

Boris Kryštufek*, Georgy I. Shenbrot, Janez Gregori, Petr Benda and Rainer Hutterer

Taxonomic and geographic setting of Royle's mountain vole *Alticola roylei* revisited

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Abstract: In the not too distant past the name *Alticola roylei* was used to encompass mountain voles which are currently classified as six different species. Such wide use of the taxonomic name still blurs the lines among species of mountain voles in northern India and adjacent Pakistan. By studying museum vouchers we redefine the taxonomic and geographical scope of *A. roylei*, a mountain vole which is characterized by a combination of dark (hair-brown) dorsal fur and moderately long tail, bowed zygomatic arches, small bullae, and moderately complex third upper molars. Two names (*lahulius* and *cautus*) are listed as junior synonyms of *roylei*. We identified 19 localities as evidence on the presence of Royle's mountain vole in Himachal Pradesh and Uttaranchal in India. Further three localities extend the range into Nepal. The total area of the species' occurrence is estimated as 15,290 km². Royle's mountain vole is allopatric with respect to further two mountain voles of Nepal and northern India, *Alticola stoliczkanus* (a single case of sympatry in Manaslu) and *Alticola montosus*.

Keywords: *Alticola montosus*; *Alticola stoliczkanus*; habitat modeling; museum collections; zoological nomenclature.

Introduction

During revisionary work on Asiatic rodents, we came across museum vouchers of mountain voles (genus *Alticola*

Blanford 1881) from Nepal which were recognizably different from Stoliczka's mountain vole *Alticola stoliczkanus* (Blanford 1875), the only species of *Alticola* reported so far for the country (Pearch 2011). Subsequent comparison with museum reference material and published data retrieved Royle's mountain vole *Alticola roylei* (Gray 1842); our new records shift the distributional border about 400 km eastwards. The more in depth we were disentangling the distributional status of *A. roylei*, the more evident it became how badly this species needs a thorough revision.

The systematic arrangement of mountain voles is far from being definitely established (cf. Lebedev et al. 2007, Litvinov et al. 2015, Bodrov et al. 2016), and the taxonomic history was particularly turbulent in the Royle's mountain vole. In the first comprehensive revision of the genus, Hinton (1926) recognized 14 species, but this number was reduced to merely three species in Ellerman and Morrison-Scott (1951). The name *roylei* was used for all mountain voles with moderately long tail and "normal" (i.e. unflattened) skull and having relatively complex third upper molar M³ (Ellerman 1947, 1961). *Alticola roylei* therefore encompassed taxa which are currently (Musser and Carleton 2005) classified as six distinct species: *Alticola argentatus* (Severtzov 1879), *Alticola montosus* (True 1894), *Alticola albicaudus* (True 1894), *Alticola semicanus* (Allen 1924), *Alticola tuvinicus* Ognev 1950, and *Alticola olchonensis* (Litvinov 1960). Within such broad definition, the range of Royle's mountain vole was regarded to cover all the major mountain ranges of Central Asia, including Himalayas, Hindu Kush, Karakoram, Pamirs, Tien Shan, Altai, and Qilian Mts., thus covering an area of about one million square kilometres (cf. Corbet 1978).

The current taxonomic setting of *Alticola* is largely based on a revision by Rossolimo and Pavlinov (1992) who split the three species of Ellerman and Morrison-Scott (1951) and Corbet (1978) into eight species and restricted *Alticola roylei* to "few localities in Kashmir". The name *roylei* however, although now only exceptionally applied for voles outside India (but see Luo et al. 2000, and Wang 2003), remained in the older literature and on museum voucher tags, and therefore blurring the lines among species of mountain voles occupying northern India and adjacent ranges in Pakistan, Afghanistan, Nepal, and China. In this contribution, we reassess the taxonomic and distributional status of the Royle's mountain vole.

