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Discriminant analysis of skull morphometric characters in *Apodemus sylvaticus*, *A. flavicollis*, and *A. alpicola* (Mammalia; Rodentia) from the Alps

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A total of 108 *Apodemus* skulls from Switzerland, Austria, Italy, France and Germany was studied to determine morphological characteristics useful in identifying individuals as *Apodemus sylvaticus* (Linnaeus, 1758), *A. flavicollis* (Melchior, 1834) or *A. alpicola* Heinrich, 1952. The original assignment of the samples to the three species was based on molar cusp morphology, body proportions, pelage coloration, and allozyme analysis. The 24 measured cranial characters used together accurately discriminated between the three species and correctly classified 100% of the individuals to species. A stepwise discriminant function analysis showed that 6 cranial characters are sufficient to differentiate between the three species, with a correct classification above 97%. Fisher's linear discriminant function coefficients can be used directly for classification of unknown specimens.

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Key words: *Apodemus*, alpine mouse, skull morphometrics, stepwise discriminant function, identification, Alps

Introduction

Mice of the genus *Apodemus* are amongst the most widely distributed rodents in Europe (Niethammer 1978). Three species occur in the Alps: the wood mouse, *Apodemus sylvaticus* (Linnaeus, 1758), the yellow-necked mouse, *A. flavicollis* (Melchior, 1834), and the alpine mouse, *A. alpicola* Heinrich, 1952. The alpine mouse, originally described as a high-altitude subspecies of the yellow-necked mouse (Heinrich 1951, 1952), was recognized as a new species based on the occurrence of three morphologically distinct forms in German and Austrian Alps (Storch and Lütt 1989). Vogel *et al.* (1991) analysed allozyme variation at 27 loci in samples of *A. sylvaticus*, *A. flavicollis,* and *A. alpicola* from Austria, Italy, and Switzerland, confirming the morphological interpretation. The specific identity of the alpine mouse was also reinforced by Filippucci's (1992) study of allozymic variation at 28-33 loci in samples of 6 *Apodemus* species.

Species identification of *Apodemus sylvaticus*, *A. flavicollis* and *A. alpicola* from the alpine region using external morphological traits such as hind foot and tail length of living specimens is not always practical because of intraspecific variation and overlap (Yoccoz 1992). Gemmeke and Niethammer (1981) showed this identification problematic already for the two original species (*A. sylvaticus* and *A. flavicollis*). Further, traits such as pelage coloration are difficult to score and are often subjectively evaluated. Spitzenberger and Englisch (1996) considered relative tail length and coloration as well as pelage characteristics (the summer pelage of adult *A. alpicola* is denser and softer than in *A. sylvaticus* and *A. flavicollis*). However, this seems rather complex and its application is not obvious. Additionally age determination is not evident.

Storch and Lütt (1989) used mensural and cranial characteristics, with morphological traits such as pelage coloration, skull proportions, body proportions, and molar cusp morphology, to differentiate between these species. They used as main skull characteristics the correlation between the sum of incisor depth and length of the upper molar row, and the length of the diastema. They further mentioned that conspicuous tail length, elongate facial skull region, and reduced cusp t9 on the second upper molar are autapomophic features in which the alpine mouse looks more specialized than the common wood mouse and the yellow-necked mouse.

The most relevant work on this subject however was done by Spitzenberger and Englisch (1996) on the Austrian *Apodemus* (n = 4165 individuals). They determined 144 specimens as *A. alpicola* by correlating the sum of incisor depth and length of maxillary tooth row with the relative length of the diastema and by considering the relative tail length and coloration as well as pelage characteristics. After performing discriminant analysis on the skull characteristics, Spitzenberger and Englisch assigned 100% of the wood mice and alpine mice and 97.4% of the yellow-necked mice to their corresponding group. Nevertheless, most of the single or combined mensural characteristics overlap, making it difficult to assign certain individuals to species. No discriminant functions have been published by these authors and the procedure was not described.

