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Phylogeny and taxonomic reassessment of pikas *Ochotona pallasii* and *O. argentata* (Mammalia, Lagomorpha)

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Lissovsky, A.A., Yatsentyuk, S.P. & Ge, D. (2016). Phylogeny and taxonomic reassessment of pikas *Ochotona pallasii* and *O. argentata* (Mammalia, Lagomorpha). — *Zoologica Scripta*, *45*, 583–594.
We examined a cranial morphometric data set consisting of 186 specimens from the entire distribution range of *Ochotona pallasii* sensu lato and *O. argentata*, as well as 67 complete sequences of the COI gene and 28 sequences of the MGF and PRKCI introns from these and closely allied species. Our results show that the two allopatric morphologically similar taxa composing *O. pallasii* sensu lato – from Mongolia and adjacent territories and Kazakhstan – are paraphyletic relative to *O. argentata*. Genetic distances between these three taxa are larger than the intraspecific variation known for the subgenus *Pika*, in which the species under consideration belong; these distances are even larger than the interspecific differences among closely related species such as *O. hyperborea*, *O. mantchurica* and *O. hoffmanni*. Thus, the three focal taxa are recognized here as distinct species. Inspection of the type specimen of *O. pallasii* indicated that this specimen was not collected in Kazakhstan, has previously been theorized. The most probable place of the holotype's origin is Russian south-eastern Altai (Chuyskaya Steppe); whatever its exact origin, it definitively originates from the 'Mongolian' taxon. Based on this evidence, the senior synonym for the Kazakh pika is *O. opaca* Argyropulo, 1930. Thus, we propose to recognize three separate species in the *O. pallasii* species group: *O. pallasii* (Mongolia and adjacent territories), *O. opaca* (eastern Kazakhstan) and *O. argentata* (Helan Shan Range, China).
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Introduction

Two species of pikas inhabiting the Gobi Desert belt of Inner Asia, *Ochotona pallasii* (Gray 1867) and *O. argentata* Howell, 1928, belong in the subgenus *Pika* Lácèpede, 1799, together with the rock-dwelling northern Asian species from the *O. alpina* species group, Nearctic *O. princeps* (Richardson, 1828) and *O. collaris* (Nelson, 1893) (Yu *et al.* 2000; Lanier & Olson 2009; Lissovsky 2014; Melo-Ferreira *et al.* 2015). Until recently (Lissovsky *et al.* 2007), *O. pallasii* and *O. argentata* were not recognized as closely related species. *Ochotona argentata* was described as and has long been considered a subspecies of *O. alpina* (Pallas, 1773) (Ellerman & Morrison-Scott 1951; Smith *et al.* 1990; Hoffmann 1993). Subsequently, it was suggested that *O. argentata* was a distinct species, on account of its coloration, skull morphology, karyotype and bioacoustics, with *O. p. helanshanensis* Zheng, 1990 as a junior synonym (Formozov *et al.* 2004; Erbajeva & Ma 2006). Yu *et al.* (2000) found that *O. argentata* (as *O. p. helanshanensis*) was a sister taxon to *O. pallasii*. The karyotype of *O. argentata* was also found to be similar to *O. pallasii* in diploid number and the number of meta- and subtelocentrics, differing only in the size of the second pair of autosomes – which is larger in *O. argentata* – and the structure of the Y-chromosome (Formozov *et al.* 2004).

Ochotona pallasii (sensu Ognev 1940; Ellerman & Morrison-Scott 1951; Smith *et al.* 1990; Hoffmann 1993; Sokolov *et al.* 1994; Hoffmann & Smith 2005) consists of four geographically separated subspecies: two with a larger distribution, *O. p. pallasii* (Kazakhstan) and *O. p. pricei* Thomas, 1911 (Mongolia and bordering territories), and two little-studied, restricted range populations, usually listed as subspecies: *O. p. hamica* Thomas 1912 (known only from type series, collected in the most eastern spur of the Tian

Shan Mountains, north of Hami, China) and *O. p. sunidica* (known from a small distribution range on the Chinese–Mongolian border near Erenhot, China). A mitochondrial study found that the two larger subspecies of *O. pallasii* were paraphyletic to *O. argentata* (Lissovsky *et al.* 2007). Morphometric data, however, have shown that *O. p. pallasii* and *O. p. pricei* are more similar to each other than to *O. argentata* (Lissovsky 2014). The pelage of *O. argentata* differs from that of the other taxa in its rufous coloration in summer and silver coloration in winter (Formozov *et al.* 2004; Erbajeva & Ma 2006; Lissovsky 2014). Because mitochondrial data sometimes give biased results in lagomorphs (Alves *et al.* 2006; Lissovsky 2014), it was hypothesized that the taxonomic rank of these three taxa could be resolved on the basis of enhanced data set, including nuclear genes.

The primary aim of this study was therefore to evaluate the taxonomic rank of *O. argentata* and the Kazakh population of *O. pallasii*. For this purpose, we analyse the extended data set of morphological data from the entire distribution of *O. pallasii* and undertake a phylogenetic analysis of the taxa in question using mitochondrial and nuclear genes. In addition, we discuss nomenclatorial problems associated with the names of these taxa in order to develop a meaningful and stable taxonomy.

Materials and methods

Morphometric analysis

We examined *O. pallasii sensu lato* and *O. argentata* in the collections of the Zoological Museum of Moscow University (ZMMU, Moscow, Russia); the Zoological Institute of the Russian Academy of Sciences (ZIN, Saint-Petersburg, Russia); the Natural History Museum (NHM, London, UK); the Institute of Zoology, Chinese Academy of Science (IOZCAS, Beijing, China); the Northwest Institute of Plateau Biology of the Chinese Academy of Science (NWIPB, Xining, China); the American Museum of Natural History (AMNH, New York, NY, USA); the Smithsonian Institution (SI, Washington, DC, USA), and the Field Museum of Natural History (FMNH, Chicago, IL, USA).

The sample consisted of 186 intact skulls (Fig. 1, Appendix S1). This number includes type series of *Ochotona* (*Ogotoma*) *pricei* Thomas, 1911; *Ochotona* (*Ogotoma*) *hamica* Thomas 1912; *Ochotona pricei opaca* Argyropulo, 1930; and *Ochotona pallasi sunidica* Ma *et al.*, 1980 (Appendix S1). *Ochotona helanshanensis* Zheng, 1990 was studied using topotypes. Holotypes of two nominal taxa, *Ogotoma pallasii* Gray 1867 and *Ochotona* (*Pika*) *alpina argentata* Howell, 1928, have broken skulls, and thus, some measurements were unavailable for these specimens.