*Corresponding author: Boris Kryštufek, Slovenian Museum of Natural History, Prešernova 20, SI-1000 Ljubljana, Slovenia, e-mail: bkryštufek@pms-lj.si

Georgy I. Shenbrot: Mitrani Department of Desert Ecology, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Midreshet Ben-Gurion, Israel

Janez Gregori: Slovenian Museum of Natural History, Prešernova 20, SI-1000 Ljubljana, Slovenia

Petr Benda: Department of Zoology, National Museum (Natural History), Václavské nám, 68, CZ-115 79 Praha 1, Czech Republic; and Department of Zoology, Faculty of Science, Charles University, Viničná 7, 128 44 Praha 2, Czech Republic

Rainer Hutterer: Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160, 53113 Bonn, Germany

The gender of *Alticola* Blanford 1881 has never been clearly defined. The name was obviously derived from Latin *cola* (one who inhabits) and *altus* (high), i.e. the mouse that inhabits high altitudes. Neither Blanford (1881: 96), who created it as a section of *Arvicola*, nor any subsequent author discussed this point. True (1894) named his new taxa (*montosa*, *albicauda*) in the genus *Arvicola*, apparently treating the genus as feminine. However, according to the Official Lists and Indexes of Names and Works in Zoology (ICZN 1987/2012), *Arvicola* is masculine, as are other Latin names ending with *cola*. We, therefore, treat *Alticola* equally as masculine and change the endings of the species names accordingly (cf. Miller 1913, Rossolimo and Pavlinov 1992).

Materials and methods

Museum vouchers

We studied extensive museum material representing all known species of mountain voles (Musser and Carleton 2005) and deposited in the following collections: BMNH – Natural History Museum, London (formerly British Museum Natural History), UK; NMNH – National Museum of Natural History, Washington D.C., USA; NMP – National Museum, Prague, Czech Republic; NMW – Natural History Museum, Vienna, Austria; PMS – Natural History Museum

of Slovenia, Ljubljana, Slovenia; SMF – Forschungsinstitut und Natur-Museum Senckenberg, Frankfurt am Main, Germany; SZM – Siberian Zoological Museum, Institute for Systematics and Ecology of Animals, Russian Academy of Sciences, Siberian Branch, Novosibirsk, Russia; ZFMK – Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany; ZIN – Zoological Institute and Zoological Museum, Russian Academy of Sciences, St. Petersburg, Russia; and ZMMU – Zoological Museum, Moscow University, Moscow, Russia.

Our study is based on visual examination of museum specimens, both macroscopically and under a stereomicroscope at different magnifications. The aim was to delimit species by using museum vouchers (skins and skulls) and to define diagnostic traits. We understand a diagnosis as “A statement in words that purports to give those characters which differentiate the taxon from other taxa with which it is likely to be confused” (ICZN 1999). Quantitative comparisons between species were done using the external and craniodental measurements. Four external measurements were obtained from specimen tags and three cranial variables were scored using a Vernier Caliper (Mitutoya, Aurora, IL, USA) adjusted to the nearest 0.1 mm (Table 1).

Mapping and habitat modeling

Most records had no original GPS coordinates, and were geo-referenced using Geographic Names Gazetteers

Table 1: Measurements (mean, minimum–maximum) in museum specimens of mountain voles (*Alticola*) from the southern margin of their range between Afghanistan and Nepal: *Alticola roylei* (specimens from BMNH, NMP, NMW, PMS), *Alticola albicaudus* (NMNH, PMS), *Alticola argentatus* from Afghanistan and western Pakistan (NMP, ZFMK), *Alticola montosus* (BMNH, ZFMK), *Alticola stoliczkanus* from Nepal and northern India (BMNH, NMP, PMS, ZFMK).

	<i>A. roylei</i>	<i>A. albicaudus</i>	<i>A. argentatus</i>	<i>A. montosus</i>	<i>A. stoliczkanus</i>
Head and body length	(18) 107.1 91–117	(2) 104.5 101–108	(66) 110.2 100–125	(30) 110.3 102–126	(19) 106.1 99–114
Tail length	(14) 39.8 29–48	(2) 28.5 28–29	(66) 46.7 39–59	(29) 49.1 41–65	(19) 18.6 13–25
Relative length of tail	(12) 39.6 29.8–47.1	(2) 27.3 26.9–27.7	(65) 43.9 36.1–54.9	(29) 44.6 36.3–60.7	(19) 17.5 13.1–22.1
Hind foot length	(19) 18.3 17.0–21.0	(2) 22.0 22.0–22.0	(66) 19.7 18.0–21.5	(31) 19.5 17.5–22.9	(19) 17.7 13.0–19.0
Ear length	(19) 13.8 12.5–15.0		(63) 15.0 12.8–19.0	(30) 14.6 13.0–17.0	(15) 12.7 10.5–18.0
Condylbasal length	(12) 26.18 24.5–27.1	(3) 25.30 24.8–25.9	(43) 26.68 25.5–28.3	(20) 26.47 25.0–27.9	(15) 25.87 22.5–28.7
Zygomatic width	(13) 15.41 15.1–15.9	(3) 14.17 13.9–14.5	(43) 14.78 13.9–15.9	(16) 14.93 14.0–15.9	(14) 14.75 13.5–16.3
Maxillary tooth-row	(14) 6.51 5.8–7.2	(3) 6.23 5.9–6.5	(54) 6.44 5.4–7.3	(20) 6.49 6.0–7.0	(16) 6.10 5.6–6.5