Several studies have differentiated between sibling species using discriminant function analysis of external and cranial measurements, such as for *Sorex araneus* and *S. coronatus* (Hausser and Jammot 1974, Handwerk 1987, Turni and Müller 1996), *Peromyscus leucopus* and *P. maniculatus* (Sternburg and Feldhamer 1997), *Talpa europaea* and *T. caeca* (Maurizio and Hausser 1990), and *Myotis myotis* and *M. blythi* (Arlettaz *et al.* 1997). Van der Straeten and Van der Straeten (1977) did the same for *Apodemus sylvaticus* and *A. flavicollis*. They established discriminant functions for distinguishing the two classical species in Belgium. These discriminant functions were also suitable for identifying skull material found in owl pellets.

Several hundred *Apodemus* specimens assigned to *A. sylvaticus* and *A. flavicollis* before the discovery of the alpine species are preserved in Swiss Museum collections and await species verification.

The aim of our study is to establish a discriminant function from limited number of skull measurements with which museum material can be reclassified with reasonable accuracy. The analyses are based on an equal number of otherwise determined specimens of the three species. They were sampled over a wide range of the Alps to avoid a bias due to local forms.

Material and methods

We analysed a total of 108 skulls, 36 of each species. To derive a discriminant function valuable for a large geographic range, we chose specimens originating from Switzerland (72 individuals), Austria (13), Italy (12), France (7) and Germany (4). The skulls used in this study are stored in the following collections: University of Lausanne (IZEA); Natural History Museum of Berne (NHMB); private collection Remo Maurizio (RM) (for addresses see Appendix 1). The individuals were identified according to morphological (tail length; hind foot length; pelage coloration), dental (reduced cusp t9 of the upper second molar), and cranial characteristics (Storch and Lütt 1989). Nineteen specimens had previously been analysed based on allozyme variations (Vogel *et al.* 1991). All localities and the identification numbers of animals examined are listed in Appendix 1.

The study is based on 24 cranial and dental variables (Niethammer 1978). Abbreviations used are (Fig. 1): Cbl – condylobasal length (1), Bll – basal length (2), Brl – basilar length (3), Cbrl – condylbbasilar length (4), Ocn – occipital length (5), Dia – length of the diastema (6), Fori – length of the foramina incisiva (7), Ges – length of the face (8), Hkl – length of the braincase (9), Nasl - nasal length (10), Ozra – length of the upper molars row (alveoli) (11), Ozrk – length of the upper molars row (crown) (12), Bull – length of the bullae (13), Iob – interorbital breadth (14), Ocb – occipital breadth (15), Nasb – nasal breadth (16), Pl – palatal length (17), Rb – rostral breadth (18), Prl – palatinal length (19), Zyg – zygomatic breadth (20), Rh – rostral height (21), Skh – height of the braincase with bullae (22), Skb – breadth of the braincase (23), Id – thickness of the incisor (24).

All the craniometric measurements were taken with a Nikon profile projector accurate to 0.01 nm, equiped with a simple optical system (Jamnot 1973). To avoid undesirable variation due to potential asymmetry, only the left side was measured in paired characteristics. No sexual dimorphism was found in a preliminary analysis and the sexes were pooled. Only adult individuals were measured (age classes 2–6) to minimize the