Twenty measurements (Lissovsky 2014) were taken on each skull using callipers with an accuracy of 0.01 mm: condylobasal length (KBD), length of palatine foramen (DNOTV), upper diastemal length (DIAST), alveolar length of the maxillary toothrow (DVKR), rostral length (from the anterior edge of the premaxillary bones to the posterior edge of the maxillary toothrow alveoli) (DLITS), length of auditory bulla (DBAR), distance between auditory bullae (RMB), length of the suture between the parietal bones (DTEM), length of the suture between the frontal

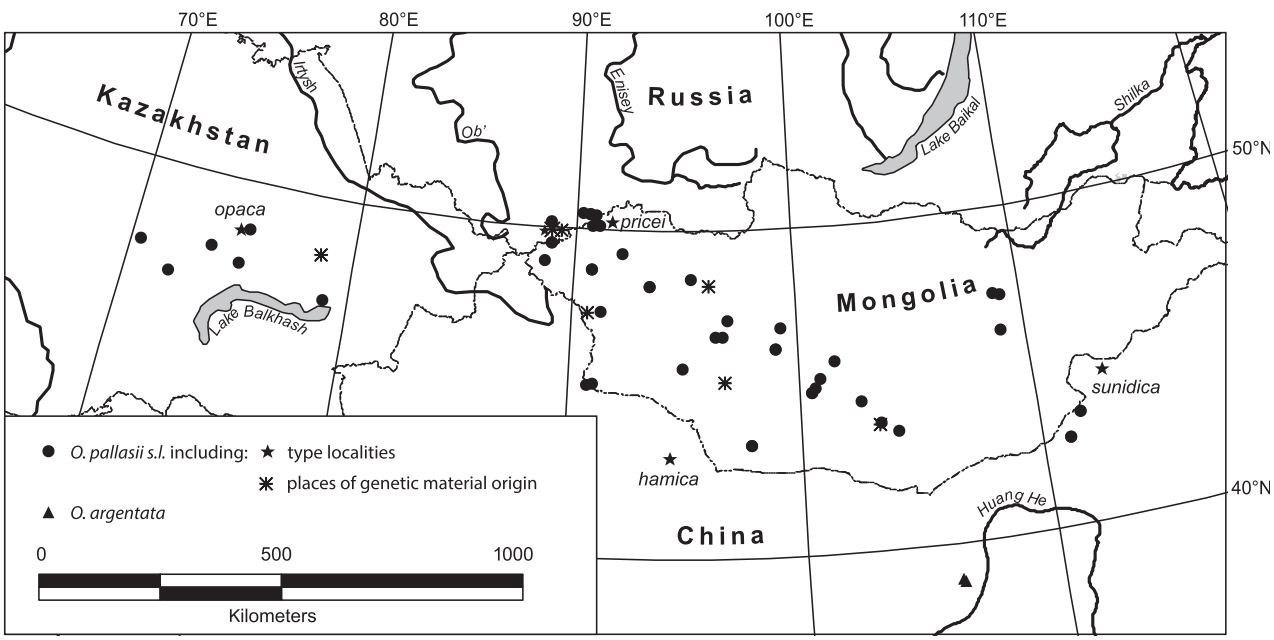

Fig. 1 Geographical distribution of studied material.

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bones (DLOB), maximal length of orbit (DG), maximal width of orbit (WG), interorbital constriction (MG), width of the rostrum between the maxillary openings (WN), zygomatic breadth (SKW), postorbital constriction (ZG), maximal width between the lateral edges of the auditory bullae (WSLB), general skull height (H), skull height on the level of the auditory bullae (HBAR), general height of mandible (HNCH) and the height of the mandible behind the toothrow (HZ). All calculations were carried out on log 10-transformed measurements in order to linearize age variation (Mina & Klevezal 1976).

Sexual dimorphism was ignored because it was not found in pika skulls after age bias was excluded (Lissovsky 2014). Age was assigned to one of three groups: (i) obvious juvenile with undeveloped crests on the mandible and arc-shaped profile of the skull, together with shortened nasals; (ii) subadults with fully developed skull profile, but with undeveloped crests on the mandible; and (iii) adults (Lissovsky 2004).

To exclude age bias, we used an orthogonal projection of the initial data along the vector of age variation (Burnaby 1966). The vector of age variation was calculated as the first eigenvector of the between-group covariance matrix computed with a nested two-factor MANOVA, in which the variable containing the three age gradations and the identifier of the geographical sample were used as the grouping variables. The age factor was nested in the geographical sample. We used five samples with more than two specimens in each age class and only used age classes 1 and 3 to calculate the covariance matrix in order to minimize errors arising from the inaccuracy in the determination of age class 2 (Lissovsky 2004; Obolenskaya *et al.* 2009).

The samples for hierarchical cluster analysis included only specimens collected in the same locality. Only samples with $n > 2$ were used in the cluster analysis (21 samples, Appendix S1). Cluster analysis was performed on the basis of a matrix of Mahalanobis distances using the unweighted pair group method with arithmetic mean. The bias induced by using samples of different sizes was corrected (Marcus 1993).

The following approach was applied as an ordination method: first, the eigenvectors of the between group covariance matrix (with geographical samples as groups) of the data set with reduced age were calculated. Secondly, the initial data matrix was multiplied with the matrix of the eigenvectors. Thus, the initial data were rotated into the space of intergroup variation without distortion of the initial space (Obolenskaya *et al.* 2009).

The position of the incomplete skulls of the holotypes of *O. pallasii* and *O. argentata* in the multidimensional space of craniometric features was determined using canonical discriminant analysis. Because these two specimens lack different measurements, we carried out two independent analyses with each of the holotypes. Taxon label (*O. pallasii* from Kazakhstan; *O. pallasii* from Mongolia and adjacent territories; *O. argentata*) was used as the grouping variable for all specimens, excluding the holotype under study. The posterior probability of assignment of the holotype to one of the three taxa was predicted.

Standard modules of Statistica, version 8 (Statsoft Inc., Tulsa, OK, USA), as well as algorithms written by the first author in Statistica Visual Basic, were used in the cranial morphometric analyses.

Genetic analysis

Sequences of the cytochrome C oxidase subunit 1 (COI) gene (657 bp); one nuclear intron of protein kinase C iota (PRKCI) (with alignment 784 bp); and the mast cell growth factor (MGF) nuclear intron (with alignment 612 bp) of representatives of the subgenus *Pika* were analysed in this study. The list of specimens with GenBank accession numbers is in Appendix S2.

