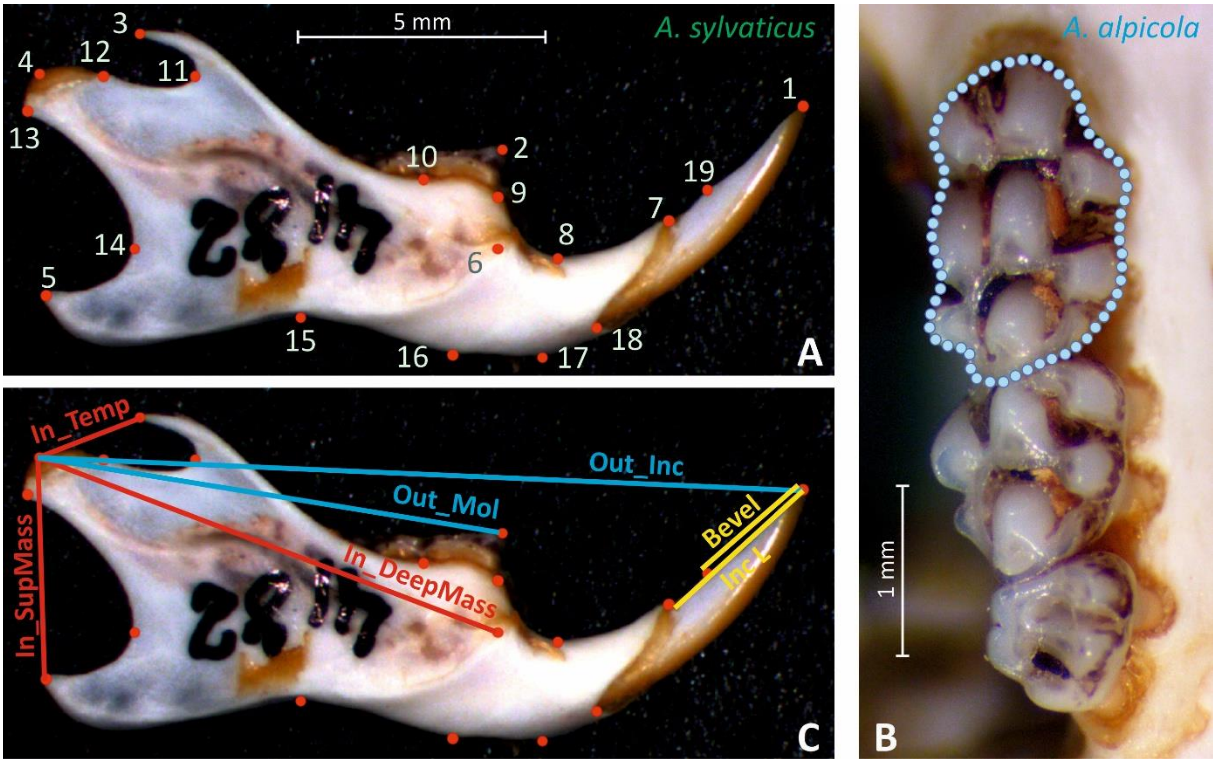

Figure 2. Morphometric and biomechanical measurements on a wood mouse right mandible and a right upper molar. A) Landmarks on the mandible, represented on a right mandible of *A. sylvaticus* (specimen #4258). B) Molar outline, depicted on a right first upper molar (UM1) of *A. alpicola* (specimen #4254). C) In-levers and out-levers, describing the mechanical performance of the mandible; length of the incisor (Inc L) and its bevel. Out-levers correspond the inter-landmark distance from the condylar articulation to the incisor tip, and to the tip of the first molar anterior cusp. In-levers correspond to inter-landmark distances from the condylar articulation to points of muscle attachments: distance from the condyle to the posterior tip of the angular process for the superficial masseter, distance from the condyle to the anterior termination of the masseteric ridge for the deep masseter, and distance from the condyle to the posterior tip of the coronoid for the temporalis muscle.

Geometric morphometrics and biomechanical estimates

Mandible morphometrics. – The 19 landmarks of the mandibular bone were adjusted using a generalized Procrustes superimposition (GPA) standardizing size, position and orientation, while retaining the geometric relationships between specimens (Rohlf and Slice, 1990). The resulting aligned (Procrustes) coordinates constituted the shape variables for subsequent analyses using the R package geomorph (Adams and Otarola-Castillo, 2013). Centroid size, the most common and explicit measure of size in geometric morphometrics, was computed as the square root of the sum of the squared distances of all landmarks from their centroid (Slice et al., 1996). The same procedure was applied to the 16 landmarks describing the mandibular bone only.

Mandibles biomechanics. – The biomechanical efficiency of the rodent mandible can be estimated in several ways. First, direct measures of bite force can be performed, but this only assesses biting at the incisors, and requires live animals (Ginot et al., 2018). Biomechanical models derived from dissections provide reliable estimates of bite force (Ginot et al., 2018) but they can only be measured on specimens with tissues. Cross-sectional indices of mandible strength also provide reliable estimates of bite force (Freeman and Lemen, 2008) but they require width measurements on the mandible, and hence to cannot be performed on simple pictures. Another estimate of the efficiency of the mandible to transmit force from the muscles to the bite point is the mechanical advantage, defined as the ratio of the in-lever (distance from the condyle to the point of muscle attachment) and the out-lever (distance from the condyle to the bite point) (Hiiemae, 1971; Thomason, 1991). Such mechanical advantages can be estimated on pictures of the mandibles, and even for prepared museum specimens (Anderson et al., 2014; Thomason, 1991). Such an approach was thus selected here for estimating the mandible biomechanical efficiency.

In-levers and out-levers were calculated as distances between the relevant landmarks. Out-levers (Fig. 2C) were estimated as the distance from the condylar articulation (playing here the role of fulcrum) to the incisor tip, and to the tip of the first molar anterior cusp. Three in-levers were measured (Fig. 2C). The effect of the superficial masseter was approximated by considering the distance from the condyle to the posterior tip of the angular process. The deep masseter action was described by the distance from the condyle to the anterior termination of the masseteric ridge. The distance from the condyle to the posterior tip of the coronoid was used to described the action of the temporalis (Anderson et al., 2014).

The temporalis is mostly used together with incisors for gnawing, whereas the masseter and molars are involved in the action of mastication. The masseter also contributes to bringing the incisors into occlusion. Four mechanical advantages were therefore considered: temporalis/incisor, superficial master/incisor, superficial masseter/molar, and deep masseter/molar.

Finally, the geometry of the incisor was described using a landmark at the bite point (tip of the incisor) and another at the basis of the bevel. The length of the incisor relative to mandible centroid size (Rel_IncL) and the length of the incisor bevel relative to incisor length (Rel_Bevel) were assessed based on inter-landmark distances (Fig. 2C).

Molars. – The 64 points delineating the occlusal surface were analyzed as sliding semi-landmarks (Cucchi et al., 2013). The outlines points were adjusted using a GPA procedure, while during the superimposition, semi-landmarks were allowed to slide along their tangent vectors until their positions minimized the shape difference between specimens, the criterion being bending energy (Bookstein, 1997), an option proven to be efficient for murine molars (Cucchi et al., 2020). Because the first point was only defined on the basis of a maximum of curvature at the anteriormost part of UM1, some slight offset might occur between specimens. The first point was therefore considered as a semi-landmark allowed to slide between the last and second points (Renaud et al., 2020).

Statistical analyses

Regarding the univariate analysis, differences between species were tested using non-parametric Kruskal–Wallis (KW) tests complemented by pairwise Wilcoxon tests. Pearson correlations were used to test for covariation between univariate variables. Linear models were used to test for the effect of multiple factors and their interaction.

Permutation-based Procrustes ANOVAs and associated pairwise tests on the aligned coordinates were used to investigate the effect of various factors on mandible and molar geometry. Multivariate regressions between size, or environmental predictor variable, and aligned coordinates provided regression scores summarizing the shape variance along the regression model while including the residual variation in that direction of shape space (Drake and Klingenberg, 2008). Details about the Procrustes ANOVA are provided as Supplementary Information.

The shape variance was summarized using Principal Component Analyses (PCA) applied to variance-covariance matrix of the shape coordinates, being aligned coordinates for Procrustes-based analyses or Fourier coefficients for outline methods. PCA provided synthetic axes to visualize the total variance among the set of specimens. Mandible shape was analyzed based on the complete set of landmarks (19 landmarks), including those located on the incisor and on the first lower molar, and based on the mandibular bone only (16 landmarks). PCA was also used to summarize the biomechanical variables (mechanical advantages, relative incisor and bevel length). PCA were performed using geomorph (Adams and Otarola-Castillo, 2013) and ade4 (Thioulouse et al., 2018).

Topologies of the specimens obtained with PCA on the whole mandible, and on the mandibular bone only, were compared with Protests (Peres-Neto and Jackson, 2001). These tests are based on a Procrustes superimposition of the two configurations, providing a Procrustes coefficient of correlation R and a permutation-based assessment of the significance of the correlation using the R package vegan (Oksanen et al., 2013).

An alternative method to display between-group differences is the canonical variate analysis (CVA). CVA aims at separating the groups by looking for linear combinations of variables that maximize the between-group to within-group variance ratio, hence distorting the relationships among groups in the resulting morphospace (Mitteroecker and Bookstein, 2011). The CVA further allows to evaluate the efficiency to correctly classify the different species. Leave-one-out cross-validated classification were considered. CVA is however sensitive to the ‘overfitting’ problem, arising when too many variables are included compared to the number of specimens (Kovarovic et al., 2011; Mitteroecker and Bookstein, 2011). This is especially the case when analyzing the molar outline as semi-landmarks, leading to 128 aligned coordinates for 110 specimens. This problem leads to non-realistic representations where groups appear much more distinct than they really are (Cardini et al., 2019). A reduction of dimensionality was therefore conducted by retaining only the first axes of the corresponding PCA optimizing the percentage of correct reclassification (Evin et al., 2013). CVA and the associated cross-validated classifications were computed using the package Morpho (Schlager, 2017).