See text for collection acronyms. Measurements are in millimeters, relative length of the tail against the length of head and body is in percentages.

available at http://earth-info.nga.mil/gns/html/cntry_files.html and old Soviet (<http://maps.vlasenko.net>) and the US (<http://www.lib.utexas.edu/maps/asia.html>) military topographic maps, and were checked for suitable habitats using Google Earth.

Environmental data for species distribution modeling (SDM) were used as 30 arc-second grids (approximately 1 km resolution) and were represented by climate, relief, and vegetation variables. The climate variables (annual mean temperature, mean monthly temperature range, mean temperatures of coldest and warmest quarters, maximal temperature of warmest month, minimal temperature of coldest month, temperature annual range, annual precipitation, and precipitation of wettest quarter) were obtained from WORLDCLIM Version 1.4 (Hijmans et al. 2005) available at <http://www.worldclim.org>. Slope data were derived from altitude [extracted from GOTOPO30 dataset distributed with ArcGIS (ESRI Corp., Redlands, CA, USA)] using the Spatial Analyst module of ArcMap. Data on Normalized Difference Vegetation Index (NDVI) were obtained from VEGETATION Programme (<http://www.spot-vegetation.com>; now <http://www.vito-eodata.be>); data for 1998–2007, each a ten-day estimate) and averaged by seasons (winter, spring, summer, and autumn) across all available years. The NDVI is an index of greenness that is directly correlated with productivity and green vegetation biomass and is widely used in ecological studies (Pettorelli et al. 2005).

The SDMs were built with MAXENT 3.3.3k software (Phillips et al. 2006). The extent of the study area or “landscape of interest” significantly affects the results of SDM (Anderson and Raza 2010, Elith et al. 2011). To define the study area of a species, we calculated the kernel density of occurrence points of this species with search radius equal 4° , reclassified the obtained raster so that original values of kernel density equal or more than 0.05 were converted to 1 and values < 0.05 to “NoData”. This reclassified raster was used as the mask for clipping environmental variables to the study area. Models were constructed with default MAXENT settings as these settings were demonstrated to be most appropriate for wide-ranging data (Phillips and Dudík 2008, Warren and Seifert 2011). We used MAXENT logistic output which provides estimates of relative habitat suitability (Elith et al. 2011). To estimate the model's performance, we used the area under the Receiver Operating Characteristic curve (AUC) test, the extensively used measure in species' distribution modeling (Elith et al. 2006). The AUC measures the ability of a model to discriminate between sites where a species is present vs. those where it is absent (Hanley and McNeil

1982). The values of AUC ranges between 0 and 1; the value of 1 means an ideally good model performance, the score of 0.5 indicates predictive discrimination that is not better than random, and values < 0.5 means performance poorer than random.

To delineate the areas of real species occurrence, the original model values, ranging continuously from 0 to 1, were transformed to binary 0 or 1 using a threshold value. The threshold value was chosen equal to the “maximum training sensitivity plus specificity”; it was demonstrated experimentally (Liu et al. 2013) that this threshold provides optimal results. After reclassification of the original raster according to chosen threshold value, the reclassified raster was transformed to polygons. Only polygons containing occurrence records were considered as areas of occurrence. Areas of these polygons were calculated on the map converted to Asia North Albers Equal Area Conic projection using command “calculate geometry” in sq. km, and the sum of areas of these polygons was used as an estimation of geographic range size. All map operations were performed using the ArcMap 10.3 software.