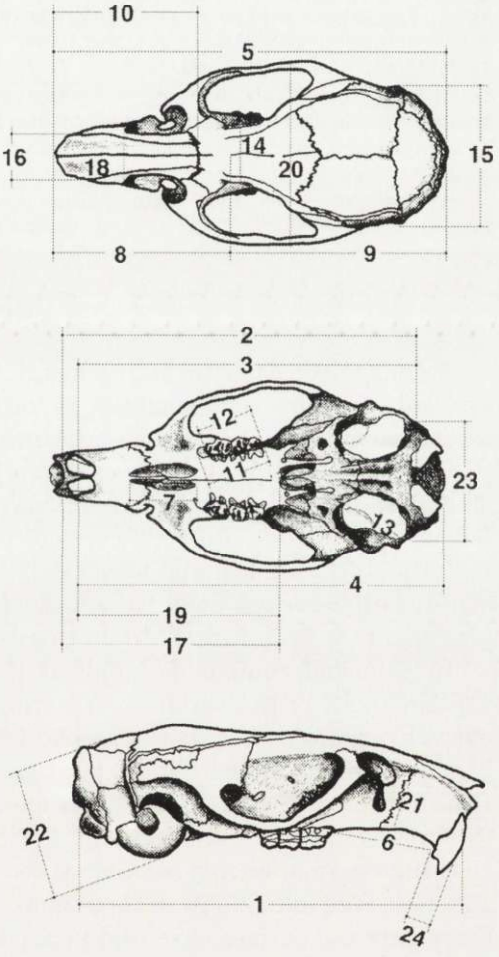

Fig. 1. Cranial measurements used in the study. See the text for number references.

effect of allometric variation associated with growth. All specimens were classified on the basis of tooth wear criteria (Steiner 1968).

We used analysis of variance (ANOVA) to detect variation among the three species for each variable. Normality was tested using Kolmogorov-Smirnov (Lillefors probability). In the further analysis, standardized variables were used in order to give an equal weight to each measurement.

As an exploratory technique for discovering structure in data, principal component analysis (PCA) is widely used in systematic studies. PCA allows ordering of individuals in space and can single out separate groups without considering *a priori* assignation of individuals.

The main analysis was a multivariate linear discriminant function analysis (DFA). The two linear functions allowed us to calculate a discriminant score for each specimen. These scores were used to classify each individual. DFA maximizes the amount of variation among groups relative to that within groups.

Stepwise discriminant function analysis, using the DISCRIM programme of SPSS (Norusis/SPSS 1994), was performed on 24 cranial measurements to predict species membership for each specimen, and to reduce the number of characters needed to discriminate between the three species (Allard *et al.* 1987). The criteria used for entering and removing variables from the stepwise discriminant function was minimization of Wilks' lambda, the *F*-test to enter or remove variables being set to 1.0 (default value) (Norusis/SPSS Inc. 1994).

Specimens positively identified to species using external characteristics and, in part, allozyme analysis were assigned *a priori* and used to form the stepwise discriminant function. The same known specimens were then reclassified using Fisher's classifcation functions to obtain the percentage classified correctly.

SYSTAT (Wilkinson 1990) was used for all statistical procedures, exept for the stepwise discriminant analysis.

Results

Standard statistics including mean, variance and standard deviation are given in Table 1. Univariate analysis of variance (ANOVA) indicates that all cranial measurements differ highly significantly in the three species *Apodemus sylvaticus*, *A. flavicollis*, and *A. alpicola*, excepted for the width of the braincase ($p < 0.021$). The most discriminating individual variables are length of the diastema (Dia), and length of the bullae (Bull). We tested the whole sample for sexual dimorphism (54 males and 54 females) and found only three variables in which the sexes differed significantly: rostral height (Rh), height of the braincase with bullae (Skh) and breadth of the braincase (Skb). In these three variables males had higher values.

In principal component analysis (PCA), the first two principal components explain 78.8% of the variation. The first factor (PC 1) accounted for 68.7% of the overall variance, whereas the second factor (PC 2) accounted for only 10.1% (Fig. 2). PC 1 was highly correlated with variables expressing skull length (ie Cbl, Bll, Brl, Cbrl, Ocn) (Table 2). PC 2 was mostly correlated with length of the diastema, foramina incisiva, and length of the bullae (Dia, Fori, Bull) (Table 2). A plot showing the relationship between these first two components (Fig. 2) clustered the 108 measured individuals in three more or less distinct groups corresponding to the three different species. A second PCA performed on the same variables adjusted for skull size (not shown) did not yield more distinct groupings.

A discriminant function analysis based on all 24 cranial measurements was 100 % accurate in assigning independently identified individuals to the correct species

Table 1. Standard statistics for 24 cranial measurements (in mm) of *Apodemus sylvaticus*, *A. flavicollis* and *A. alpicola*. Statistics given are mean, variance and standard deviation.