Allometry was investigated using Procrustes ANOVA (see above). When significant, complementary analyses were run on the residuals of the aligned coordinates vs. centroid size (‘size-free’ shape) in order to check for the influence of size-related variations on the morphometric signals. Size-in and size-free morphometric spaces (based on aligned coordinates or their residuals) were compared using Protests.

Habitat preferences were investigated using a Multiple Correspondence Analysis (MCA) (Tenenhaus and Young, 1985) on the table of factors describing the landscape where the mice were trapped. This analysis was performed using ade4 (Thioulouse et al., 2018).

The effect of species, habitat and altitude on molar and mandible morphology was finally assessed using multivariate analyses of variance using the R package ffmanova (Langsrud and Mevik, 2012), providing the percentage of variance explained (pve) by each set of explanatory variables and the associated P-value. This method is based on type II sum of squares, which has the advantage of being invariant to ordering of the model terms; the ffmanova also handles colinear responses. It may inflate the pve but allows an estimation of the relative importance of the explanatory variables.

When relevant, probabilities were based on 9999 permutations. All analyses were performed under R (R Core Team, 2018).

Results

Habitat differences between species

The first axis of the MCA on habitat data, explaining 21.0% of variance, opposed open landscapes (grasslands, forest edges and bocage hedges) on the positive side to close, forest landscape on the negative side (Fig. 3A). Along this axis, the yellow-necked mouse appeared restricted to negative scores and hence to forest habitats (Fig. 3B), while the Alpine field mouse was characterized by scores around the center of the axis, pointing to mixed environments. The wood mouse displayed scores along almost all the range of the axis, suggesting a generalist ranging from extremely open to close environments.

The three species differed along this axis ($P_{KW} = 0.0005$), a signal driven by the peculiar habitat of *A. flavicollis*, associated with deciduous forests and wetlands (FLAV vs ALP, $P_{Wilcox} = 0.0003$; FLAV vs SYLV, $P_{Wilcox} = 0.0007$) whereas the two other species did not differ ($P_{Wilcox} = 0.9920$).

The second MCA axis, explaining 17.0% of variance, mostly corresponded to the type of forest, with negative scores associated with coniferous trees among which larch, and the occurrence of altitude meadow. *A. alpicola* displayed extreme negative scores corresponding to this environment, but overlapped with the two other species. As a consequence, the difference was close to the significant threshold ($P_{KW} = 0.0506$).

The three species displayed clearer differences in their altitudinal distribution ($P_{KW} < 0.0001$), despite some overlap (Fig. 3C). The *A. alpicola* of course was found at higher altitude than both other species (pairwise Wilcoxon tests: ALP-FLAV $P < 0.0001$; ALP-SYLV $P < 0.0001$). The yellow-necked mouse tended to inhabit at lower altitudes than the wood mouse *A. sylvaticus* (FLAV-SYLV $P = 0.0008$).

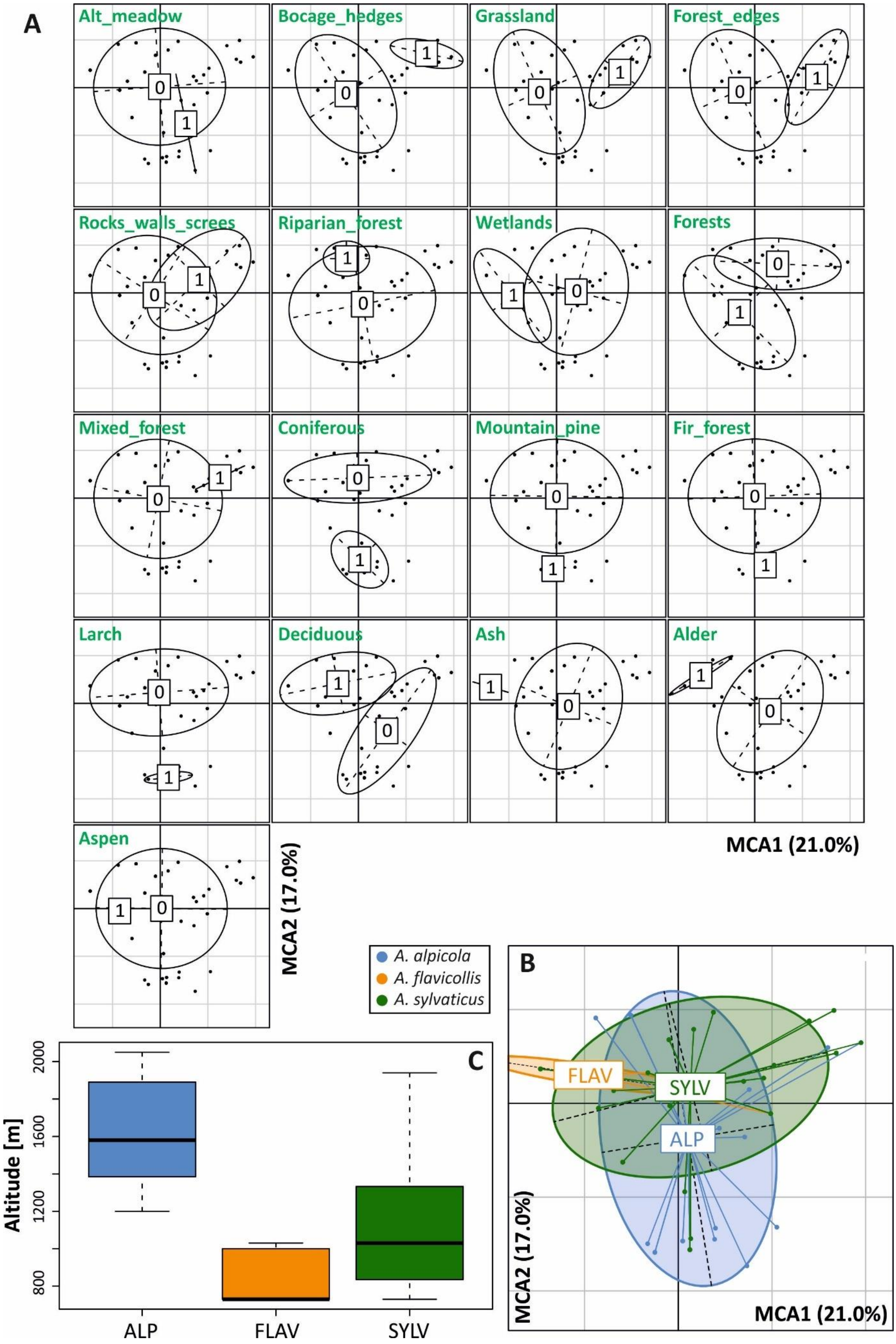
A
Alt_meadow
Bocage_hedges
Grassland
Forest_edges
Rocks_walls_screes
Riparian_forest
Wetlands
Forests
Mixed_forest
Coniferous
Mountain_pine
Fir_forest
Larch
Deciduous
Ash
Alder
Aspen
0
1
MCA1 (21.0%)
MCA2 (17.0%)
A. alpicola
A. flavicollis
A. sylvaticus
B
FLAV
SYLV
ALP
MCA1 (21.0%)
MCA2 (17.0%)
C
Altitude [m]
800
1200
1600
2000
ALP
FLAV
SYLV

Figure 3. Multiple correspondence analysis of the habitat preferences of the three *Apodemus* species. All graphs represent the specimens in the space defined by the first and second MCA scores. A) Repartition of the different habitat factors along these axes. For each habitat variable, 1 corresponds to the occurrence of the given habitat type at the trapping site, and 0 to its absence. B) Repartition of the three species along the axes. C) Altitudinal distribution of the three *Apodemus* species.

Size differences between species

The mandible, both when including the incisor and molars or not, differed in their centroid size between the three species ($P_{KW} < 0.0001$, Fig. 4A). *Apodemus sylvaticus* displayed the smallest mean mandible (mean centroid size = 23.1 ± 1.2 standard deviation [s.d.]), while *A. flavicollis* and the *A. alpicola* displayed mandibles of similar size (FLAV mean centroid size = 24.5 ± 1.1 s.d.; ALP mean centroid size = 24.2 ± 1.5 s.d.; Table 2), a pattern maintained when focusing on the mandibular bone only (Fig. 4B, Table 2), since the centroid sizes of the mandible including molars and incisor, and of the mandibular bone only, were tightly correlated ($R^2 = 0.9778$, $P < 0.0001$).

The three species did also differ in their molar size, estimated by the centroid size of the outline points considered as semi-landmarks ($P_{KW} < 0.0001$; Fig. 4C). This was due to the larger molar size of the yellow-necked mouse *A. flavicollis* (mean centroid size = 6.5 ± 0.2 s.d.) compared to the two other species sharing a similar size (ALP mean centroid size = 6.1 ± 0.2 s.d.; SYLV mean centroid size = 6.1 ± 0.2 s.d.; Table 2).

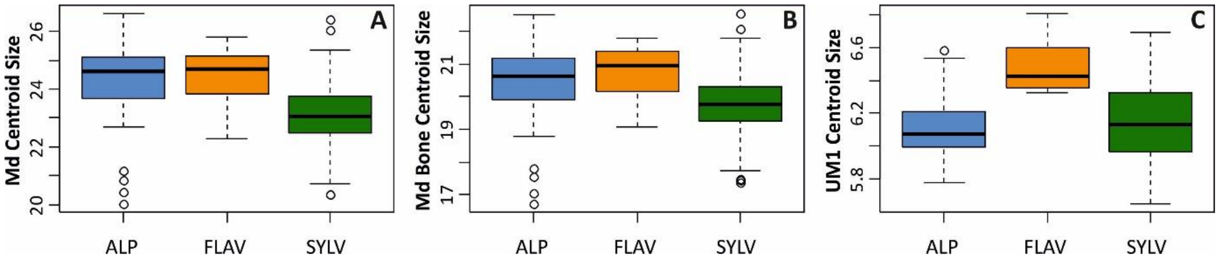

Figure 4. Size differences among the three *Apodemus* species. A) Centroid size of the mandible, including molar and incisor. B) Centroid size of the mandibular bone. C) Centroid size of the first upper molar (UM1). Box-plots are represented: the thick line corresponds to the median, the box is enclosed between the first (Q1) and third (Q3) quartiles, defining the interquartile range (IQR). The dotted 'whiskers' correspond to Q1 – 1.5*IQR and Q3 + 1.5 IQR. The open circles correspond to outliers outside the ranges mentioned above.