Results and discussion

Taxonomic scope

We searched the literature (Hinton 1926, Rossolimo and Pavlinov 1992) for diagnostic traits and these were verified on museum vouchers. We examined 13 types (see below) representing four species of mountain voles in the region, i.e. all except *Alticola albicaudus*. In taxonomy, “Type specimens are the objective standard of reference for the application of zoological names”, and therefore act as onomatophores (ICZN 1999). On these grounds, we safely linked diagnostic morphological traits with the species of mountain voles.

Alticola roylei is characterized by a combination of dark (hair-brown) dorsal fur and moderately long tail (Figure 1A, Table 1), bowed zygomatic arches, small bullae (Figure 2A), and moderately complex M^3 with three lingual salient angles (Figure 3B). *Alticola stoliczkanus* is morphologically the most unique mountain vole in the region and this distinctiveness was fully appreciated throughout the 20th century (e.g. Corbet 1978). The tail is decidedly shortest of any mountain vole (Figure 1D, Table 1), and the third upper molar shows a simplified enamel pattern, with two prominent salient angles on

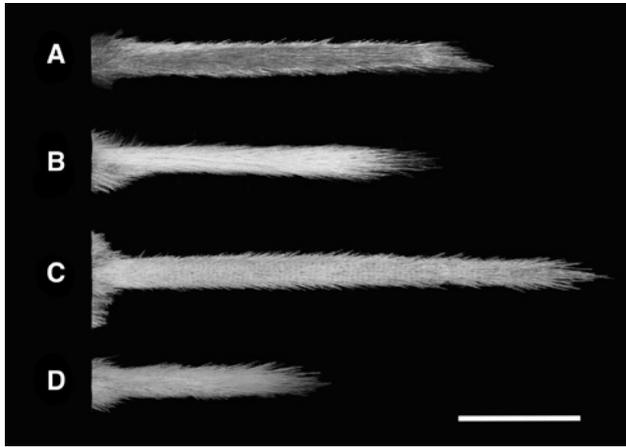


Figure 1: Tails of mountain voles *Alticola*: (A) *Alticola roylei* (NMP 40206; Manaslu, Nepal); (B) *Alticola albicaudus* (NMNH 198531; Phyang Nullah Lake, Jammu and Kashmir, India); (C) *Alticola argentatus* (NMP 39793; Tirich Valley, Pakistan); (D) *Alticola stoliczkanus* (NMP 40205; Manaslu, Nepal). Scale bar = 5 mm.

the lingual side; the posterior angle is shallow or absent (Figure 3E). *Alticola albicaudus* is of light color, has a short and densely haired light tail (Figure 1B, Table 1), and a relatively narrow skull with large bullae (Figure 2B); M^3 is as in *A. roylei* (Figure 3B). *Alticola montosus* is as dark as *A. roylei*, has a relatively long tail (Figure 1C, Table 1), and small bullae (Figure 2D). Distinctive is the morphology of M^3 which is the most complex in *Alticola*. The lingual side bears three or four salient angles and the antero-buccal triangle BT1 is large and closed (Figure 3D), while it is reduced and widely opened into the anterior loop in all other mountain voles (Figure 3A–C, E). *Alticola*

argentatus is lighter than *A. roylei* and has larger bullae (Figure 2). The tail is less densely clad with hairs in *A. argentatus* than in *A. roylei* and frequently exposes annulation (Figure 1C). In *A. stoliczkanus* and *A. albicaudus* dense hair conceal the annulation; both species also have prominent terminal pencils (Figure 1B, D).

Species of mountain voles can be conventionally keyed as follows:

- 1a M^3 with 3–4 lingual salient angles; antero-buccal triangle BT1 large and isolated from the anterior loop (Figure 3D) *A. montosus* 2
- 1b M^3 with 2–3 lingual salient angles; antero-buccal triangle BT1 small and widely confluent with the anterior loop (Figure 3A–C, E) 2
- 2a Tail short, about same length as hind foot (Table 1); M^3 with two prominent lingual salient angles (Figure 3E) *A. stoliczkanus* 2
- 2b Tail decidedly longer than hind foot (Table 1); M^3 with three prominent lingual salient angles (Figure 3A–C) 3
- 3a Tail relatively shorter (<30% of head and body length; Table 1), light (white or light grey) throughout, densely haired (annulation concealed), with a distinct pencil (Figure 1B) *A. albicaudus* 3
- 3b Tail relatively longer (more than 30% of head and body length; Table 1), darker (grey to brown), thinly haired, and lightly pencilled (annulation frequently exposed), terminal pencil less prominent (Figure 1A, C) 4
- 4a Dorsal pelage dark hair-brown; bullae smaller (Figure 2A) *A. roylei* 4
- 4b Dorsal pelage lighter, smoke-grey, cloudy-rusty, or fawn-brown; bullae larger (Figure 2C) *A. argentatus* 4