Variable	*A. sylvaticus*			*A. flavicollis*			*A. alpicola*		
	Mean	Var	SD	Mean	Var	SD	Mean	Var	SD
1 Cbl	23.10	0.87	0.93	25.20	2.20	1.48	24.99	0.71	0.84
2 Bll	21.27	0.80	0.90	23.40	2.07	1.44	23.19	0.69	0.83
3 Brl	19.78	0.79	0.89	21.86	1.79	1.34	21.45	0.66	0.81
4 Cbrl	22.20	0.91	0.96	24.10	1.52	1.23	23.81	0.60	0.78
5 Ocn	25.55	1.11	1.05	27.64	1.91	1.38	27.76	0.68	0.82
6 Dia	6.62	0.16	0.40	7.19	0.29	0.54	7.96	0.13	0.35
7 Fori	5.42	0.08	0.29	5.46	0.16	0.40	5.89	0.13	0.35
8 Ges	11.26	0.51	0.71	12.41	0.83	0.91	12.44	0.27	0.52
9 Hkl	14.30	0.25	0.50	15.24	0.33	0.57	15.34	0.17	0.41
10 Nasl	8.34	0.27	0.52	9.26	0.58	0.76	9.75	0.21	0.46
11 Ozra	4.20	0.03	0.18	4.63	0.04	0.20	4.40	0.03	0.17
12 Ozrk	3.88	0.03	0.18	4.24	0.02	0.15	4.02	0.03	0.16
13 Bull	4.42	0.04	0.19	4.96	0.05	0.22	4.48	0.03	0.17
14 Iob	4.10	0.03	0.18	4.30	0.03	0.17	4.19	0.02	0.16
15 Ocb	11.08	0.18	0.43	11.61	0.20	0.45	11.56	0.11	0.33
16 Nasb	2.90	0.03	0.17	3.20	0.04	0.21	3.04	0.03	0.18
17 Pl	12.57	0.37	0.61	13.86	0.73	0.85	14.16	0.22	0.47
18 Rb	3.71	0.04	0.21	4.09	0.05	0.22	3.87	0.05	0.22
19 Prl	11.08	0.39	0.62	12.31	0.57	0.76	12.41	0.22	0.47
20 Zyg	13.16	0.38	0.61	14.10	0.50	0.70	13.98	0.28	0.53
21 Rh	4.33	0.04	0.20	4.83	0.09	0.29	4.60	0.06	0.24
22 Skn	8.87	0.09	0.29	9.56	0.07	0.27	9.16	0.08	0.28
23 Skb	9.25	0.13	0.36	8.46	0.14	0.37	8.42	0.09	0.30
24 Id	1.47	0.01	0.08	1.60	0.01	0.10	1.52	0.01	0.10

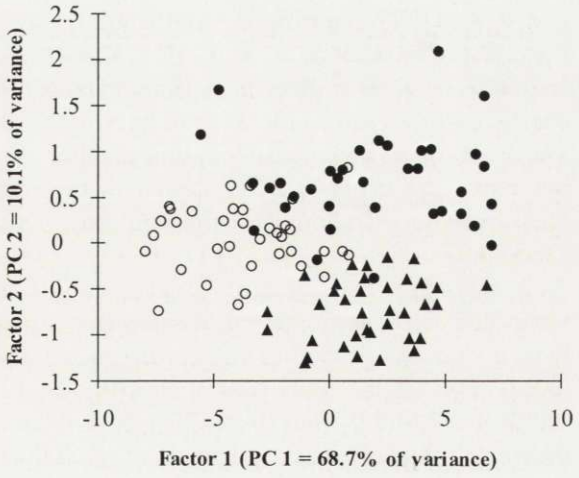

Fig. 1. Morphological relationship between *Apodemus sylvaticus* (○), *A. flavicollis* (●), and *A. alpicola* (▲). Principal component analysis (PCA) for 108 skulls.