				Aalp/Aflav	Aalp/Asylv	Aflav/Asylv
Md Csize	P_{KW}	**< 0.0001**	P_{Wilcox}	0.7210	**< 0.0001**	**0.0010**
Md Bone Csize	P_{KW}	**< 0.0001**	P_{Wilcox}	0.3102	**0.0006**	*0.0020*
UM1 Csize	P_{KW}	**< 0.0001**	P_{Wilcox}	**< 0.0001**	0.4900	**< 0.0001**
MA Temp/Inc	P_{KW}	0.1614	P_{Wilcox}	-	-	-
MA SupMass/Inc	P_{KW}	**< 0.0001**	P_{Wilcox}	*0.019*	**< 0.0001**	0.0720
MA DeepMass/Inc	P_{KW}	**< 0.0001**	P_{Wilcox}	**< 0.0001**	**< 0.0001**	0.6400
MA Temp/Mol	P_{KW}	**0.0002**	P_{Wilcox}	**0.0016**	**0.0004**	0.9512
MA SupMass/Mol	P_{KW}	*0.0157*	P_{Wilcox}	0.3410	0.0590	0.0570
MA DeepMass/Mol	P_{KW}	**< 0.0001**	P_{Wilcox}	0.1520	**< 0.0001**	0.0790
IncL/MdBoneCsize	P_{KW}	**0.0002**	P_{Wilcox}	*0.0244*	***0.0003***	0.6783
Bevel/IncL	P_{KW}	*0.0044*	P_{Wilcox}	0.9106	*0.0051*	0.1565
Md Shape	ProcD.lm	**0.0001**	P_{perm}	**0.0001**	**0.0001**	0.0642
Md Bone Shape	ProcD.lm	**< 0.0001**	P_{perm}	**0.0001**	**0.0001**	0.0837
UM1 Shape	ProcD.lm	**< 0.0001**	P_{perm}	**< 0.0001**	**< 0.0001**	**0.0009**

Table 2. Pairwise differences between groups. Probabilities are given, in italics $P < 0.05$, in bold $P < 0.001$. Univariate test: Kruskal Wallis (P_{KW}) and pairwise Wilcoxon test (P_{Wilcox}). Multivariate statistics: Procrustes ANOVA and associated pairwise test. Aalp: *A. alpicola*; Aflav: *A. flavicollis;* Asylv: *A. sylvaticus*. Md: mandible. Csize: centroid size. MA: mechanical advantages of the mandible. UM1: first upper molar. UM1 Shape: LMs, analysis on the aligned coordinates. In italics $P < 0.05$, in bold $P < 0.001$.

Mandible shape

The analysis of the mandible including incisor and molar (Fig. 5A) showed an important morphological difference between the two well-sampled species, *A. sylvaticus* plotting towards positive values and *A. alpicola* towards negative values along the PC1 axis (28.1% of total variance), with little overlap. This axis corresponds to a more compact anterior part of the mandible (Fig. 5B). The specimens of *A. flavicollis* plotted in the same area of the morphospace as *A. sylvaticus*. This visual impression was confirmed by a Procrustes ANOVA (P = 0.0001) and pairwise tests (Table 2). The difference between *A. sylvaticus* and *A. flavicollis* was close to the significance threshold but not significant (P-value = 0.0642).

The differences appear as even clearer in the morphospace of the CVA calculated on a subset of PCs (11 PCs retained, maximizing the correct cross-validated classification rate at 93%, see Table 3) (Fig.

5C), with *A. alpicola* diverging along CV1 explaining the vast majority of the between-group variance (93%) while *A. flavicollis* segregated from *A. sylvaticus* along CV2 (only 6.8% of between-group variance).

An additional CVA was performed using species x localities as grouping factor (Supp. Figure 3A). In this morphospace, species in sympatry were not closer or more differentiated than the same species found in allopatry. No trend was observed according with the month of trapping. To check for the influence of allometry on mandible shape differentiation, a similar CVA was performed on PC axes based on residuals of the aligned coordinates vs. centroid size (Supp. Figure 3B). The resulting pattern was very similar to the topology obtained based on raw data (Protest on group means, first two CV axes: Procrustes R = 0.9702, P = 0.0001).

CV classif			Classif. accuracy	Aalp	Aflav	Asylv
		PCs				
Md	Aalp	11 PCs	93.2%	40	0	0
	Aflav			0	8	5
	Asylv			1	2	61
Md Bone	Aalp	8 PCs	90.6%	42	0	0
	Aflav			0	6	7
	Asylv			1	3	60
UM1		32 PCs	76.3%			
	Aalp			33	1	5
	Aflav			0	7	5
	Asylv			3	7	52

Table 3. Leave-one-out cross-validated classification based on CVAs computed on the set of PC axes maximizing correct classification. For each analysis, the number of specimens of each species attributed to the three species is provided together with the overall classification accuracy.

The difference in shape from *A. sylvaticus* to *A. alpicola* involves an expansion of the anterior part of the mandible, including the bone and the incisor. Compared with the wood mouse *A. sylvaticus*, the *A. alpicola* is characterized by a long incisor and a posterior shift of the molar row and of the extremity of the masseteric ridge (Fig. 5D). The differences between *A. sylvaticus* and *A. flavicollis* are very tenuous (Fig. 5E).

Allometric variation of the mandible was investigated using Procrustes ANOVA (shape ~ Species * Csize). Species and centroid size had highly significant effects (P = 0.0001). A significant interaction (P

= 0.001) indicated that allometric slopes were different depending on the species (Fig. 5F). Pairwise comparisons between slope vectors showed that *A. alpicola* displays a steeper allometric slope than *A. sylvaticus* and *A. flavicollis* (ALP:FLAV P = 0.0063, ALP:SYLV P = 0.0043), while *A. sylvaticus* and *A. flavicollis* are characterized by closer but significantly different allomeric relationships (FLAV:SYLV P = 0.0194). All three species converged towards a similar large-sized shape of mandibular bone, showing a slight expansion of the angular process and anterior shift of the ventral molar region (Fig. 5G).

The patterns were very similar when focusing on the mandibular bone only (Supp. Fig. 4), with the distributions in the first three axes of the morphospaces based on the mandible and the mandibular bone only being highly related (Protest R = 0.9432, P = 0.0001).

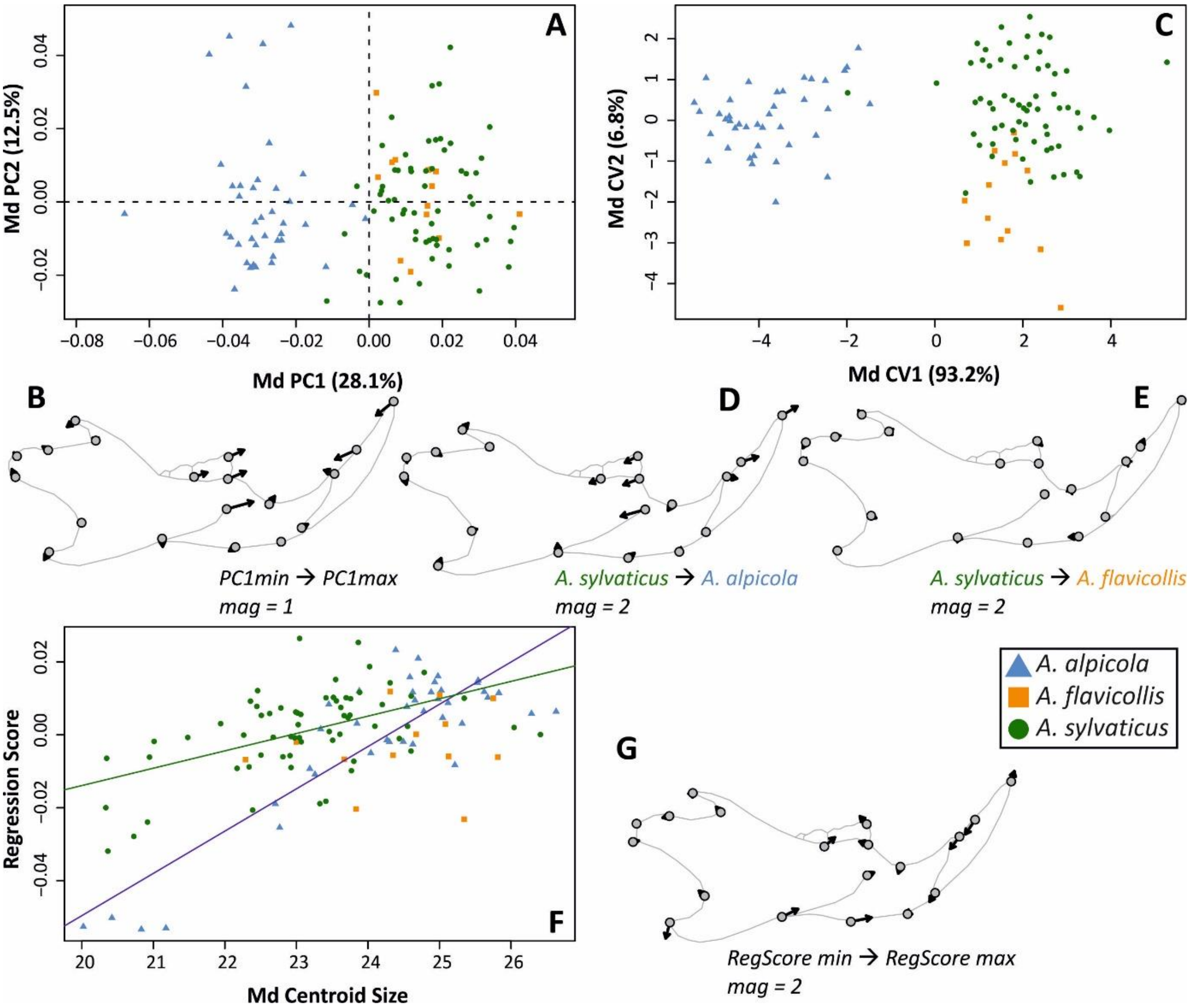

Figure 5. Shape differentiation of the mandible. A) Morphospace based on a Procrustes analysis of mandible shape, including molar and incisor (19 landmarks). B) Shape difference from minimum to maximum PC1 scores. C) CVA on the set of PC axes maximizing correct reclassification (11 axes). D) Visualization of the shape change from *A. sylvaticus* to *A. alpicola* and E) from *A. sylvaticus* to *A.*

flavicollis. Shape change magnified x2 in D) and E). F) Regression scores, based on a Procrustes ANOVA of aligned coordinates vs species and centroid size, allowed to visualize allometric change within each species. Color lines represent significant within-species regressions ($P < 0.05$). G) Shape change from minimum to maximum size according with the same allometric model.