Total genomic DNA was extracted from 5 mg samples using a DNA-sorb-C kit (InterLabService Ltd., Moscow, Russia). The genes were amplified by polymerase chain reaction and sequenced using primers: COI – VF1d (TTCTCAACCAACCACAARGAYATYGG) + VR1d (TAGACTTCTGGGTGGCCRAARAAYCA) (Ivanova *et al.* 2006); PRKCI – PRKCI-F (AAACAGATCGCATTTATGCAAT) + PRKCI-R (TGTCTGTACCCAGTCAATATC) (Matthee *et al.* 2004); MGF – MGF-F (AAATATCAGTCTTGAATCTTAC) + MGF-R (TTTTAGATGAATTACAGTGTCC) (Matthee *et al.* 2004) or MGF-F1 (ACGCATCTCCAACTTTATT) + MGF-R1 (TGCGTCAGTGTTATATGGTTTTA). We amplified PRKCI under the following conditions: 94 °C for 3 min, 42 cycles of 94 °C for 10 s, 55 °C for 10 s and 72 °C for 10 s and 1 cycle of 94 °C for 10 s, 55 °C for 10 s and 72 °C for 3 min. The PCR conditions for MGF were as follows: 94 °C for 3 min followed by 42 cycles of 94 °C for 20 s, 48 °C for 20 s and 72 °C for 20 s. The final 3-min elongation step was at 72 °C. Amplification of the COI gene was performed in one cycle consisting of 5 min at 94 °C, followed by 42 cycles consisting of 10 s at 94 °C, 10 s at 63 °C and 10 s at 72 °C, with a final 3-min elongation step at 72 °C using a Tercic Thermal Cycler (DNA-Technology, Russia). Sequences were assembled in Geneious 8.1.5 for Windows (http://www.geneious.com, Kearse *et al.* 2012) and aligned manually using the program Bioedit 7.2.5 (Hall 1999).

Nuclear loci demonstrated some heterozygous nucleotide positions. Only the PRKCI sequences contained insertions and deletions, and allelic haplotypes were determined easily in all cases from overlapping sequences (Flot *et al.* 2006).

Eight MGF sequences had one heterozygous site, and four sequences had more than one such site. All these four cases were represented by one specimen per species only; therefore, we always had sequences from the same species without multiple heterozygous sites for comparison. MGF haplotypes were reconstructed for each individual using PHASE v2.1 (Stephens & Donnelly 2003), implemented in DnaSP v5.10.01 (Librado & Rozas 2009), with output probability threshold of 0.9. Gaps were coded using FastGap 1.2 (Borchsenius 2009) and were used as a separate binary data partition in Bayesian analysis (Ronquist *et al.* 2011).

We used *O. pusilla* Pallas, 1769 and *O. curzoniae* (Hodgson, 1858) as an outgroup as these species were shown to be external to the group under study (Lissovsky 2014; Melo-Ferreira *et al.* 2015).

Phylogenetic analyses were performed on individual locus data sets as well as a combined data set with all three loci concatenated. Maximum-likelihood (ML) analyses, including selection of the optimal model of molecular evolution, phylogenetic reconstruction, calculation of patristic distances and bootstrapping, were performed using Treefinder (Jobb 2011). The Akaike information criterion was used to determine the most appropriate model of molecular evolution in the Propose Model dialog. Standard deviations of ML distances and bootstrap values were calculated using 1000 replicates. Nucleotide substitution models are listed in Table S3.

A Bayesian analysis for each data set was performed in MrBayes 3.2.5 (Ronquist *et al.* 2012) with 50 000 000 generations [the standard deviations of split frequencies were below 0.0015; potential scale reduction factors were equal to 1.0; stationarity was examined in Tracer v1.6 (Rambaut *et al.* 2014)], two runs with five independent chains, a sampling frequency of 5000 and the GTR + I + Γ model. The model was selected as the next more complex model after Treefinder results available in MrBayes (Ronquist *et al.* 2011). The heating parameter was selected in preliminary runs following Ronquist *et al.* (2011). It was set to 0.1 (default value) in the analyses of MGF and PRKCI and to 0.01 in the analysis of COI and combined data set.

A Bayes factor comparison (Nylander *et al.* 2004) for COI showed that the codon-partitioned model was not positively better than the single partition model [2*ln (B_{10}) = 0.219] and only the results of the single partition model were used. The MGF and PRKCI were analysed as a single partition each. Combined data set was gene-partitioned. The first 25% of generations were discarded as burn-in. Maximum clade credibility trees were constructed using TreeAnnotator v2.2.1.

We did not separate *O. alpina* and *O. turuchanensis* in calculations of intergroup distances, because phylogenetic relationship of these two species slightly disagrees in two nuclear genes and needs additional investigation. Such an investigation was not part of the aim of this study.

Results

Morphology

All the specimens studied displayed a high degree of morphological similarity (Table 1). The first two components of the intersample variation (Fig. 2) explain 32% and 14% of overall variance, respectively. Specimens of *O. argentata* tend to form a distinct morphological group (Figs 2 and 3). The pikas from Kazakhstan were weakly separated from the Mongolian specimens; it appears that methods used cannot resolve this taxon completely. The samples from the type localities of *hamica* and *sunidica* do not segregate from pikas from Mongolia with adjacent territories in our analysis.

From the perspective of species identification, *O. argentata* has wider interorbital constriction than other taxa (Table 1). The Kazakhstan taxon and *O. argentata* differ in KBD, DLITS, DLOB, SKW: *O. argentata* is always bigger. The more widely distributed Mongolian taxon shows a greater degree of variation in all characteristics examined; its variation overlaps completely with the variation of the Kazakhstan taxon and differs from *O. argentata* only in above-mentioned interorbital constriction. Thus, the Mongolian and Kazakhstan taxa could be considered sibling forms solely on the basis of cranial measurements.

Pikas from Chuya (SE Altai) and pikas from the type locality of *O. pricei* (including the holotype) (i.e. mountains W of the Achit Nor in NW Mongolia) were situated very closely in the dendrogram (Fig. 3, 'KoshAgach_pa' and

Table 1 Cranial measurements of adult specimens of recognized taxa from *Ochotona pallasii* group: Mean ± SD (Min–Max)

	N	KBD	MGLW	SKW	WSLB	H
argentata	7	45.6 ± 0.6 (44.7–46.5)	4.9 ± 0.2 (4.7–5.2)	24.1 ± 0.3 (23.7–24.4)	20.5 ± 0.7 (19.6–21.7)	16.9 ± 0.3 (16.5–17.3)
pallasii s.l. (Kazakhstan)	8	42.6 ± 1.2 (40.6–44.7)	3.8 ± 0.2 (3.3–4.1)	22.9 ± 0.3 (22.6–23.6)	19.3 ± 0.3 (18.9–19.8)	16.2 ± 0.6 (15.1–16.8)
pallasii s.l. (Mongolia, etc)	61	44.1 ± 1.5 (41–47.1)	3.7 ± 0.4 (2.7–4.4)	23.6 ± 0.7 (22.1–25.6)	20.3 ± 1 (18–22.3)	16.4 ± 0.4 (15.4–17.4)
sunidica	16	43.4 ± 1.6 (40.9–46.5)	4 ± 0.4 (3.2–4.8)	23.3 ± 0.7 (22.5–24.4)	19.5 ± 0.5 (18.7–20.4)	16 ± 0.4 (15.3–16.6)
hamica	4	45.4 ± 1.2 (44.3–46.5)	4.1 ± 0.1 (4–4.2)	24.7 ± 0.4 (24.2–25.2)	20.8 ± 0.8 (19.6–21.5)	16.9 ± 0.2 (16.7–17.2)

'Ur_Achit_pa', respectively). The posterior probability of the assignment of the holotype of *O. pallasii* to the taxon from Mongolia and adjacent territories is equal to 1.00 (Fig. S1). The holotype of *O. argentata*, which was not included in the training sample, is situated in the same cloud with other pikas from the Helan Shan Mountains, including the topotypes of *O. helanshanensis* (Fig. S2). Thus, there is no reason to suggest existence of two separate taxa (*argentata* and *helanshanensis*) in the Helan Shan Mountains.