Table 2. Principal component (PC) and canonical variate loadings (CV) for 24 cranial morphometric variables in *Apodemus sylvaticus* (n = 36), *A. flavicollis* (n = 36), and *A. alpicola* (n = 36).

Variable	PC 1	PC 2	CV 1	CV 2
1 Cbl	0.98	0.09	−1.73	−0.13
2 Bll	0.97	0.10	2.68	0.09
3 Brl	0.97	0.05	−3.24	0.79
4 Cbrl	0.97	0.06	−0.92	−1.60
5 Ocn	0.97	0.17	−1.56	−2.92
6 Dia	0.78	0.54	2.28	−0.11
7 Fori	0.58	0.62	0.09	−0.72
8 Ges	0.93	0.18	0.37	1.17
9 Hkl	0.89	0.11	1.37	1.72
10 Nasl	0.84	0.40	0.19	0.97
11 Ozra	0.73	−0.39	0.08	0.23
12 Ozrk	0.68	−0.47	0.14	0.28
13 Bull	0.61	−0.59	−0.37	0.47
14 Iob	0.59	−0.38	0.39	−0.01
15 Ocb	0.89	−0.01	−0.17	−1.02
16 Nasb	0.78	−0.18	−0.19	0.04
17 Pl	0.95	0.25	−1.12	0.90
18 Rb	0.79	−0.33	−0.26	0.03
19 Prl	0.95	0.18	2.42	0.76
20 Zyg	0.91	0.03	0.58	0.34
21 Rh	0.89	−0.15	−0.47	−0.15
22 Skh	0.69	−0.45	−0.03	0.56
23 Skb	0.66	0.03	−0.02	−0.37
24 Id	0.61	−0.38	0.27	0.02

[canonical correlation coefficient (ccc) = 0.93; Wilks' Λ = 0.024; χ^2 = 368.84; $p < 0.0001$]. The results showed that the first canonical dimension accounted for most of the variation (R^2 = 94.7%). A scatter plot of the first and second canonical scores showed clear discrimination of the three species (Fig. 3). From the canonical coefficients (CV) in Table 2 it can be concluded that Brl, Bll, Prl, Dia, Cbl, Ocn, Hkl and Pl (1st CV) are measurements playing an important role in the discrimination between *A. alpicola* and the other two species, while Ocn, Hkl, Cbrl, Ges, Ocb and Nasl are those that mostly discriminate between *A. flavicollis* and *A. sylvaticus* (2nd CV).

A stepwise discriminant function analysis allowed us to identify a set of 6 variables with a sufficient discriminating ability. The analysis classifies the variables in the following descending order: Dia (0.38), Cbl (0.12), Bull (0.08), Ozra (0.06), Hkl (0.05), Fori (0.05), Skb (0.04), Pl (0.04), Brl (0.03), Skh (0.03), Ocb (0.03), Nasl (0.03), Ocn (0.02). The first 6 variables alone account for 92.4% of the total variation between species (Fig. 4). Therefore, they were included in the two

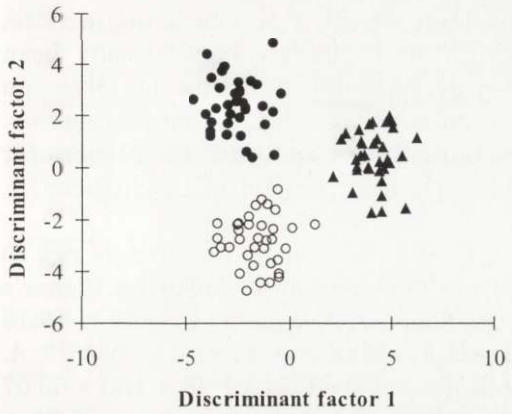

Fig. 3. Discrimination of *Apodemus sylvaticus* (o; n = 36), *A. flavicollis* (•; n = 36), and *A. alpicola* (▲; n = 36). The analysis is based on 24 variables (univariate F-test, $p < 0.01$); 94.7% of the total variance is explained by 2 discriminant factors.