Biomechanical analysis of mandible shape

No significant pairwise differences were observed for the temporal/incisor and superficial masseter/molar mechanical advantages (Table 2). The species differed regarding the mechanical advantages involving the superficial masseter/incisor, deep masseter/incisor, deep masseter/molar and to a lesser degree temporal/molar (Supp. Fig. 5). In all these cases, *A. alpicola* differed from *A. sylvaticus*; it also differed from *A. flavicollis* except for the deep masseter/molar mechanical advantage. Pairwise differences between *A. sylvaticus* and *A. flavicollis* were never significant.

The analysis of the whole mandible suggested differences in incisor morphology. This was investigated by considering the incisor length relative to mandibular bone centroid size (relative incisor length), and the length of the bevel related the incisor length (relative bevel length). Both were significantly different among the *Apodemus* species (Table 2; Supp. Figure 6). In agreement with the shape changes shown by the landmark analysis, *A. alpicola* displayed a relatively longer incisor than *A. sylvaticus*. *A. flavicollis* displayed values similar to *A. sylvaticus*.

The variation in biomechanical ratios was summarized using a PCA (Fig. 6), clearly separating *A. alpicola* towards positive PC1 scores and *A. sylvaticus* towards negative PC1 scores. *A. flavicollis* tended to plot towards intermediate scores, sharing some traits with either of the other two species (see Supp. Figure 5). *A. alpicola* displayed higher ratios than *A. sylvaticus* only regarding the temporal-related mechanical advantages, and the relative incisor length.

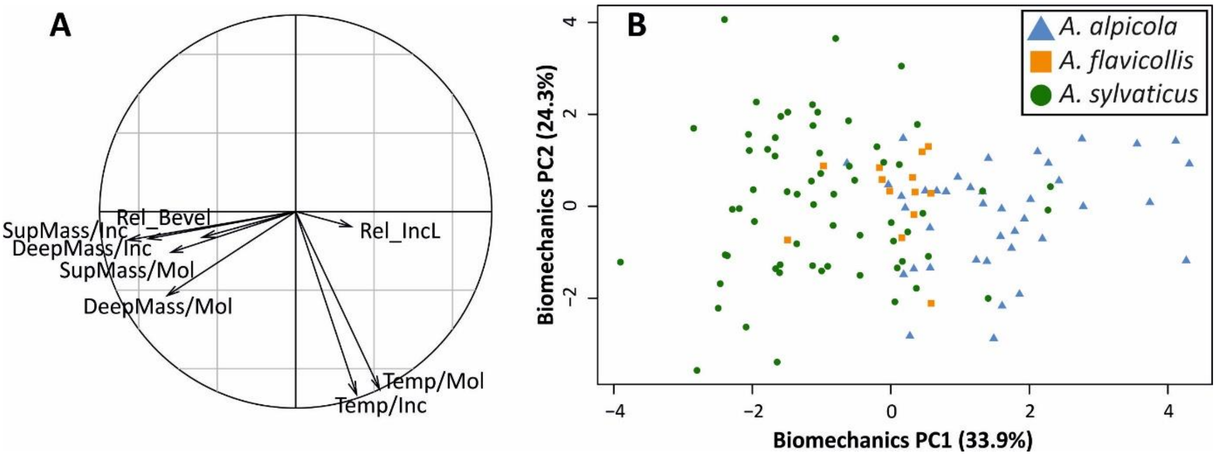

Figure 6. Principal component analysis summarizing the biomechanical variations in the three *Apodemus* species. A) Circle of correlation, indicating the contribution of each variable to the PC axes. B) Scores of the specimens on the first principal plane.

First upper molar shape

The three species differed regarding UM1 shape (Procrustes ANOVA P = 0.0001; Table 2). The overlap between *A. alpicola* and *A. sylvaticus* along the first axis of the PCA on the aligned coordinates of the molar outline (Fig. 7A) was more pronounced than for the mandible; as for the mandible, *A. flavicollis* tended to share the same range than *A. sylvaticus* in the PCA space. However, these two species were significantly different regarding UM1 shape (Table 2), and accordingly, they were better separated along the second axis of the CVA (Fig. 7B) calculated on a subset of PCs (32 PCs retained, maximizing the correct cross-validated classification rate at 81%, see Table 3). As for the mandible, an additional CVA was performed using species x localities as grouping factor (Supp. Figure 3C). In this morphospace, species in sympatry were not closer or more differentiated than the same species found in allopatry. No trend was observed according with the month of trapping.

The difference in shape between the three species were tenuous (Fig. 7C). from *A. sylvaticus* to *A. alpicola* involves a decrease in width of the molar, and a backward shift of the posterior labial cups. The change from *A. sylvaticus* to *A. flavicollis* is much subtler, with a forward shift of most cusps leading to a more massive anterior part of the tooth.

Allometric variation of the UM1 was investigated using Procrustes ANOVA (shape ~ Species * Csize). Species had highly significant effects (P = 0.0001) but not centroid size (P = 0.2823), indicating the absence of allometric variation for the UM1.

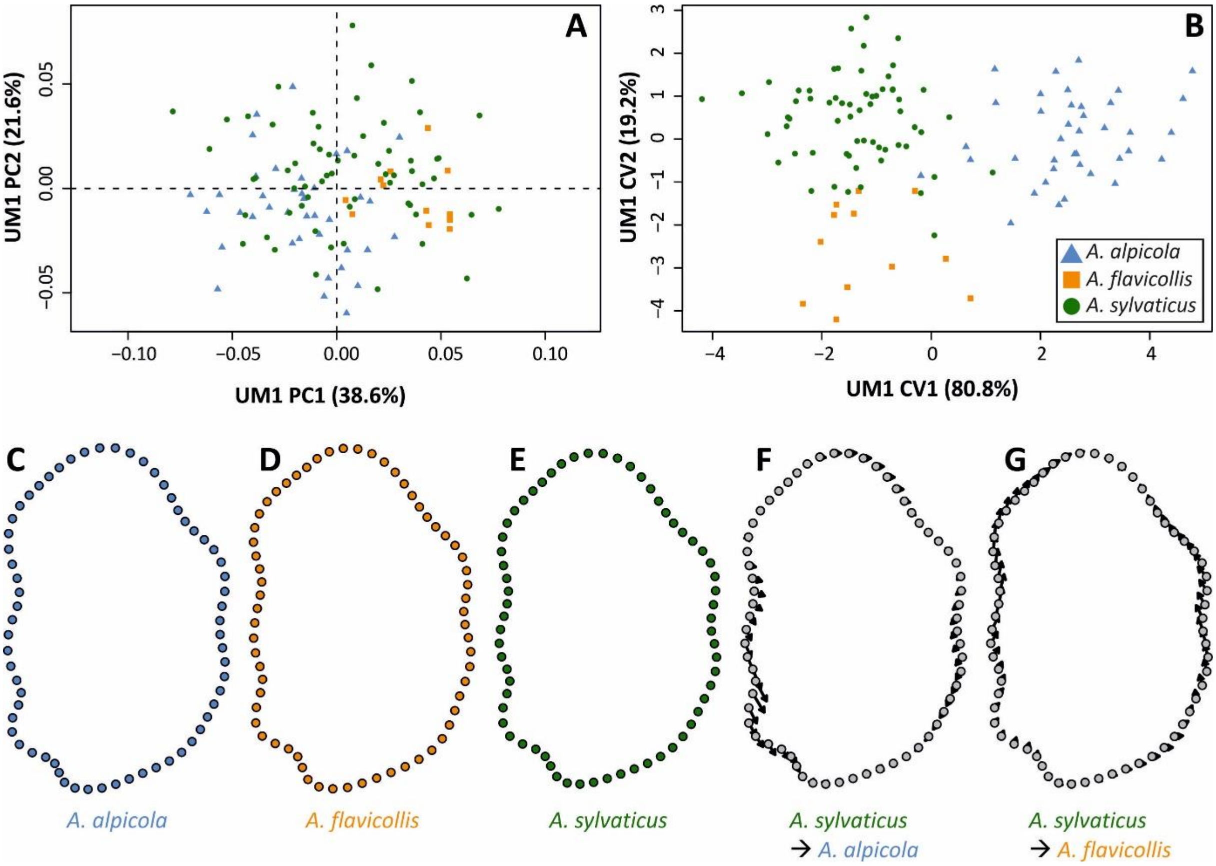

Figure 7. Shape differentiation of the UM1. A) Morphospace based on a Procrustes analysis of UM1 shape (64 semi-landmarks). B) CVA on the set of PC axes maximizing correct reclassification (32 axes). C, D, E) Visualization of the mean UM1 shape of the three *Apodemus* species; E,F) shape change from *A. sylvaticus* to *A. alpicola* and from *A. sylvaticus* to *A. flavicollis* (magnification = x2).

Variation of morphology with environmental factors

The variation in size, biomechanics, and shape with altitude and habitat, quantified by the first two axes of the MCA, were finally investigated using ffmanovas (Table 4). In all cases, habitat was found to explain little morphological variance. Its influence was never significant for mandible size nor shape, but UM1 size was significantly related with the first two axes of the MCA describing the habitat. The effect was close to the significance threshold regarding UM1 shape. For UM1 size and shape however, altitude had no effect.

In contrast, mandible shape and mandible biomechanics were significantly influenced by altitude, but not habitat (Table 4).