During our investigation of *O. argentata* specimens in IOZ, we found that one of the skulls (30886) was identified erroneously and belongs in fact to *O. mantchurica* (Lissovsky 2014). The skin of this specimen belongs undoubtedly to *O. argentata*. We did not find any signs that specimens were mixed in the Beijing collection: all of the ID numbers and labels point to the fact that the skin and the skull of the specimen came together. According to the opinion of Prof. Ma, who donated this series to IOZ, it is most probable that the collector from Huh Hotto, who also collected in the distribution range of *O. mantchurica*, confused the skull. This specimen was not mentioned in the paper of Formozov *et al.* (2004); however, Erbajeva & Ma (2006) based their discussion partly on this specimen.

Genetics

All pairs of trees resulted from Bayesian and ML analyses were very similar in topology; however, ML bootstrap values were always lower than corresponding values of Bayesian posterior probabilities (*100). Our result derived from the COI gene (Fig. 4) obtains unresolved relations between *O. pallasii* and *O. argentata*. The two nuclear introns are not in agreement as to the sister taxon relationships of *O. argentata*. The MGF gene unites *O. argentata* with *O. pallasii* from Kazakhstan with a high posterior probability (Fig. 5). The PRKCI gene in contrast joins *O. argentata* with *O. pallasii* from Mongolia with posterior probability 1.0 (Fig 6 and S3). The combined data set also joins *O. argentata* with *O. pallasii* from Mongolia with

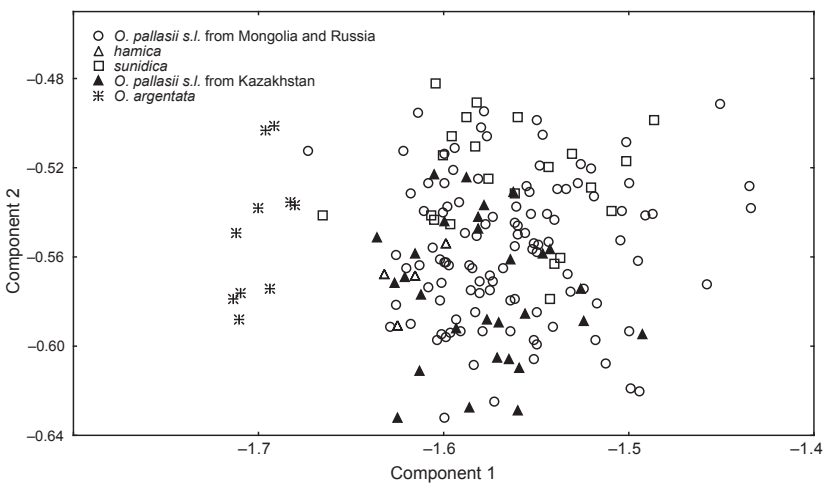

Fig. 2 Distribution of the pika specimens in the space of maximized between-sample craniometric differences.

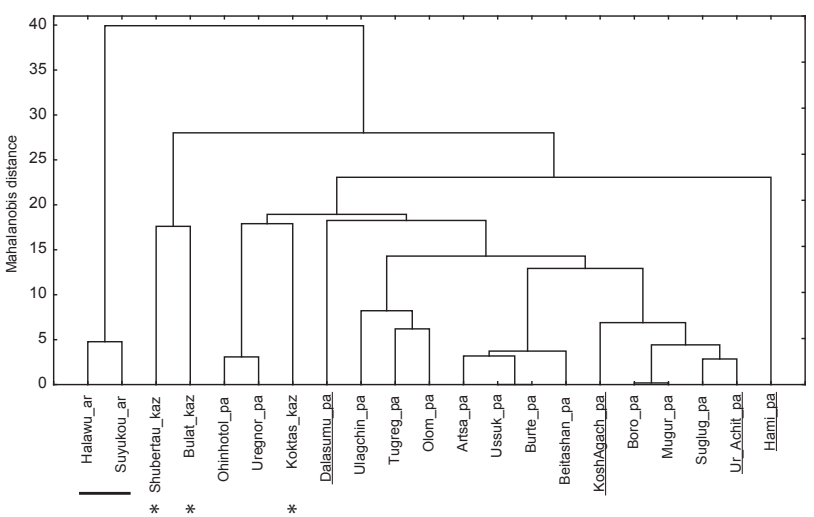

Fig. 3 Dendrogram showing results of hierarchical cluster analysis of craniometric features of geographical samples of *Ochotona pallasii* s.l. and *O. argentata*. Samples of *O. argentata* are marked with horizontal line; samples from Kazakhstan are marked with asterisk; samples, containing holotypes of pricei, hamica, sunidica and proposed topotypes of *pallasii*, are underlined. For explanation of sample labels, refer to Appendix S1.