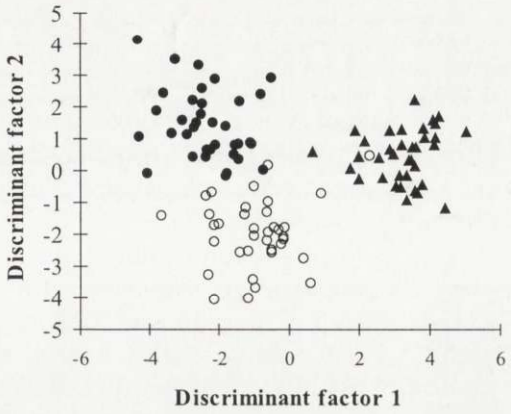

Fig. 4. Discrimination of *Apodemus sylvaticus* (o; n = 36), *A. flavicollis* (•; n = 36), and *A. alpicola* (▲; n = 36). The analysis is based on the 6 variables (Cbl, Bull, Dia, Fori, Hkl, Ozra) found to be significant discriminators by stepwise discriminant function analysis (univariate F-test, $p < 0.01$); 92.4% of the total variance is explained by 2 discriminant factors.

discriminant functions: Z_1 = Cbl × –2.1 + Bull × –2.55 + Dia × 4.88 + Fori × 0.44 + Hkl × 1.38 + Ozra × 0.71 + 1.45 and Z_2 = Cbl × –0.55 + Bull × 2.48 + Dia × 2 + Fori × –1.71 + Hkl × 0.73 + Ozra × 3.41 – 28.77. With this new combination, 105 of 108 individuals (97.2%) were assigned correctly.

Discussion

Specific identification of skulls from yellow-necked, wood and alpine mice from the Alps cannot be made consistently on the basis of a single cranial characteristic. Although variable means were significantly different between the three species, ranges overlapped within all groups for all characteristics. A principal component analysis (PCA) shows, however, that interspecific differences actually exist and are not blurred by the large geographic range of our sample. Therefore, a discriminant function seems the most appropriate technique to evidence these interspecific differences and to use them for practical purpose. Stepwise discriminant function analysis of cranial variables was successful in selecting measurements to accurately distiguish between skulls of the three *Apodemus* species. Excluding young animals, we demonstrated that an efficient distinction between individuals of the three *Apodemus* species is possible on the basis of a linear combination of 6 cranial characters only: condylobasal length, length of the bullae, length of the diastema, length of the foramina incisiva, length of the braincase, and length of the upper molars row. Only three specimens (out of 108) were not classified correctly.

Some of these criteria (length of the diastema, length of the foramina incisiva, length of the upper molars row, and length of the bullae) have already been proposed as identification criteria by Van der Straeten and Van der Straeten (1977), who also used a discriminant function analysis of cranial measurements. However, the discriminant functions proposed in the present work are efficient for three species and offer a more powerful tool for the identification of *A. sylvaticus*, *A. flavicollis*, and *A. alpicola*.

The use of the two discriminant functions simultaneously, however, is not so easy. For practical determination, we suggest the use of the following Fisher's classification functions derived from the same analysis: *A. sylvaticus* = Cbl × −18.13 + Bull × 71.68 + Dia × −0.25 + Fori × 7.88 + Hkl × 62.53 + Ozra × 81.4 − 588.53; *A. flavicollis* = Cbl × −17.07 + Bull × 83.65 + Dia × −0.34 + Fori × 1.48 + Hkl × 63.07 + Ozra × 91.96 − 689.49; *A. alpicola* = Cbl × −28.31 + Bull × 66.98 + Dia × 25.06 + Fori × 5.61 + Hkl × 70.1 + Ozra × 92.66 − 655.18. Unknown individuals should be attributed to the species for which the function gives the highest score.

The biogeographical range of *A. alpicola* is unknown. Our work reports the first records of *A. alpicola* from France. They were found on the southern slope of the Col du Mont Cenis, close to the Italian border. The application of this discriminant analysis to Museum collections should help to gain better knowledge about *Apodemus* populations of the Swiss region and French Alps and may help to better understand the ecology and evolution of this long-ignored species.