			Species		Habitat		Altitude	
			pve	P	pve	P	pve	P
Size	Md	Csize	17.1	**< 0.0001**	3.3	0.1030	0.0	0.9200
	UM1	Csize	9.8	*0.0011*	4.7	*0.0354*	0.1	0.6796
Shape	Md Shape	5 PCs	12.6	**< 0.0001**	1.6	0.4355	3.3	**0.0009**
	UM1 Shape	4 PCs	7.6	**< 0.0001**	3.2	0.0637	0.5	0.5820
	Md Biomechanics	4 PCs	14.3	**< 0.0001**	1.8	0.3020	5.9	**< 0.0001**

Table 4. Effect of species, habitat and altitude on UM1 and mandible morphology. For UM1 and mandible, size is estimated by centroid size. Shape is estimated by the set of PC axes explaining more than 5% of total variance. Mandible biomechanics is summarized by the first four PC axes based on biomechanical ratios. Habitat is described by the first two axes of the MCA on the habitat variables. Percentage of variance explained (pve) and p-value are given for each effect, based on ffmanova models. In bold P < 0.001, in italics P < 0.05.

The relationship between mandible biomechanics and altitude was further investigated using a linear model (PC1 biomechanics ~ Species * altitude). Species and altitude had highly significant effects but no interaction ($P_{species} < 0.0001$, $P_{altitude} = 0.0001$, $P_{interaction} = 0.9238$), showing that the different species shared similar trends with altitude (Fig. 8A). When analyzing the species separately, the trend was significant within *A. sylvaticus*, which displays the wider altitudinal range (P = 0.0015), close to the significance threshold within *A. alpicola* (P = 0.0593) and not significant within *A. flavicollis* (0.6902). The pattern suggests an intraspecific decrease of PC1 biomechanics, associated with an increase in the masseter-related mechanical advantage but a decrease of the temporal-related ones (Fig. 6A), with increasing altitude, a trend over-compensated in *A. alpicola* by the interspecific difference compared to *A. sylvaticus* (Fig. 8A).

Altitudinal effects on whole mandible shape was investigated using a Procrustes ANOVA and associated multivariate regression (Fig. 8B). Here again, species and altitude were highly significant but not their interaction (Procrustes ANOVA: $P_{species} = 0.0001$, $P_{altitude} = 0.0001$, $P_{interaction} = 0.0584$). Very similar results were obtained when considering size-free shape data (residuals of aligned coordinates vs. centroid size; see Supp. Information), showing that the relationship between mandible shape and altitude was not a by-product of size variations. This relationship suggested discrete changes involving a posterior extension of the coronoid process, an extension of the angular process, and a shortening of the mandibular bone along the upper part of the incisor (Fig. 8C). The significance of the relationship was confirmed by intraspecific models for *A. sylvaticus* (regression line vs altitude, P = 0.0281; Procrustes ANOVA shape vs altitude = 0.0001) and *A. alpicola* (regression line vs altitude, P < 0.0001; Procrustes ANOVA shape vs altitude = 0.0381).

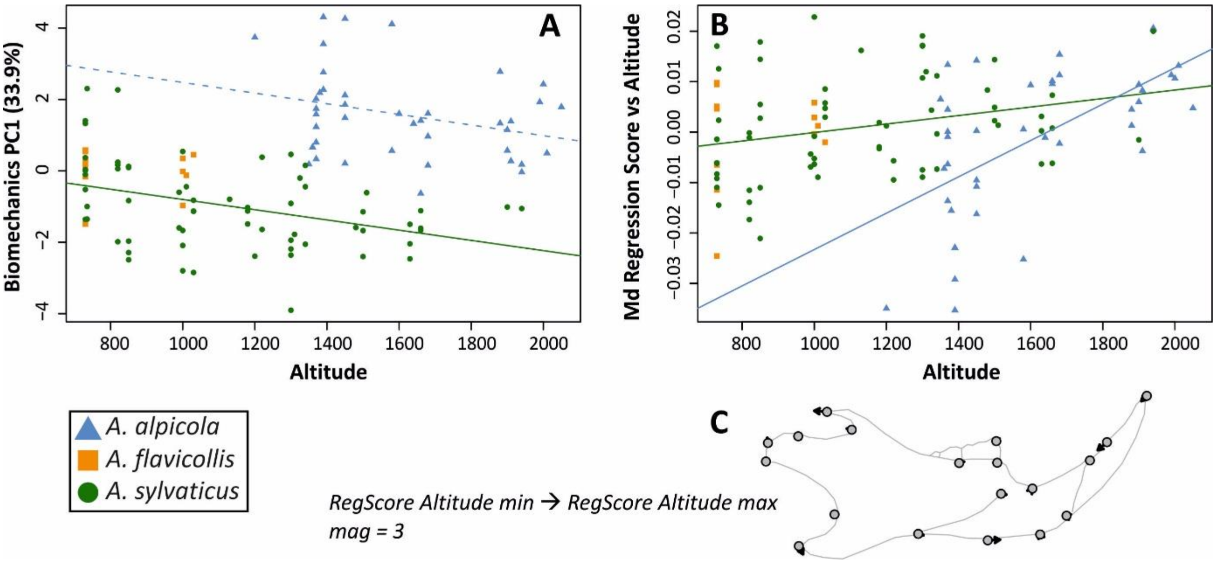

Figure 8. Relationship between mandible morphology and altitude. A) First axis of the PCA on biomechanical ratios vs altitude. B) Regression scores, based on a Procrustes ANOVA of aligned coordinates vs species and altitude. C) Shape change according with the same model, from minimal to maximal altitude (magnification x3). Full lines represent significant within-species regressions (P < 0.05). The dotted line corresponds to a regression close to the significant threshold (P=0.059).

Discussion

Limited morphological differences between the forest dwellers A. sylvaticus *and* A. flavicollis

Although they diverged *ca.* two million years ago (Michaux et al., 2002; Suzuki et al., 2008), the species from the *Sylvaemus* subgenus are reputedly difficult to identify based on their morphology, especially regarding the forest dwellers *A. sylvaticus* and *A. flavicollis*. This even led to propose alternate approaches for field identification, such as patterns of vocalization (Ancillotto et al., 2017). This is due to the combination of low between-species but important within-species differences (Jojić et al., 2014; Michaux, 2005) including within-lineage geographic variation (Renaud and Michaux, 2007). However, especially over a restricted geographic scale, the two species *A. sylvaticus* and *A. flavicollis* can be distinguished based on differences in skull shape [e.g. (Barćiová and Macholan, 2009; Chassovnikarova and Markov, 2007; Jojić et al., 2014)]. The mandible has been less frequently investigated, but a former study suggested that *A. flavicollis* had a longer coronoid process and a forwardly shifted molar region compared with *A. sylvaticus* (Barćiová, 2009).

In contrast, the present results failed to identify any significant difference between *A. flavicollis* and *A. sylvaticus* regarding mandible shape. However, *A. flavicollis* displayed larger mandibles and first upper molars than *A. sylvaticus*, and a significant difference in molar shape. A morpho-functional analysis of the mandible of the two species previously suggested that the yellow-necked mouse was better adapted to biting at large gap angle than the wood mouse (Kerr et al., 2017). The large mandible and molar size may allow the forest-dweller *A. flavicollis* to consume larger food items, including seeds of deciduous trees such as acorns or beechnuts. In agreement, this species was only found in the Massif des Écrins area within high deciduous forests and more rarely at their border. The difference in molar shape appears too subtle to allow any functional interpretation.

Mandible shape suggests adaptive divergence of the Alpine field mouse

In contrast to the morphologically close wood and yellow-necked mice, the Alpine field mouse appears as well differentiated, both regarding UM1 and mandible shape. The difference between *A. alpicola* and the two other species is distributed all over the anterior part of the mandible, involving a backward shift of the molar row and of the masseteric ridge, and a forward expansion of the incisor. This echoes finding on skull morphology, where the length of the diastema appeared as an important factor discriminating *A. alpicola* (Reutter et al., 1999).

The mandible constitutes the moving tool bringing teeth into occlusion, but in rodents, due to the large diastema, incisors and molars cannot be occluded at the same time (Cox et al., 2012) and they are involved in different functions, namely biting and chewing, respectively. The teeth are primarily moved by different masticatory muscles, the temporal being mainly involved during incision and masseter muscles during chewing. An approximation of the functional performance of these lever systems can be assessed using simple mechanical advantages corresponding to the ratio of the in-lever length (distance from the articulation to the point of muscle attachment) and the out-lever length (distance from the articulation to the bite point) (Anderson et al., 2014). This approach allows assessing functionally-relevant morphological changes on simple pictures, while indices derived from cross-sections require 3D measurements on the mandible (Freeman and Lemen, 2008). *In vivo* bite-force measurements and mechanical estimates based on dissections (Ginot et al., 2018) are inapplicable on prepared museum specimens.

A comparison between commensal domestic mice (*Mus musculus domesticus*) and Sub-Antarctic populations, which incorporate more invertebrate preys in their diet (Le Roux et al., 2002), showed a difference in the biomechanical characteristics of the mandible. Jaw shape appeared optimized for chewing at the molars for commensal mice feeding grains and other hard food items, while an optimization for incisor biting was observed in Subantarctic mice preying on invertebrates (Renaud et al., 2015a; Renaud et al., 2018). The comparison between *A. alpicola* and the two other species, *A. sylvaticus* and *A. flavicollis*, did not provide such a clear pattern, probably because differences in diet only correspond to modulation of a basic omnivorous-granivorous habit, as observed for the domestic mouse and the Cypriot mouse in Cyprus (Renaud et al., 2024a).

Even if less pronounced than between commensal and Sub-Antarctic mice, *A. alpicola* however differ in habitat and diet compared to the lowland *A. sylvaticus* and *A. flavicollis*. The Alpine field mouse was trapped in the Massif des Écrins from 1000 m to above 2000 m of altitude, in environments ranging from deciduous forest to larch forests and Alpine grassland. In such habitats, it relies mostly on fruits and seeds from small herbaceous dicotyledons, with invertebrates being the second most important food category in its diet (Reutter et al., 2005). Elongated mandibles, with an extended anterior part, are associated with predator behavior within murine rodents, a protruding incisor allowing to size prey more easily (Michaux et al., 2007). The long incisor of *A. alpicola* may thus contribute to efficiently capture invertebrates (Renaud et al., 2019). In agreement, mechanical advantages related to the temporal appeared to be comparable between the Alpine field mouse and its lowland relatives, suggesting a maintained functional demand for incisor functioning. In contrast, mechanical advantages related to the masseter appeared to be lower in *A. alpicola*, in agreement with lesser functional requirement for mastication in a species relying more on invertebrate preys.