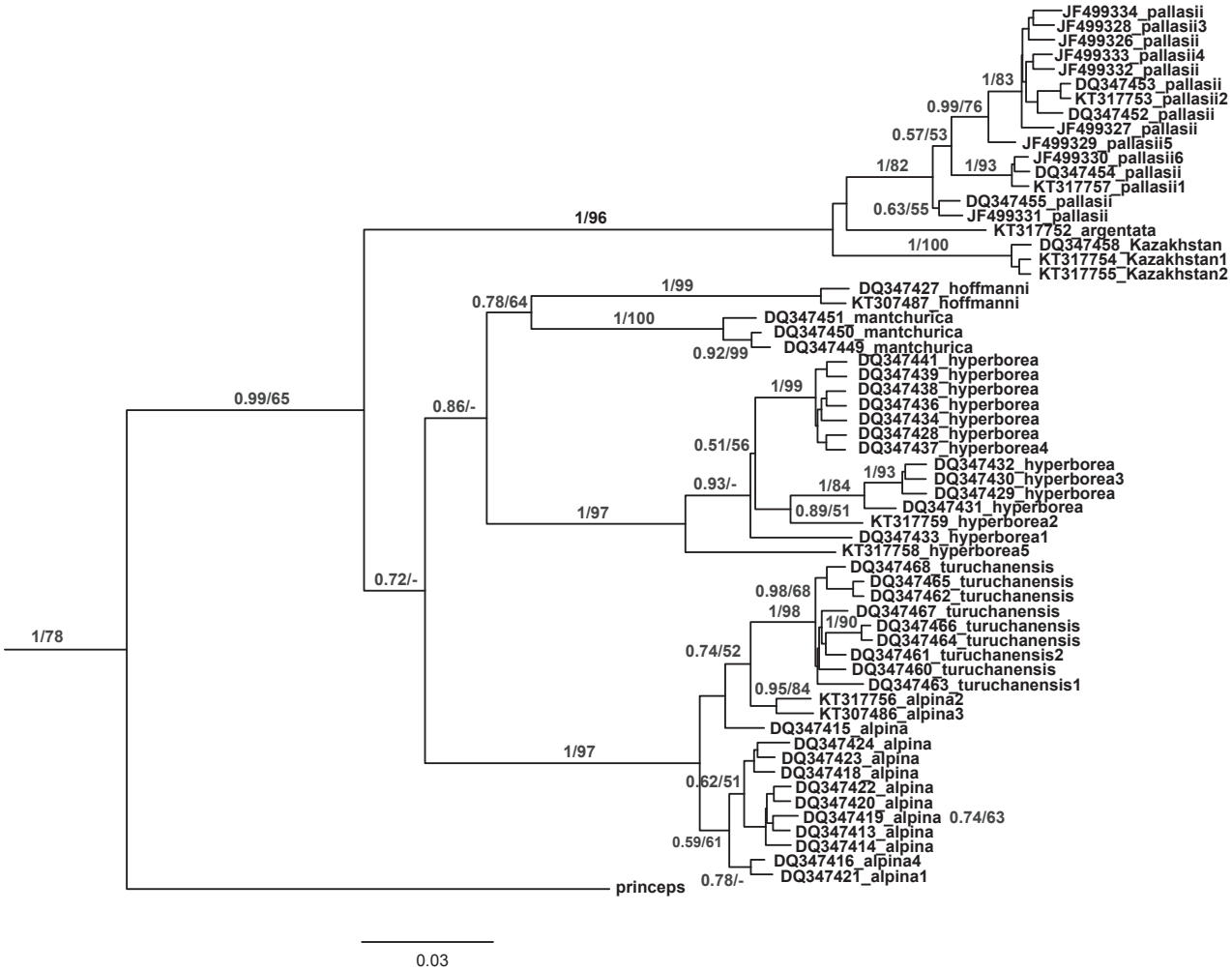

Fig. 4 Maximum clade credibility tree of Bayesian analysis based on COI sequences. Numbers on branches indicate Bayesian probabilities/ML bootstrap values. Outgroup is not shown. For explanation of labels, refer to Appendix S2.

posterior probability 1.0 (Fig. S4). Thus, nuclear genes agree on the paraphyletic status of *O. pallasii* relative to *O. argentata*, and COI does not resolve this group.

Maximum-likelihood distances among taxa are listed in Table 2. The average within-group distances in *O. princeps* were 1.2 ± 0.8% (PRKCI) and 0.1 ± 0.1% (MGF), whereas those in *O. hyperborea* (Pallas, 1811) were 0.5 ± 0.4% (PRKCI) and 0.1 ± 0.1% (MGF).

The subgenus *Pika* is well supported by the PRKCI gene; however, this gene does not support the monophyly of *O. hyperborea*, *O. mantchurica* Thomas, 1909, or *O. hoffmanni* Formozov, Yakhontov, and Dmitriev, 1996. The MGF gene supports a subgenus *Pika* in Bayesian analysis only (with posterior probability 0.79), but does not differ between closely related *O. hyperborea*, *O. mantchurica* and *O. hoffmanni*. The internal structure of subgenus *Pika* is also conflicting in two genes.

Nomenclature

Taxon *pallasii* was described by Gray (1867). The entire description is cited below.

'1. Ogotoma. Skull: the orbits very large; space between the orbits narrow; nose narrow, bent down.

Ogotoma Pallasii. (*Lagomys ogotoma*, Cuvier, Waterh. Glir. 17. *Lepus ogotoma*, Pallas, Glires, 30, t. 3, 4 a. f. 16a.) B.M.' (Gray 1867: 220).

Thus, Gray describes a new genus, *Ogotoma* (distinguishing it from *Lagomys*), and a new species, *O. pallasii*. In parentheses are references to publications (some with page or table numbers), describing '*Lagomys ogotoma*' (Cuvier 1817; Waterhouse 1848) and '*Lepus. ogotoma*' (Pallas 1778). 'B.M.' indicates that the specimen is in the collection of the British Museum. In the book cited above, Waterhouse (1848) gave a description of the *L. ogotona* Pallas, 1778 specimen from the collection of the British Museum.

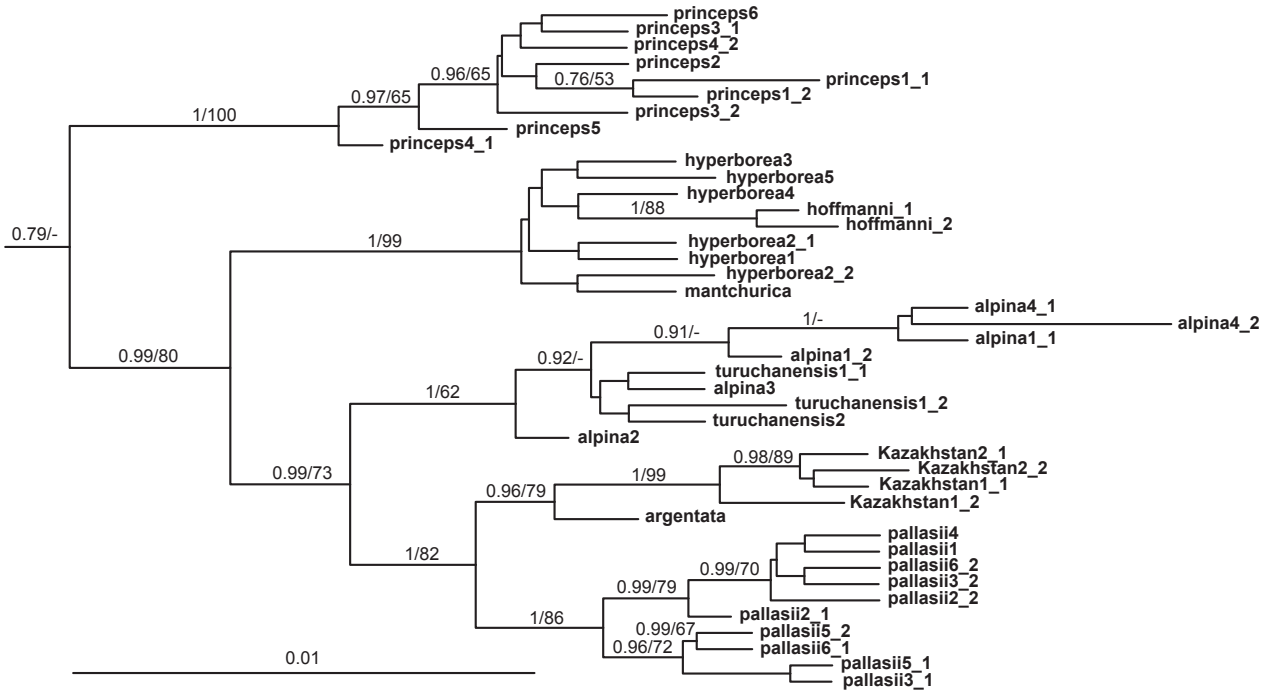

Fig. 5 Maximum clade credibility tree of Bayesian analysis based on MGF sequences. Numbers on branches indicate Bayesian probabilities/ML bootstrap values. Outgroup is not shown. For explanation of labels, refer to Appendix S2.