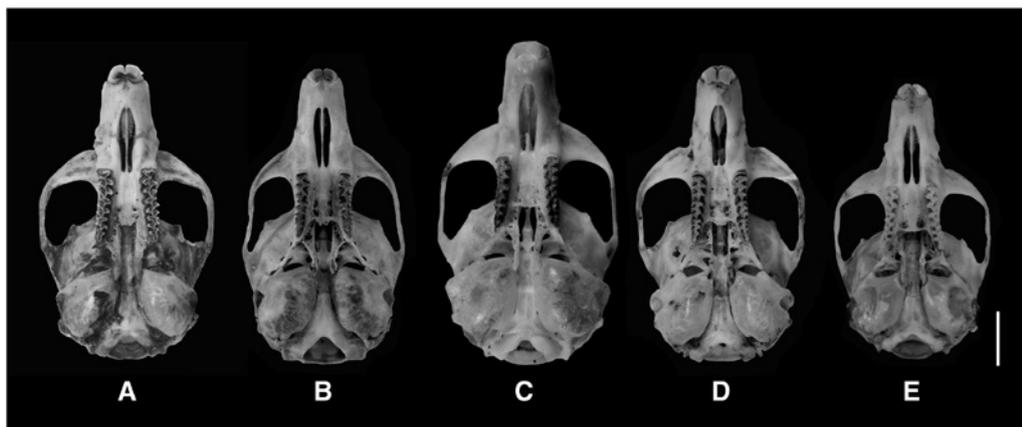


Figure 2: Skulls of mountain voles *Alticola* in dorsal view: (A) *Alticola roylei* (BMNH 2002a; type of *roylei*); (B) *Alticola albicaudus* (PMS 5340; Liligo, Paju, Broad Peak, Pakistan); (C) *Alticola argentatus* (ZFMK 78.143; Pandja near Kachu, Afghanistan); (D) *Alticola montosus* (BMNH 10.1.18.60; Mai Dunn, Kashmir, India); (E) *Alticola stoliczkanus* (PMS 4553; Makalu, Nepal). Scale bar = 5 mm.

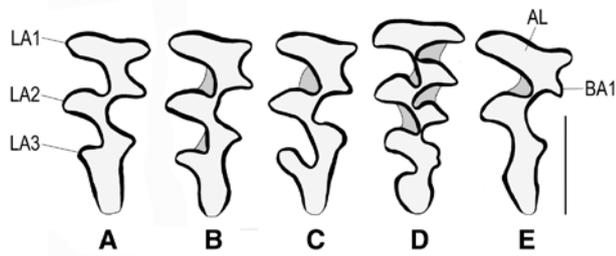


Figure 3: Occlusal surface of third upper molar M3 in mountain voles *Alticola*: (A) *Alticola roylei* (PMS 7098; Pisang, Dhukure Pokhari, Anapurna, Nepal); (B) *Alticola albicaudus* (NMNH 198531; Phyang Nullah Lake, Jammu and Kashmir, India); (C) *Alticola argentatus* (NMP 39791; Tirich Valley, Pakistan); (D) *Alticola montosus* (ZFMK 84.829; Liddar Valley, Pahalgam, Kashmir and Jammu, India); (E) *Alticola stoliczkanus* (ZFMK 84.813; Khumbu, Lobuche, Nepal). LA, lingual angle; BA, buccal angle; AL, anterior loop. Scale bar = 1 mm.

The taxonomic scope of *Alticola roylei* (Gray 1842) is summarized as follows:

Arvicola roylei Gray 1842: 265.

Type: BMNH 2002a, skin and skull. Type examined in June 2015.

Type locality as reported by Gray [“India (Chasmere)” i.e. Kashmir] is erroneous as *roylei* does not occupy Kashmir; see Wroughton (1914: 299) who argued that the type originates from “the higher Ranges of Kumaon”, Uttaranchal, India (cf. also Wroughton 1920: 59). Wroughton’s act of fixation was accepted by Hinton (1926: 313) and subsequent authors.