Molar shape evolution

The first upper molar shape of *A. alpicola* appeared to be slender compared to the more massive *A. sylvaticus and A. flavicollis* occlusal outlines. First upper molar morphology was however not mentioned as a discriminant character of *A. alpicola*, to the contrary of the second molar (Storch and Lütt, 1989). It is a character with both an important phylogenetic and adaptive signal in murine rodents (Gómez Cano et al., 2013; Misonne, 1969). At a large phylogenetic scale, slender first upper molar outlines have been associated with diet incorporating animal preys (Gómez Cano et al., 2013) whereas broad molars seem associated with herbivorous diet, by providing a larger occlusal surface allowing to deal with hard, abrasive food items (Renaud et al., 2005). A similar trend was observed at the intraspecific scale within the wood mouse *A. sylvaticus* and interpreted as a response to a latitudinal trend in changing food resources (Renaud and Michaux, 2007). The variation between slender and broad molars is also the prime component of the within-population variation, in *Apodemus* (Renaud et al., 2015b) as other murines (Renaud and Auffray, 2013) and this preexisting genetic / developmental variation may fuel rapid adaptive response to differences in diet, even at the scale of intraspecific divergence (Hayden et al., 2020). The divergence in molar shape of the Alpine field mouse may surf on similar processes, allowing for an adaptive response to a diet shift even on a relatively short time-scale.

Phylogenetic studies do not show an association of *A. sylvaticus* and *A. flavicollis* as sister species opposed to *A. alpicola*; rather, they suggest an association between *A. alpicola* and *A. flavicollis* (Michaux et al., 2002). The morphological divergence of *A. alpicola* from the very similar *A. sylvaticus* and *A. flavicollis* is therefore not a mere phylogenetic signal. The congruent molar and mandible differentiation, in line with adaptive interpretations, suggests that the niche shift of the Alpine field mouse triggered morphological evolution, in contrast to *A. flavicollis* and *A. sylvaticus* sharing very similar habitat and probably submitted to stabilizing selection regarding their masticatory apparatus (Renaud et al., 2007).

Intraspecific variation with altitude

The two well-sampled species, *A. sylvaticus* and *A. alpicola*, displayed intraspecific variation related to environmental variables, even at the regional scale of the Massif des Écrins. Surprisingly, molar size appeared to be slightly influenced by habitat, although in murine rodents, molars are not subjected to any plasticity once erupted. Molars are however abraded along the animal's life, and the pace of wear can vary depending on the food ingested (Renaud et al., 2024b). Possibly, open habitats in high altitude may expose the mice to an increased abrasion, due to dust and grit adhering to low-lying plants in open habitats (Janis et al., 2002).

In contrast, mandible morphology is remodeled at the scale of an animal's life in response to food consistency and hence diet (Anderson et al., 2014), causing modulations along a growth trajectory primarily determined by heritable developmental constraints (Atchley and Hall, 1991; Dubied et al., 2025). Plasticity and microevolutionary processes *sensu stricto* (i.e. heritable changes due to variations in allele frequency among individuals and populations) cannot usually be disentangle in wild populations, but both can contribute to morphological variation with an adaptive value, in the sense of providing a functional advantage (Anderson et al., 2014). Both processes can therefore be involved in the intraspecific variation in mandible shape observed in the two well-sampled species *A. sylvaticus* and *A. alpicola*, in relation with altitude but not habitat. Both species display a wide altitudinal range, especially pronounced for the wood mouse which can be found from lowlands up to almost 2000 m of altitude. Facing this altitudinal gradient, both species displayed similar trends in mandible morphology, suggesting common responses to the changes in environmental conditions. The parallel change in mandible biomechanics of *A. sylvaticus* and *A. alpicola* maintain a difference between the two species whatever the altitude. Together with the larger mandible size of *A. alpicola*, allowing it to consume larger preys, this may allow the two species to maintain niche partitioning and species coexistence (Dayan and Simberloff, 1998; Rowsey et al., 2020). The trends in mandible shape observed in *A. sylvaticus* and *A. alpicola* also share a same direction, but *A. alpicola* displays divergent mandible morphologies in populations foraging at the lower end of their altitudinal range.

The wood mouse *A. sylvaticus* is known for its generalist habits (Marsh and Harris, 2000) and its ability to forage on diversified food resources (Butet, 1986). Accordingly, latitudinal gradients over a larger geographic scale have been reported for mandible morphology (Renaud and Michaux, 2003) and even molar shape (Renaud and Michaux, 2007). The present study showcase that similar trends can evolve for mandible morphology at a much smaller geographic scale, according with altitudinal gradient in a mountainous massif. It further suggests that the Alpine field mouse also presents evidence of short-term adaptation to the local resources, despite its more restricted altitudinal preferences.

Conclusions

The present study confirmed habitat differences between the three *Apodemus* species thriving in the French Alps, and the generalist habits of the wood mouse *A. sylvaticus*. From a morphological point of view, *A. alpicola* appeared well differentiated from both, *A. sylvaticus* and *A. flavicollis*, regarding molar shape, mandible size and shape. Its morphological characteristics presumably involve an adaptive response to a diet enriched in invertebrate preys, requiring an elongated incisor, but not so powerful chewing. The morphological differentiation was pronounced enough to pinpoint problems in the initial genetic tests. In contrast, the two forest dwellers *A. sylvaticus* and *A. flavicollis* appeared extremely close in their morphology, hindering any robust identification based on molar or mandible morphology, at least with the available sampling.

The Alpine field mouse *A. alpicola* is a relatively poorly investigated species due to its restricted geographic distribution. By integrating former results on dietary preferences with a morphometric analysis of different components of its masticatory apparatus (mandible and first upper molar), this study provide evidence of adaptation to local food resources on different time-scales. The differences in molar shape between the Alpine field mouse and the two other species occurring in the area, *A. sylvaticus* and *A. flavicollis*, suggests long-term adaptation to the basic dietary preferences of each species. Mandible morphology diverged as well between the species, with complex functional consequences suggesting fine-tuning around a morphology adapted to the omnivorous-granivorous diet shared by the three species.

Mandible morphology is further prone to short-term adjustment in response to diet, and in agreement, altitudinal trends were evidenced for both, the highly generalist *A. sylvaticus*, and the high-altitude specialist *A. alpicola*. Morphological trends were parallel in both species, suggesting that the Alpine field mouse is also able to adapt to local resources on a short-time scale. Given the current global warming, deeply affecting Alpine environments, this ability to respond to changing resources may be crucial for its mid-term survival, while facing the reduction of its preferred high-altitude habitat and increased competition with the generalist *A. sylvaticus*.

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Supplementary material

Supplementary information. Details about the Procrustes ANOVA. SS: sum of squares.

1. Procrustes ANOVA: Md shape ~ Species

```
Analysis of Variance, using Residual Randomization
Permutation procedure: Randomization of null model residuals
Number of permutations: 10000
Estimation method: Ordinary Least Squares
Sums of Squares and Cross-products: Type I
Effect sizes (Z) based on F distributions

           Df       SS        MS     Rsq      F      Z Pr(>F)
Species     2 0.057864 0.0289320 0.24539 18.535 7.2463  1e-04 ***
Residuals 114 0.177944 0.0015609 0.75461
Total     116 0.235808
```

2. Procrustes ANOVA: Md shape ~ Species * Csize

```
               Df       SS        MS     Rsq       F      Z Pr(>F)
Species         2 0.057864 0.0289320 0.24539 20.2767 7.4113  1e-04
Csize           1 0.012954 0.0129538 0.05493  9.0786 6.0320  1e-04
Species:Csize   2 0.006609 0.0033043 0.02803  2.3158 3.1186  0.001
Residuals     111 0.158381 0.0014269 0.67165
Total         116 0.235808

Pairwise distances between slope vector
            (end-points), plus statistics
                    d  UCL (95%)         Z Pr > d
ALP:FLAV  0.017139016 0.014634351 2.496544 0.0063
ALP:SYLV  0.008631142 0.007234536 2.635000 0.0043
FLAV:SYLV 0.015781852 0.014545068 2.096794 0.0194
```

3. Procrustes ANOVA: UM1 shape ~ Species

```
           Df      SS        MS     Rsq      F      Z Pr(>F)
Species     2 0.04339 0.0216940 0.13246 8.3977 5.1194  1e-04 ***
Residuals 110 0.28417 0.0025833 0.86754
Total     112 0.32755
```

4. Procrustes ANOVA: UM1 shape ~ Species * Csize

```
               Df      SS        MS     Rsq      F       Z Pr(>F)
Species         2 0.04339 0.0216940 0.13246 8.3779  5.1087  1e-04 ***
Csize           1 0.00314 0.0031364 0.00958 1.2112  0.5787 0.2823
Species:Csize   2 0.00396 0.0019807 0.01209 0.7649 -0.4457 0.6724
Residuals     107 0.27707 0.0025894 0.84587
Total         112 0.32755
```

5. Procrustes ANOVA: Md shape ~ Species * Latitude

```

                                   Df       SS        MS     Rsq
Md_Species                          2 0.057864 0.0289320 0.24539
fac_Md_Ecrins$Altitude              1 0.005841 0.0058408 0.02477
Md_Species:fac_Md_Ecrins$Altitude   2 0.004441 0.0022207 0.01883
Residuals                         111 0.167661 0.0015105 0.71101
Total                             116 0.235808
                                        F      Z Pr(>F)
Md_Species                        19.1544 7.3116  1e-04 ***
fac_Md_Ecrins$Altitude             3.8669 3.8725  1e-04 ***
Md_Species:fac_Md_Ecrins$Altitude  1.4702 1.5718 0.0584 .
Residuals
Total
```