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Appendix 1. List of localities and collection numbers of animals investigated. Specimen with asterisk are from the allozyme study of Vogel *et al.* (1991).

Apodemus sylvaticus (Linnaeus, 1758)

Switzerland: *Valais:* Grimisuat: (IZEA, 1917 and 1912); Martigny: (IZEA, 1085); La Tarpe: (NHMB, 1009847); Suen: (IZEA, 4204 and 4205); Grand St. Bernard: (IZEA, 4313); Bourg St. Bernard: (IZEA, 4800); Pfynwald: (IZEA, 4860); Les Fays: (NHMB, 1009841); *Graubünden*: Trimmis: (IZEA, 4246* and 4247*); *Vaud:* Solalex: (IZEA, 4792 and 4793); *Fribourg:* Charmay: (IZEA, 4831 and 4832); *Bern:* Haslital: (IZEA, 5159); Plateau de Diesse: (NHMB, 1009740 and 1009739); Belp, Hunzigenau: (NHMB, 1009690); *Solothurn:* Nennigkofen: (NHMB, 1008346, 1008338 and 1008342); *Ticino:* Losone: (IZEA, 1384); Cevio: (NHMB, 1009786); *Zürich:* Rümlang: (NHMB, 1009929).

Italy: Lage Sirio: (IZEA, 4270*); San Bernardo: (IZEA, 4272*, 4276*, 4278* and 4279*); Ronc San Bernardo: (IZEA, 4809).

Austria: Langen: (IZEA, 4293*).

France: Mt. Cenis: (IZEA, 4808); Malamot Mt. Cenis: (IZEA, 4820).

Apodemus flavicollis (Melchior, 1834)

Switzerland: *Vaud:* Forel Lavaux (IZEA, 1427O and 1427P); Prévérenges (IZEA, 4168 and 4169); *Valais:* Grimisuat (IZEA, 1914 and 1919); Martigny (IZEA, 4219*); *Bern:* Justistal, Gibelegg (NHMB, 1009600); Plateau de Diesse (NHMB, 1009564, 1009556 and 1009558); *Graubünden:* Jenaz (IZEA, 4249, 4250, 4251 and 4252); *Ticino:* Mergozzo, Gordevio: (IZEA, 4227* and 4306); Cevio: (NHMB, 1009570 and 1009571); *Fribourg:* Charmay: (IZEA, 4829 and 4833); *Solothurn:* Nennigkofen: (NHMB, 1008542 and 1008666); *Schwyz:* Riemenstalden, Hüsern: (NHMB, 1009629); *Schaffhausen:* Neunkirch (NHMB, 1009633 and 1009632); *St. Gallen:* Altstätten: (NHMB, 1009549 and 1009550).

Germany: Grainau Garmisch: (IZEA, 4259*, 4260*, 4261* and 4262*).

Austria: Silbertal: (IZEA, 4294 and 4295); Silbertal Montafon (73393).

France: Morzine Les L'Hottys: (IZEA, 4806).

Apodemus alpicola Heinrich, 1952

Switzerland: *Graubünden:* Casaccia Bergell: (RM, 2, 4 and 100); Vicosoprano, Bergell: (RM, 11 and 68); Bergell: (RM, 28, 31, 39, 48, 52, 67 and 71); *Bern:* Haslital: (IZEA, 5160, 5161 and 5188); *Valais:* Sanetsch: (IZEA, 4850).

Italy: Aostatal, Entrèves: (IZEA, 4273*, 4274* and 4275*); St. Bernardo (IZEA, 4601, 4602 and 4798).

Austria: Vorarlberg, Klösterle: (IZEA, 4290*, 4291* and 4311); Stuben: (IZEA, 4594, 4595, 4597, 5051 and 4312); Silbertal, Montafon: (73382).

France: Col du Mt. Cenis: (IZEA, 4796, 4797, 4822 and 4851).

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