[Microtus] royliei Miller 1896: 54. Misprint of *roylei*.

Alticola roylei Hinton 1926: 310. First use of current name combination.

Alticola blanfordi lahulius Hinton 1926: 309.

Type: 26.3.1991, skin and skull. Type seen in June 2015.

Type locality: “Kyelang, Lahul, Altitude 10,380 feet”, Northern India.

Remark: Musser and Carleton (2005) synonymized *lahulius* with *Alticola argentatus*. The type is characterized by dark dorsal pelage and small bullae, and the type locality is well inside the range of *Alticola roylei*. We, therefore, propose *lahulius* as a junior synonym of *A. roylei*.

Alticola roylei cautus Hinton 1926: 313.

Type: 26.3.9.2, skin and skull. Type seen in June 2015.

Type locality: “Rahla, Kulu Valley, Lahul”, Himachal Pradesh, India.

We further examined 10 types in the collections of BMNH (June 2015) and ZIN (October 2014). These types represent three nominal species from the region; the subsequent synonymy is according to Rossolimo and Pavlinov (1992) and Musser and Carleton (2005).

Alticola argentatus (Severtsov 1879): *Arvicola blanfordi* Scully, 1880 (BMNH 8.3.9.17, skin and partly damaged skull); *Alticola worthingtoni* Miller 1906 (BMNH 5.12.4.110, skin and broken skull); *Microtus (Alticola) argurus* Thomas 1909 (BMNH 8.4.3.100, skin and skull); *Alticola phasma* Miller 1912 (BMNH 12.4.1.120, skin and skull); *Alticola worthingtoni subluteus* Thomas 1914 (BMNH 14.5.10.186, skin and skull). In its current scope, *A. argentatus* is paraphyletic, at least with respect to *Alticola albicaudatus* (Litvinov et al. 2015), and is in urgent need of revision. The inspection of the above type specimens, together with large series representing the majority of subspecific forms (e.g. Shenbrot and Krasnov 2005) retrieves this species to be a “garbage basket” rather than a natural taxon. None of the types we saw, however, can be aligned either with *A. roylei*, *Alticola montosus* or *Alticola stoliczkanus*.

Alticola montosus (True 1894): *Microtus imitator* Bonhote 1905 (BMNH 5.1.5.12, skin and broken skull).

Alticola stoliczkanus (Blanford 1875): *Arvicola stracheyi* Thomas, 1880 (BMNH 60.5.4.113, skin and broken skull); *Microtus (Alticola) lama* Barrett-Hamilton 1900 (BMNH 97.1.21.3, skin and broken skull); *Microtus kaznakovi* Satunin 1903 (ZIN 45002, skin and fragment of left maxilla with molars); *Microtus nanschanicus* Satunin 1903 (ZIN 6000, skin and skull).

Geographic scope

The classification of mountain voles as *Alticola roylei* has a long history of dispute and already Blanford (1891) discredited reports of his predecessors as improbable or wrong. The unsettled taxonomic scope disabled any mapping attempt. During the last decade however authors writing on the Royle’s mountain vole mainly agreed that the species is endemic to high elevations (2500–4300 m a.s.l.) in Himachal Pradesh and Uttarakhand in northern India (Agrawal 2000, Chakravarthy et al. 2005, Shenbrot and Krasnov 2005, Molur and Nameer 2008, Prakash et al. 2015). A closer look at the evidence, however, discloses important differences among contemporary studies. For example, Chakravarthy et al. (2005) identified only