6. Procrustes ANOVA: Md shape ~ altitude – *A. alpicola*

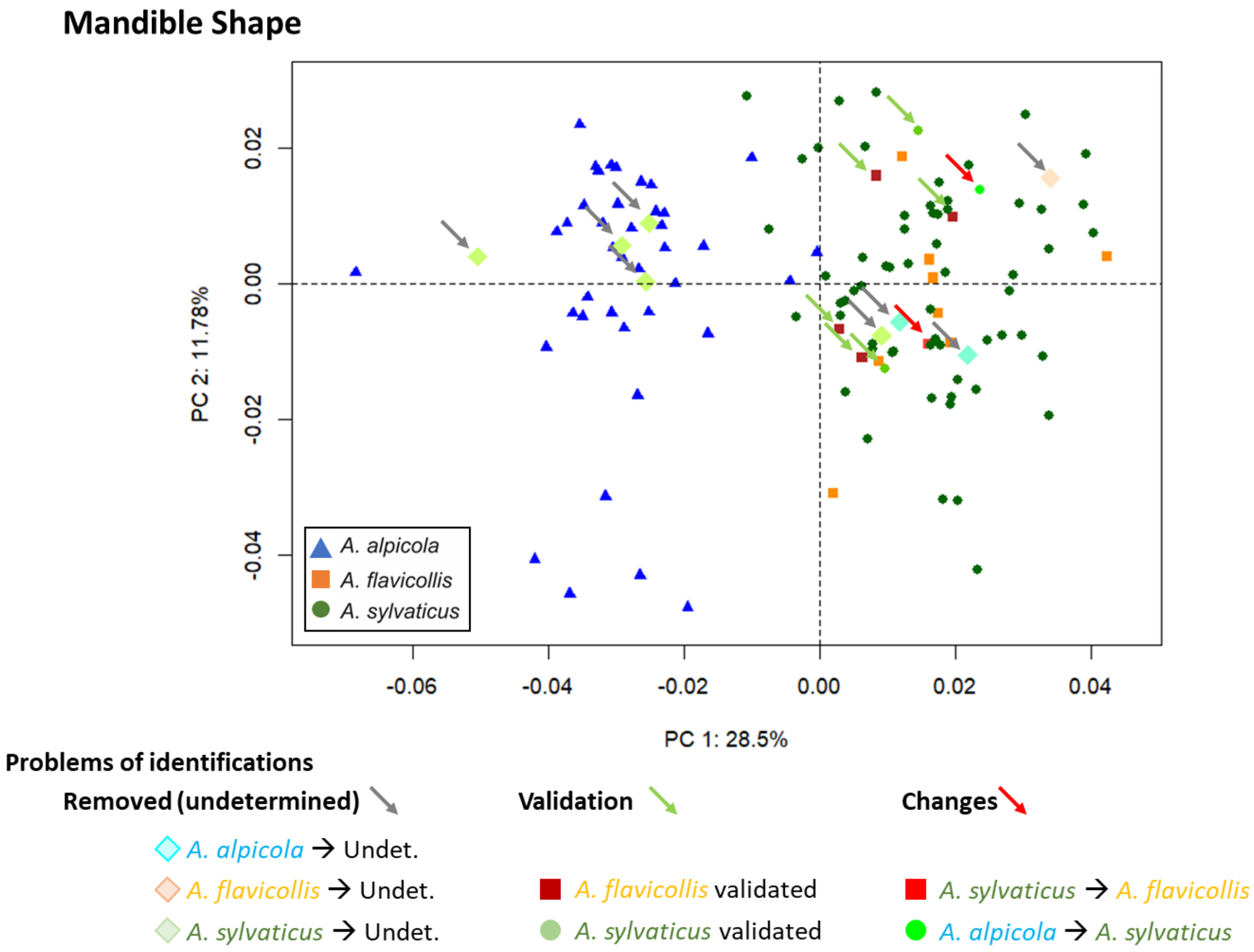
```
          Df       SS        MS    Rsq     F      Z Pr(>F)
Alt_aalp   1 0.003120 0.0031202 0.0501 2.004 1.8019 0.0381 *
Residuals 38 0.059164 0.0015569 0.9499
Total     39 0.062284
```

7. Procrustes ANOVA: Md shape ~ altitude – *A. sylvaticus*

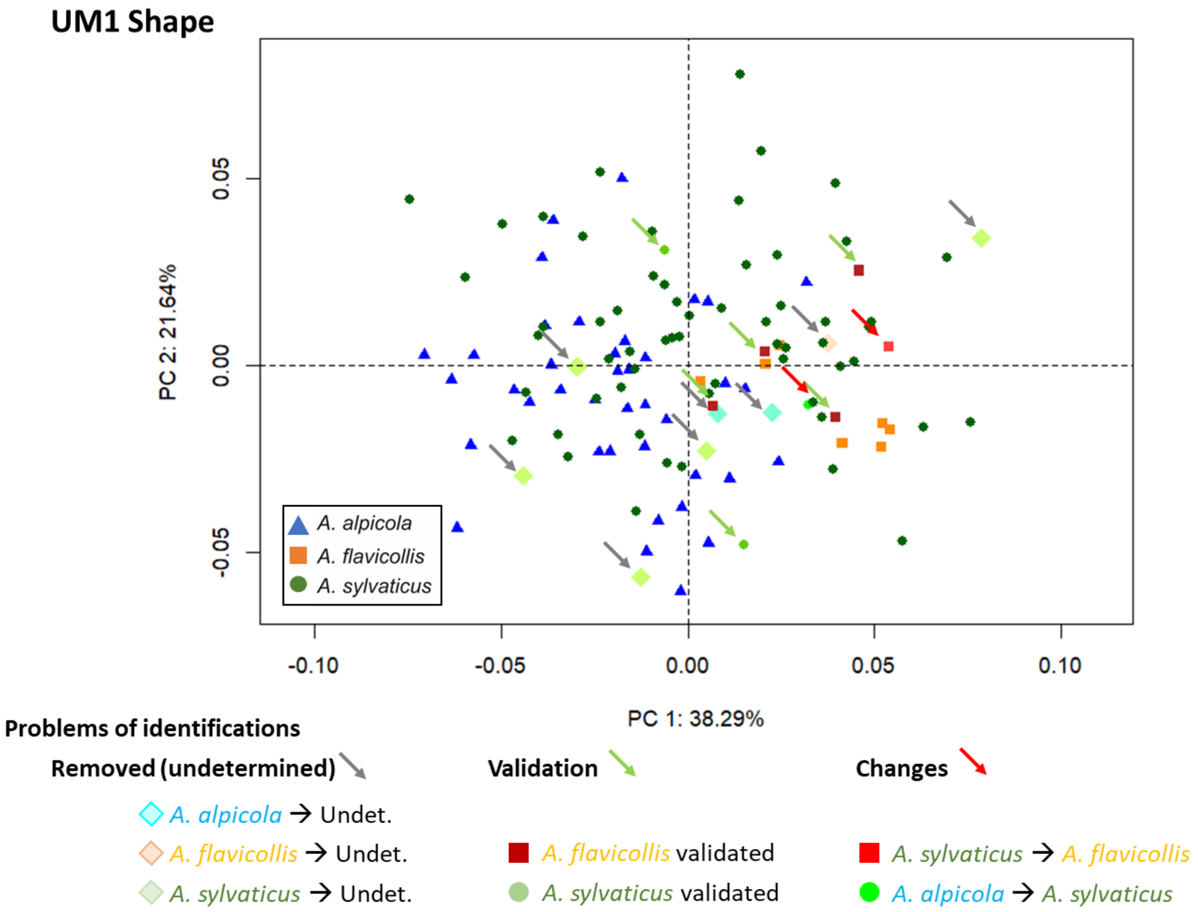
```
          Df       SS        MS     Rsq      F      Z Pr(>F)
Alt_asylv  1 0.005149 0.0051488 0.05179 3.3863 3.3356  1e-04 ***
Residuals 62 0.094270 0.0015205 0.94821
Total     63 0.099419
```

8. Procrustes ANOVA: size-free Md shape ~ Species * Latitude

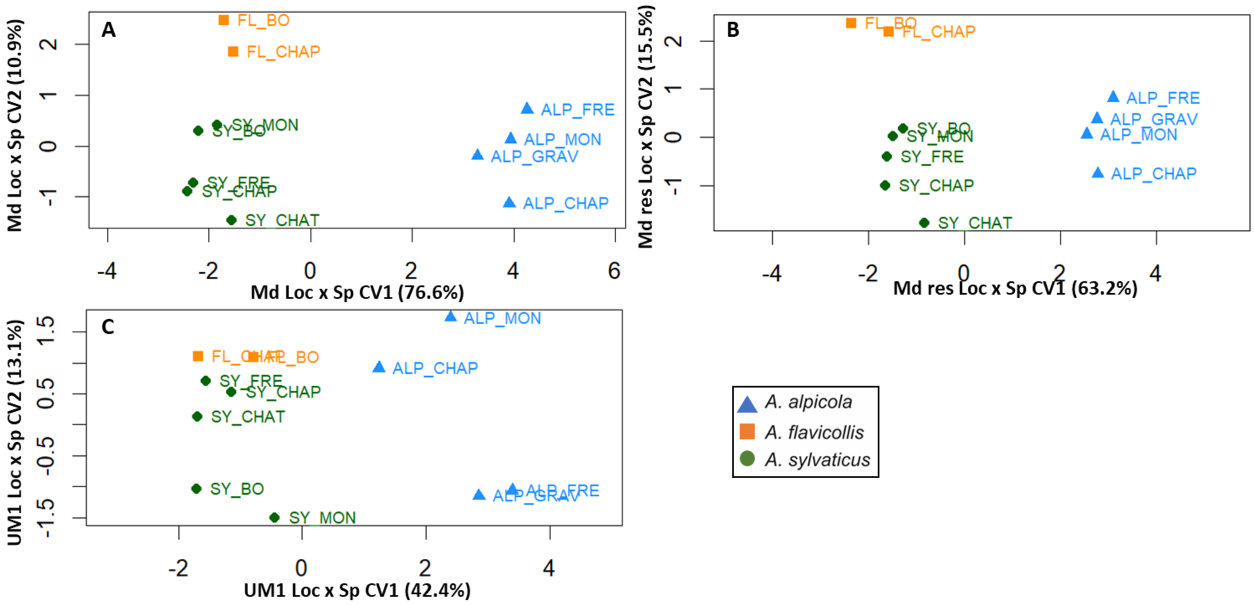
```
                                   Df       SS        MS     Rsq
Md_Species                          2 0.050895 0.0254477 0.23078
fac_Md_Ecrins$Altitude              1 0.005316 0.0053158 0.02410
Md_Species:fac_Md_Ecrins$Altitude   2 0.004072 0.0020361 0.01846
Residuals                         111 0.160253 0.0014437 0.72665
Total                             116 0.220537
                                        F      Z Pr(>F)
Md_Species                        17.6264 7.0369  1e-04 ***
fac_Md_Ecrins$Altitude             3.6820 3.8677  1e-04 ***
Md_Species:fac_Md_Ecrins$Altitude  1.4103 1.4569 0.0732 .
Residuals
```