It should be noted that Pallas and Waterhouse (Pallas 1778; Waterhouse 1848) used '*ogotona*' and not '*ogotoma*'. Thus '*ogotoma*' as a specific epithet in Gray's description constitutes an incorrect subsequent spelling. Another incorrect subsequent spelling was used by Cuvier (1817: 212): '*ogotonna*'. Waterhouse (1848) and Bonhote (1904) wrongly applied the name '*ogotona*' through misidentification. These authors blended Pallas's and Daurian pikas (in modern understanding) together under the name *Lagomys ogotona*; they provided distribution of Daurian pika, *O. dauurica*, after Pallas (1778) and the morphological description of the single specimen of *O. pallasii* from the British Museum. Thus, according to Art. 49 (International Commission on Zoological Nomenclature 1999), the names *ogotona* Waterhouse, 1848 and *ogotona* Bonhote, 1904 cannot be used as available names for *O. pallasii*, as wrongly applied to denote a species-group taxon because of misidentification. Consequently, the names *ogotona* Waterhouse, 1848 and *ogotona* Bonhote, 1904 erroneously marked in Hoffmann & Smith (2005) as junior synonyms of *O. pallasii* (wherein there also is listed an erroneous date for Bonhote's paper: although listed as '1905' in the publication, it was on fact published 15 of November 1904).

There is in fact no mention of any exact specimen in the original description of *O. pallasii* by Gray (1867). Bonhote (1904) wrote that he examined only one individual 'of this species' (he wrote about *O. ogotona* as he understood it, but explicitly cited *O. pallasii* as a synonym). Thomas (1908) also explicitly wrote about only one specimen, described by Waterhouse, Gray and Bonhote. We also found only one specimen of *O. pallasii* (and none of *O. dauurica* Pallas, 1776 = *O. ogotona*) collected before the 20th century in the collection of the NHM. The specimen with numbers 537a and 45.12.22.10 (the number of the skull) on the skull and 45.4.21.5 on the label (the number of the stuffed skin) were marked with red ink. This specimen was first mentioned as the 'type' of *O. pallasii* by Thomas (1908). Thus, the initial description by Gray was based on the single specimen (45.4.21.5), which is the holotype fixed by monotypy (Art. 73.1.2, 72.4.1.1; ICZN 1999).

Another major issue is the place of origin of said holotype of *O. pallasii*. The specimen came to the NHM between 1843 (it is absent in Gray (1843) catalogue) and 1845 (when it was registered). The original label contains only one word: 'Russia'. The register entry for 1845.4.21.5 is: 'stuffed skin. Asiatic Russia, Keigisen (or Kigisen in different handwriting)' (P. Jenkins pers. com.). Thomas (1908: 109) stated that 'the Museum specimen No. 45.4.21.5, which was bought from the dealer Brandt under the name vof *Lagomys ogotona*, and said to come from 'Asiatic Russia – Kirgisen'.

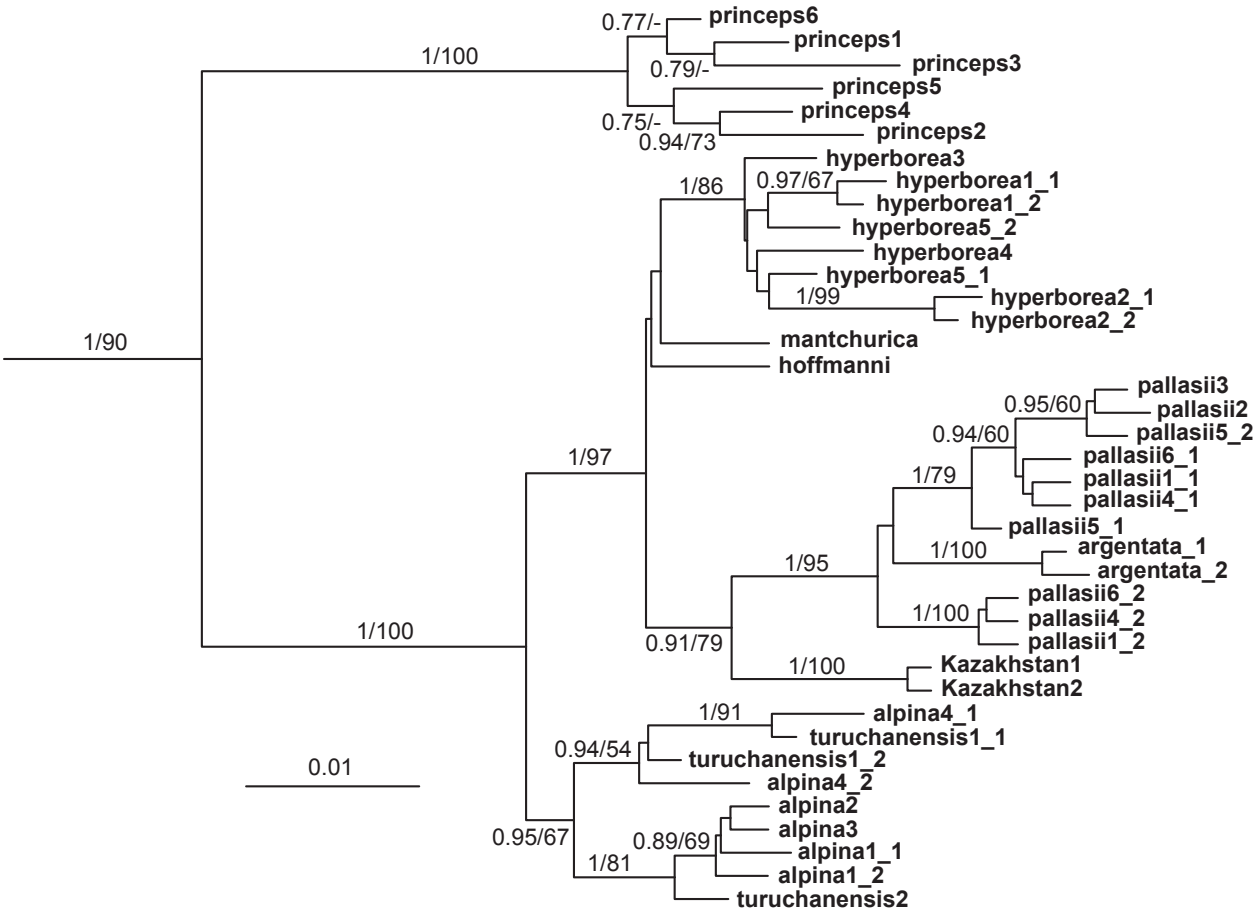

Fig. 6 Maximum clade credibility tree of Bayesian analysis based on PRKCI sequences, gap information excluded. Numbers on branches indicate Bayesian probabilities/ML bootstrap values. Outgroup is not shown. For explanation of labels, refer to Appendix S2.