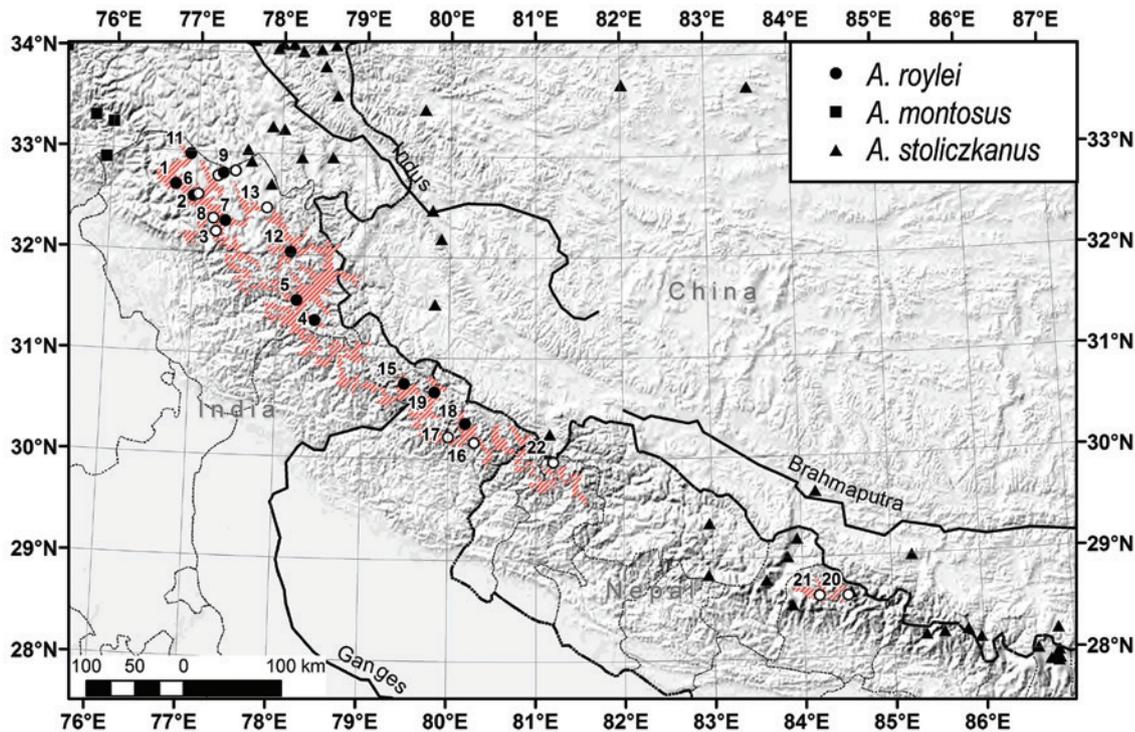


Figure 4: Localities of *Alticola roylei* in northern India and Nepal.

Suitable habitat is highlighted red. White circles indicate records with specimens examined by one of us. Localities and supporting references are the following: India, Himachal Pradesh: 1 – Chamba, Sindwan (Lewis 1981); 2 – Chamba, Tindi (Lewis 1981); 3 – Jagatsukh Nullah, Kulu Valley (BMNH); 4 – Kinnaur, Chitkul (Lewis 1981); 5 – Kunawar near Chini (Blanford 1891); 6 – Kyelang (type of *lahulius* BMNH; ZMMU); 7 – Lahul, Chhetru (Lewis 1981); 8 – Lahul, Kulu valley, Rahla [=Rahala] (type of *cautus* BMNH); 9 – Lahul, Panchina La [between Chenab and Lingti-Chu valleys] (NMW); 10 – Lahul, Patseo (NMW, ZMMU); 11 – Pattan [=Dhar Than Pattan] (Heptner and Rossolimo 1968); 12 – Spiti Valley, Guling (Museum of Zoology, University of Michigan); 13 – Spiti Pattan, Hansa (ZMMU); 14 – Zingzingbar (Heptner and Rossolimo 1968). India, Uttaranchal: 15 – Chamoli, Badrinath (Lewis 1981); 16 – Kumaon [the higher ranges; see comments in the taxonomic summary of *A. roylei*] (type of *roylei* BMNH); 17 – Kumaon, Pindar Valley, Phurkia (Wroughton 1914; Field Museum of Natural History, Chicago, USA); 18 – Martoli (Wroughton 1914); 19 – Nanda Devi NP, Chamoli (Chakravarthy et al. 2005). Nepal, Pashchimanchal: 20 – Manaslu (NMP); 21 – Pisang, Dhukure Pokhari (PMS). Nepal, Sudur Pashchimanchal: 22 – Seti, Garanphu (BMNH).

three localities of *A. roylei* and estimated the range at 20,000 km², while a simultaneous revision by Shenbrot and Krasnov (2005) retrieved 11 localities and estimated the area as encompassing 78,292 km², i.e. a four-fold difference between two existing sources.