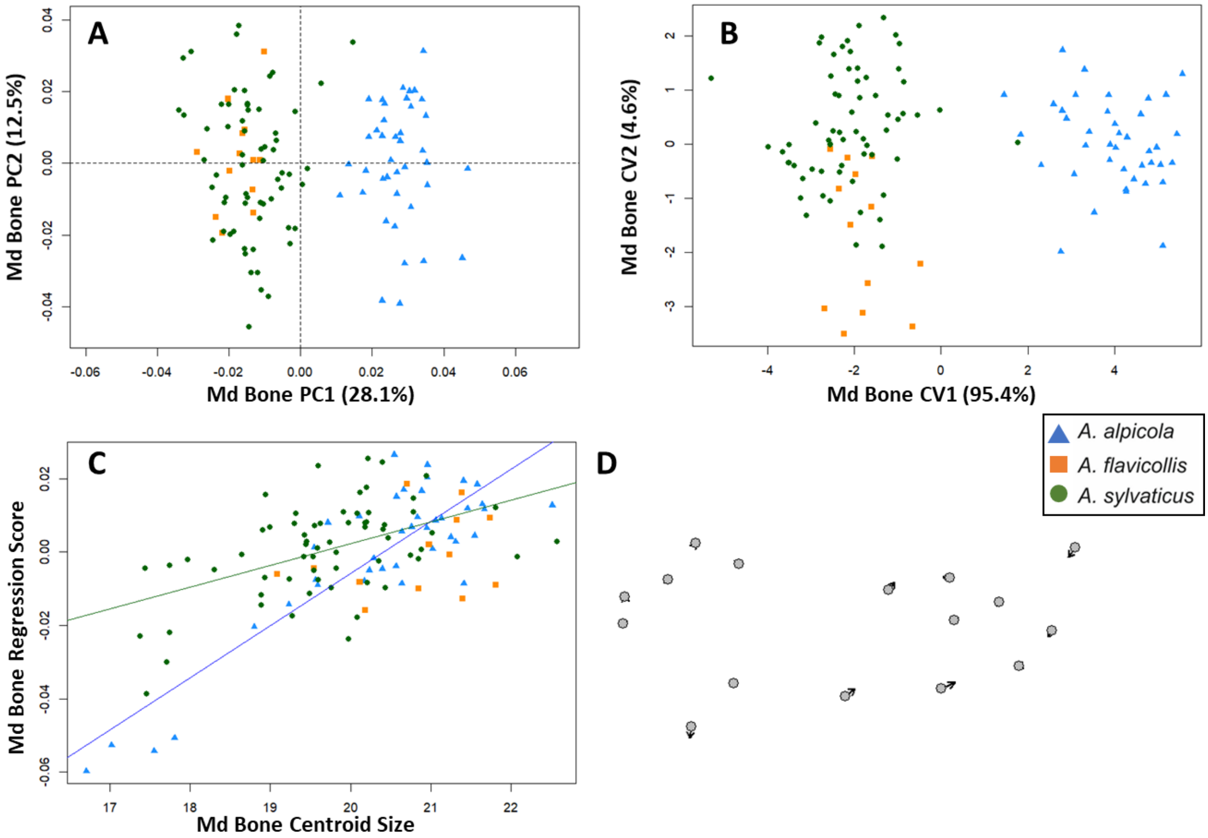
Supp. Figure 1. Preliminary analysis of mandible shape. Specimens which attribution was checked with cyt *b* sequencing are highlighted. The specimens without clear validated attribution were classified as "undetermined" and discarded from the final analysis.



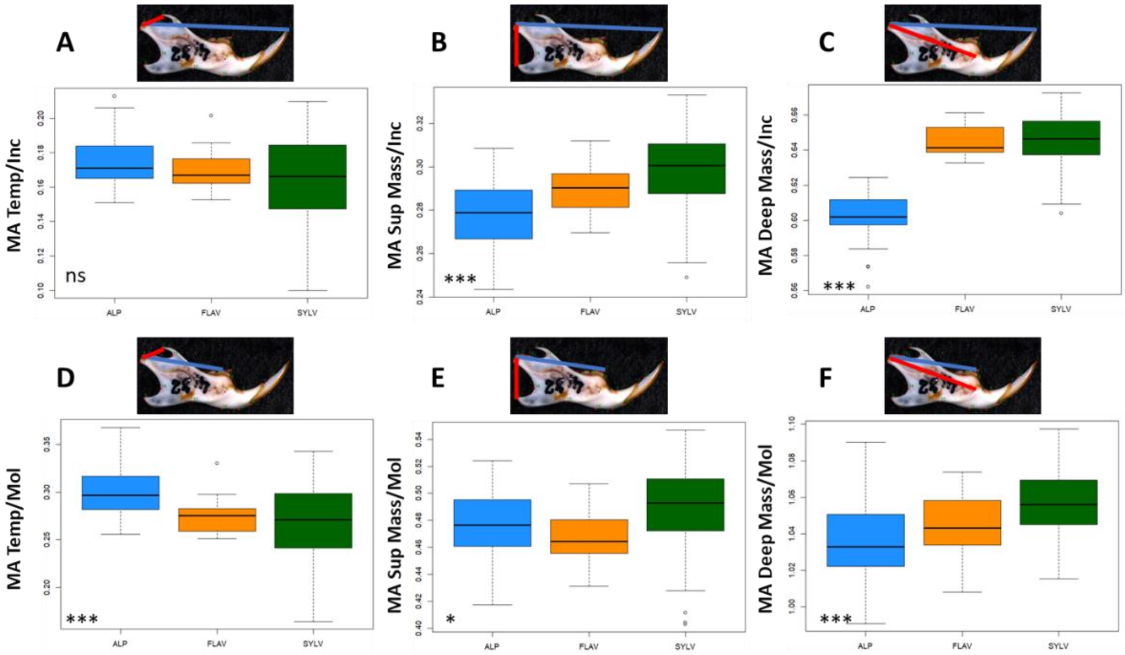
Supp. Figure 2. Preliminary analysis of UM1 shape. Specimens which attribution was checked with cyt *b* sequencing are highlighted. The specimens without clear validated attribution were classified as “undetermined” and discarded from the final analysis.



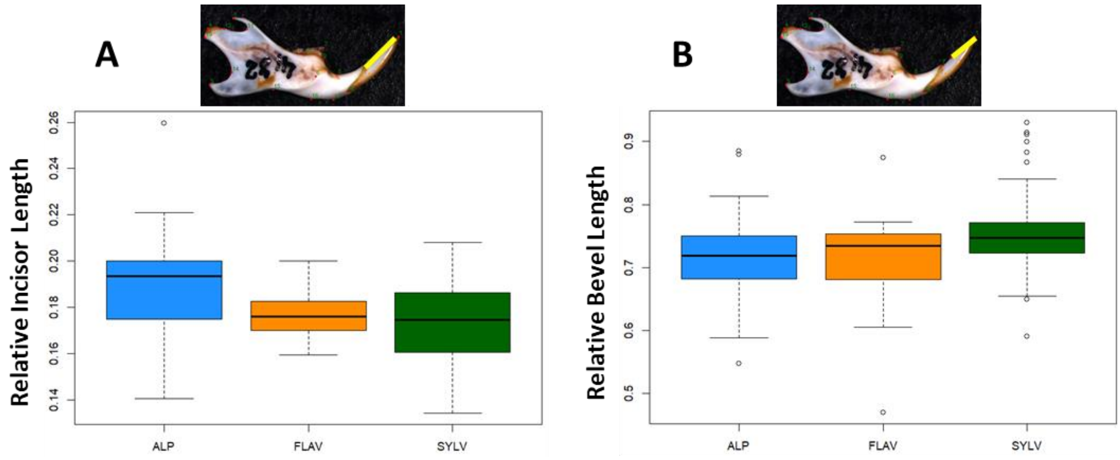
Supp. Figure 3. Shape differentiation of the mandible and the UM1, according with a CVA with species x localities as grouping factor. The CVAs are based on the set of PC axes maximizing correct reclassification between species (11 for the mandible and 8 for the UM1). Group means are represented. A) Mandible shape. B) ‘Size-free’ mandible shape, corresponding to a CVA on the residuals of the aligned coordinates ~ Centroid size. C) UM1 shape.



Supp. Figure 4. Shape differentiation of the mandibular bone. A) Morphospace based on a Procrustes analysis of mandibular bone shape, excluding molar and incisor (16 landmarks). B) CVA on the set of PC axes maximizing correct reclassification for mandibular bone shape (8 axes). C) Regression scores, based on a Procrustes ANOVA of aligned coordinates vs species and centroid size, allowed to visualize allometric change within each species. Color lines represent significant within-species regressions ($P < 0.05$). D) Shape change from minimum to maximum size according with the same allometric model.



Supp. Figure 4. Biomechanical advantages (= In/Out lever arms) of the mandible in the three species of *Apodemus*. A) Temporal/incisor; B) superficial masseter/incisor; C) deep masseter/incisor; D) temporalis/molar; E) superficial masseter/molar; F) deep masseter/molar. Above each graph, a representation of the biomechanical ratio, in-lever in red and out-lever in blue.



Supp. Figure 5. Relative incisor length and bevel length in the three species of *Apodemus*. A) Incisor length relative to mandibular bone centroid size. B) Bevel length relative to incisor length.

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