Table 2 Maximum-likelihood patristic distances between group (%, ±SD) in pikas species calculated on the basis of mast cell growth factor (below diagonal) and protein kinase C iota (above diagonal) genes

	O. pusilla	*O. princeps*	*O. hyperborea*	*O. hoffmanni*	*O. mantchurica*	*O. alpina* + *O. turuchanensis*	*O. argentata*	*O. pallasii* (Kazakhstan)	*O. pallasii* (Mongolia, etc)
O. pusilla		7.03 ± 2.21	6.87 ± 2.64	6.73 ± 2.5	6.73 ± 2.5	6.55 ± 2.53	7.98 ± 3.21	7.38 ± 2.82	7.68 ± 3.16
O. princeps	3.73 ± 1.49		5.7 ± 1.9	5.56 ± 1.77	5.56 ± 1.91	5.37 ± 1.85	6.8 ± 2.45	6.21 ± 2.08	6.51 ± 2.32
O. hyperborea	4.28 ± 1.84	2.97 ± 1.51		0.94 ± 1.18	0.94 ± 0.6	1.82 ± 1.33	2.19 ± 1.29	1.6 ± 0.9	1.89 ± 1.23
O. hoffmanni	3.98 ± 1.65	2.68 ± 1.32	0.37 ± 0.26		0.79 ± 1.04	1.68 ± 1.19	2.05 ± 1.75	1.45 ± 1.36	1.75 ± 1.7
O. mantchurica	3.96 ± 1.61	2.65 ± 1.28	0.04 ± 0.03	0.35 ± 0.23		1.68 ± 1.19	2.05 ± 1.18	1.45 ± 0.79	1.75 ± 1.12
O. alpina + *O. turuchanensis*	4.3 ± 2.11	2.99 ± 1.78	2.42 ± 1.37	2.72 ± 1.56	2.4 ± 1.33		2.92 ± 1.91	2.33 ± 1.51	2.63 ± 1.85
O. argentata	3.93 ± 2.02	2.62 ± 1.68	2.05 ± 1.27	2.35 ± 1.46	2.03 ± 1.24	1.71 ± 1.26		2.2 ± 1.05	1.16 ± 1.02
O. pallasii (Kazakhstan)	4.43 ± 2.2	3.12 ± 1.87	2.55 ± 1.45	2.85 ± 1.64	2.53 ± 1.42	2.21 ± 1.44	0.83 ± 0.52		1.9 ± 1.1
O. pallasii (Mongolia, etc)	4.16 ± 2.16	2.86 ± 1.83	2.29 ± 1.42	2.59 ± 1.61	2.27 ± 1.38	1.94 ± 1.41	0.9 ± 0.83	1.4 ± 1.01	

The first person who placed *O. pallasii* in Kazakhstan was Heptner (1941). All previous authors who revised this pika gave the name *O. pricei* to the taxon under discussion and wrote about *O. pallasii* as a doubtful taxon, one originating from an unknown place (Thomas 1912; Argyropulo 1932; Ognev 1940). Heptner did not study the holotype of

O. pallasii; his statement: 'in the same locality [Karkaralinsk Mountains] Brandt's material was procured and sent to the British Museum and that this form must be considered as nominal' was not supported by any analysis.

Pallas' pikas were found in Kazakhstan in the late 1920s for the first time. They were described by Argyropulo (1932), who did not give them any name 'up to clarification of taxonomic position of *Och. pallasii*'. However, Argyropulo later described *O. pricei opaca*, which is the senior synonym for Pallas's pikas from Kazakhstan (Argyropulo 1939).

We cannot find any mammal specimens collected by Russian explorers from the modern range of *O. pallasii* in Kazakhstan before 1845 in the ZIN and ZMMU collections. Altai, however, was explored by a number of investigators (Strauch 1889). One of them, P. Romanov, a laboratory assistant of Eversmann, collected several specimens of *O. pallasii* on the Chuya River (SE Altai) in 1841 (Garanin 2002). Eversmann identified these specimens as *Lagomys ogotona*. Three specimens from this series are now in the ZIN (nos. 68976, 68977 and 69094); they were bought in 1877 together with the large collection of Eversmann after the latter's death (Strauch 1889). These three specimens, collected before 1845, are the only *O. pallasii* specimens found in Russian collections.

J.G.W. Brandt, from Hamburg, who sold pikas to the NHM, was a dealer in taxidermy specimens (Stresemann 1967), who intensively traded with Russian collectors and a number of European museums, including the NHM in London. Eversmann had some trade relations with J.G.W. Brandt; at least one specimen of *O. pusilla* (1845.4.21.6) collected by P. Romanov was sold to the British Museum; another specimen of *O. alpina* was sold to Heidelberg (Hutterer & Peters 2010). Consequently, there is a high probability that the specimen identified as *Lagomys ogotona* that came to London in early 1840s was collected by Romanov for Eversmann and arrived via J.G.W. Brandt.

Another nomenclaturally complicated nominal taxon is *Ochotona helanshanensis* Zheng, 1990. The initial description was published in a book by Wang (1990) as '*Ochotona helanshanensis* Zheng, 1987 sp. nov'. There is a footnote associated with the description: 'Zheng Tao named and described this species'. Any explanation of the contradictory combination of '1987' and 'sp. nov.' is absent. There is no information about any mention of *O. helanshanensis* published in 1987. Most probably, '1987' is an erroneous indication of the date, when the unpublished description was compiled. As a result, we suggest using the name and date combination '*O. helanshanensis* Zheng, 1990', following Formozov *et al.* (2004), until the 1987 publication is found or clarified.

There is one additional name that has not been listed in connection with *O. pallasii* previously: *O. pusilla angustifrons* Argyropulo 1932. The holotype ('type' in the original publication) of this taxon is ZIN number 17421. The skin of this specimen belongs to *O. pusilla* (Pallas, 1769), while the skull is from *O. pallasii*. The composite nature of the specimen was first discovered by Erbajeva (1988). Subsequently, the skull of the specimen was re-numbered as 68975. It is clear from the original description that Argyropulo described the Steppe pika with some peculiarities (derived from an erroneous identification of the skull) and not deviating Pallas's pika. Both paratypes mentioned in the paper apparently belong to *O. pusilla*. Erbajeva (1988) suggested considering the skin of the specimen as a lectotype and the skull as paralectotype. This action does not, however, fit the rules of the Code; we suggest in contrast excluding the skull from the holotype of *O. pusilla angustifrons* after Erbajeva (1988) according to the Art. 73.1.5 (ICZN 1999). Fixation of the Steppe pika skin as a holotype of *O. pusilla angustifrons* will maintain the stability of scientific names in pikas.