After a careful examination of historical records and museum vouchers, we identified 22 localities as reliable evidence on the presence of Royle's mountain vole (Figure 4). The majority of records (14) were from Himachal Pradesh, five records came from Uttaranchal, and three localities are from Nepal. We saw museum specimens from 11 of these localities, and three of them were type localities (for *roylei*, *lahulius*, and *cautus*). As defined here, the range of Royle's mountain vole is stretching about 840 km across a rough and broken terrain from Chumba and Dhar Than Pattan in Himachal Pradesh (pts. 1, 2, and 11 in Figure 4) to Pashchimanchal in Central Nepal (pts. 20 and 21 in Figure 4).

The obtained habitat model demonstrates good performance (AUC=0.991). Environmental variables with the highest contribution in the model are winter (21.9%) and spring (17.6%) precipitation, spring NDVI value (15.7%), altitude (12.1%), and slope (9.7%). Logistic maximum training sensitivity plus specificity threshold equal 0.303. Summary area of occurrence of the species with this threshold is estimated as 15,290 km². This low estimate is evidently a consequence of the highly fragmented nature of the habitat of Royle's mountain vole. As is typical for mountain voles in general (Gromov and Erbajeva 1995) the Royle's mountain vole is also tied to rocky habitats above the tree line, and therefore its habitat is fragmented already at the landscape scale. In this respect, the Royle's mountain vole closely resembles other rock dwelling arvicolines, e.g. *Dinaromys bogdanovi* (Kryštufek and Bužan 2008) and snow voles *Chionomys* (Shenbrot and Krasnov 2005) which cope with naturally fragmented “continental

archipelagos" of accumulated rocks, cliffs, and escarpments (Kryštufek et al. 2015).

Uncertainties regarding the exact geographic scope of Royle's mountain vole abound on all sides of its range. As one can conclude from Figure 4 the species may be marginally present in China. The only mountain vole identified in the country along the border with Nepal, however, is *A. stoliczkanus* (Rossolimo et al. 1994, Zhang et al. 1997; see also Figure 4) which is morphologically clearly distinct from the Royle's mountain vole. To the east of Nepal, the Royle's mountain vole was reported for Arunachal Pradesh (Choudhury 2003, Kumawat et al. 2013) and Sikkim (Wroughton 1920, Choudhury 2003, 2013). Although our new records shift the known range of Royle's mountain vole eastwards into Central Nepal, the putative presence in Sikkim is still about 400 km away from the most exposed records, and the gap is double that distance for Arunachal Pradesh. Not surprisingly, any of these reports is quoted in present-day reviews of south Asian mammals (Chakravarthy et al. 2005, Prakash et al. 2015). The Royle's mountain vole was also reported from places to the west of Himachal Pradesh, namely in Jammu and Kashmir (Blanford 1891, Sclater 1891, Lewis 1981) and in northern Areas in Pakistan (Fakhri 2009). In the absence of vouchers, it is not possible to conclude how reliable these data are. Reports by Lewis (1981, 1981) e.g. predate the revision by Rossolimo and Pavlinov (1992) and certainly reflect a broad understanding of *Alticola roylei*.

Petrophilous small mammals coexist with difficulty and competing tandems of rock dwelling voles are only exceptionally found in sympatry (Kryštufek and Bužan 2008). This is probably also the situation with mountain voles. For example, *Alticola argentatus* is only marginally sympatric with *Alticola strelzowi* in Kazakhstan (Sludskiy et al. 1978) and does not co-occur with sympatric *Alticola stoliczkanus* in Qilian Mts. (Li et al. 2003). The Stoliczka's mountain vole and Royle's mountain vole have mutually exclusive distributions (Figure 4) and we recorded their sympatry only in Manaslu (Pt. 20 in Figure 4). Similarly, Schwartz (1938) found Stoliczka's mountain vole to be only marginally sympatric with *Alticola albicaudus* in Jammu and Kashmir (on Sobu). Furthermore, *Alticola roylei* is clearly allopatric against *Alticola montosus* (Figure 4) and we found no evidence of its co-occurrence with *A. albicaudus* and *A. argentatus*. Anyhow, before drawing a firm conclusion on spatial relationships of mountain voles much more sampling is needed in Himachal Pradesh, Jammu and Kashmir, and northern areas in Pakistan, where species diversity of *Alticola* voles is particularly high.

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