Discussion

The pikas under discussion are widely distributed in the arid zone of Inner Asia. Their range extends from the Betpak Dala Desert in Kazakhstan to the Eastern Gobi Desert and the Helan Shan Range (Fig. 1). The modern distribution in Kazakhstan is separated from the Mongolian part of the range by a gap of about 700 km. The very limited distribution range of *O. argentata* at Helan Shan Range (Formozov *et al.* 2004) is separated from the closest points of *O. pallasii* sensu lato distribution by 600 km. The Helan Shan Range is situated on the left bank of Huang He River and thus separated from the Mongolian Upland only by the Alashan Desert. One could speculate that an ancestral form might have potentially penetrated the Helan Shan Range through the Yin Mountains, the nearest mountains to the north.

The group under study displays conservative morphology, displaying high levels of similarity among different geographical populations. Both in its morphological traits (Fig. 2 and 3) and in its pelage coloration (Formozov *et al.* 2004; Erbajeva & Ma 2006; Lissovsky 2014), *O. argentata* occupies a more distinct position.

Our results based on the more intensely sampled mitochondrial COI gene support the current view that there exist three distinct taxa in the group: *O. argentata* in the Helan Shan Mountains, *O. pallasii* from Kazakhstan and *O. pallasii* from Mongolia and adjacent territories (Fig. 4). Despite the fact that the nuclear introns are in conflict as to the topology of the relationships, all the genes examined, as well as the previously studied *cytb* gene (Lissovsky *et al.* 2007), contradict contemporary taxonomy (e.g. Hoffmann & Smith 2005), which suggests the same taxonomic status

for *O. pallasii* and *O. argentata*. Nuclear genes, *cytb* and combined data set agree on paraphyletic status of *O. pallasii* relative to *O. argentata*. Although our genetic samples of *O. argentata* and *O. pallasii* from Kazakhstan are quite limited, it is unlikely that additional sampling will radically change the topology of the trees, because the previous studies on *cytb* gene (Yu *et al.* 2000; Lissovsky *et al.* 2007) were carried out on the basis of other specimens.

Thus, genetic data do not support contraposition of *O. pallasii* from Kazakhstan, together with *O. pallasii* from Mongolia from the one hand and *O. argentata* from another. Recognition of all the three taxa in question as a separate species or uniting them in one polytypic species may be considered as a more appropriate taxonomic solutions. Because three taxa in question are allopatric, a potential taxonomic solution can be approximated on the basis of genetic distances. The genetic distances between *O. argentata* and the two geographical forms of *O. pallasii* in the two nuclear genes we examined are notably larger than the intraspecific distances within *O. princeps* and *O. hyperborea*; they are larger also than distances among *O. hyperborea*, *O. mantchurica* and *O. hoffmanni* (Table. 1). In the PRKCI gene, they are even larger than the distance between *O. hyperborea* and *O. alpina*. Thus, within the framework of the subgenus *Pika*, our data support the recognition of the three taxa under consideration herein (*O. argentata* and two major geographical forms of *O. pallasii*) as three distinct species. Apparently, they represent three fragmented descendant populations of a putative ancestral species that have been isolated for a long period of time.

Phylogenetic relationships among these three species are in conflict in the nuclear introns studied; however, combined data set supports a sister relationship between *O. argentata* and the Mongolian species. Such a relationship also is concordant with the geographical distribution of the taxa.

We did not study genetic material from the two poorly known taxa: *O. p. hamica* and *O. p. sunidica*. Nevertheless, our morphological analysis does not support a distinction between them. These two taxa are usually cited as being isolated from the main distribution range; however, the entire range of Mongolian species is constituted by isolates of varying size (Fig. 1). A large population is located in eastern Mongolia, south of Ulan Bator; samples from this enclave are also indistinguishable from samples from western Mongolia (Fig. 3). The south-western limit of the distribution also includes several isolated populations (Fig. 1). The patched distribution, together with low level of genetic and in a less degree morphological variation, may point to recent range fragmentation. Recent drying of the climate in the Gobi Desert (Smith *et al.* 1990) seems to be a reasonable explanation of this phenomenon. In this case, the current distribution of *hamica* and *sunidica* should be recognized as the result of recent isolation events that have not to date resulted in these populations even reaching the subspecies level. This hypothesis should be tested on the larger genetic material.

The names of the three taxa: Helan Shan pika, pika from Kazakhstan and Pallas pika from Mongolia require separate discussion. The name of the species from the Helan Shan Mountains presents the simplest case. Two nominal taxa have been described within the distributional range in Helan Shan: *O. alpina argentata* Howell, 1928 and *O. helanshanensis* Zheng, 1990. These two names were considered synonyms by Formozov *et al.* (2004), albeit absent any quantitative analysis. Our morphometric results support this view. Thus, the name for the species should be *O. argentata*, as the senior synonym, with *O. helanshanensis* as a junior synonym.

It is clear from our data that the name '*O. pallasii*' was assigned erroneously to the pikas from Kazakhstan. Nothing points to Kazakh origin. Most likely, the type specimen originated from the Chuya Steppe of the south-eastern Russian Altai Mountains, less than 150 km from the *terra typica* of *O. pricei*. In any case, our morphological analysis assigned the type specimen of *pallasii* to the Mongolian taxon with the highest probability. Given that there is no notable difference between pikas from the SE Altai and NW Mongolia (type locality of *O. pricei*), the name *O. pallasii* should be recognized as the senior synonym for the Mongolian taxon, while *O. pricei* should be considered a junior synonym. It should be noted that according to article 33.4 (ICZN 1999), the correct spelling of the name in question is '*pallasii*'; the commonly used spelling '*pallasi*' constitutes an incorrect subsequent spelling.

There is only one available name for the species from Kazakhstan – *O. pricei opaca*. Thus, the valid name for this species is *O. opaca*.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. List of specimens, analyzed in morphometric study.

Appendix S2. List of specimens analyzed in genetic study.

Table S1. Nucleotide substitution models.

Fig. S1. Distribution of the pika specimens in the canonical space of craniometric differences.

Fig. S2. Distribution of the pika specimens in the canonical space of craniometric differences.

Fig. S3. Maximum clade credibility tree of Bayesian analysis based on PRKCI sequences, gap information included.

Fig. S4. Maximum clade credibility tree of Bayesian analysis based on combined dataset.

Fig. S5. Skulls of pikas.