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MOLECULAR PHYLOGENETICS AND TAXONOMY OF THE SUBGENUS *PIKA* (*OCHOTONA*, LAGOMORPHA)

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A phylogenetic analysis based on partial sequences of 2 mitochondrial genes (cytochrome *b* and cytochrome *c* oxidase subunit I) confirmed that *Ochotona alpina* (Pallas, 1773) and *O. turuchanensis* Naumov, 1934, are sister taxa to all other Palearctic species of the subgenus *Pika*. *O. hyperborea* (Pallas, 1811) contains sufficient genetic heterogeneity to define 2 or 3 races within this species. Examination of genetic data supports the recognition of *O. scorodumovi* Skalon, 1935, as a distinct species. The proper name of the taxon (either *O. scorodumovi* Skalon, 1935, or *O. mantchurica* Thomas, 1909) remains to be established. *O. hoffmanni* Formozov et al., 1996, is probably the closest relative of *O. scorodumovi*. These 2 taxa constitute a sister group to *O. hyperborea*. All the above-mentioned Palearctic taxa constitute the monophyletic *alpina–hyperborea* group. The *pallasi* group contains at least 3 taxa: *O.* (*p.*) *pallasi* (Gray, 1867), *O.* (*p.*) *pricei* Thomas, 1911, and *O.* (*p.*) *argentata* Howell, 1928. The taxonomic rank of these 3 taxa requires additional careful investigation. Nearctic pikas *O. princeps* (Richardson, 1828) and *O. collaris* (Nelson, 1893) constitute a monophyletic group separate from Palearctic taxa.

Key words: mitochondrial DNA, *Ochotona*, phylogeny, pika, taxonomy

The subgeneric taxonomy of the genus *Ochotona* Link, 1795, is somewhat confused (Yu et al. 2000). One of the few notions where the views of different researchers coincide is the existence of a group of closely related Palearctic species: *O. alpina* (Pallas, 1773), *O. hyperborea* (Pallas, 1811), *O. pallasi* (Gray, 1867), and an array of allied races whose status remains vague (Argiropulo 1948; Ellerman and Morrison-Scott 1951; Erbajeva 1988; Yu et al. 2000). Most authors group these taxa into the subgenus *Pika*; some also include here the Nearctic representatives of the genus—*O. princeps* (Richardson, 1828) and *O. collaris* (Nelson, 1893). Monophyly of this subgenus including the Nearctic taxa has been shown using mitochondrial DNA markers (Yu et al. 2000).

To date, the ''*alpina–hyperborea*'' species group has been defined by a considerable amount of data on variation of morphological, bioacoustical, and other features. Examination of our data on mitochondrial DNA helps to clarify the phylogenetic affinities of the subgenus *Pika*, as well as establish a baseline for future investigations of the taxonomy of poorly known taxa such as the ''*pallasi*'' group.

Brief historical overview.—Most works dealing with the systematics of the subgenus *Pika* have focused on the taxonomy of the ''*alpina–hyperborea*'' species group. Lissovsky (2003) provided a detailed review of this literature. In essence, 2 alternative points of view were concurrent during recent decades. The 1st proposed the existence of 2 Eurasian species, *O. alpina* and *O. hyperborea*, in this group. Alternatively, all races of the ''*alpina–hyperborea*'' complex were referred to as 1 species—*O. alpina*. The study of karyotypic diversity (Vorontsov and Ivanitskaya 1973) corroborated that *O. alpina* and *O. hyperborea* are 2 distinct species.

A study of geographical variation of skull measurements and the structure of palatal foramina of pikas (Lissovsky 2003) revealed the existence of 3 morphologically distinct species within the ''*alpina–hyperborea*'' complex: *O. alpina*, *O. hyperborea*, and *O. turuchanensis* Naumov, 1934. The latter was shown to be specifically distinct from *O. hyperborea* because of partial sympatry of the 2 species. Karyological study demonstrated close similarity between the karyotypes of *O. turuchanensis* and *O. alpina* (Formozov et al. 1999).

In addition, 2 taxa were postulated to be distinct based on the earlier morphological study (Lissovsky 2003). The 1st, taxon *scorodumovi* Skalon, 1935, which inhabits the area between the Shilka and Argun' rivers, is usually considered a junior synonym of *O. alpina* (Hoffmann 1993; Hoffmann and Smith 2005; Ognev 1940; Sokolov et al. 1994; Yakhontov and Formozov 1992). The 2nd is taxon *mantchurica* Thomas, 1909, described from Manchuria, which is usually considered a subspecies of *O. hyperborea* (Hoffmann 1993; Hoffmann and Smith 2005; Ognev 1940; Sokolov et al. 1994).

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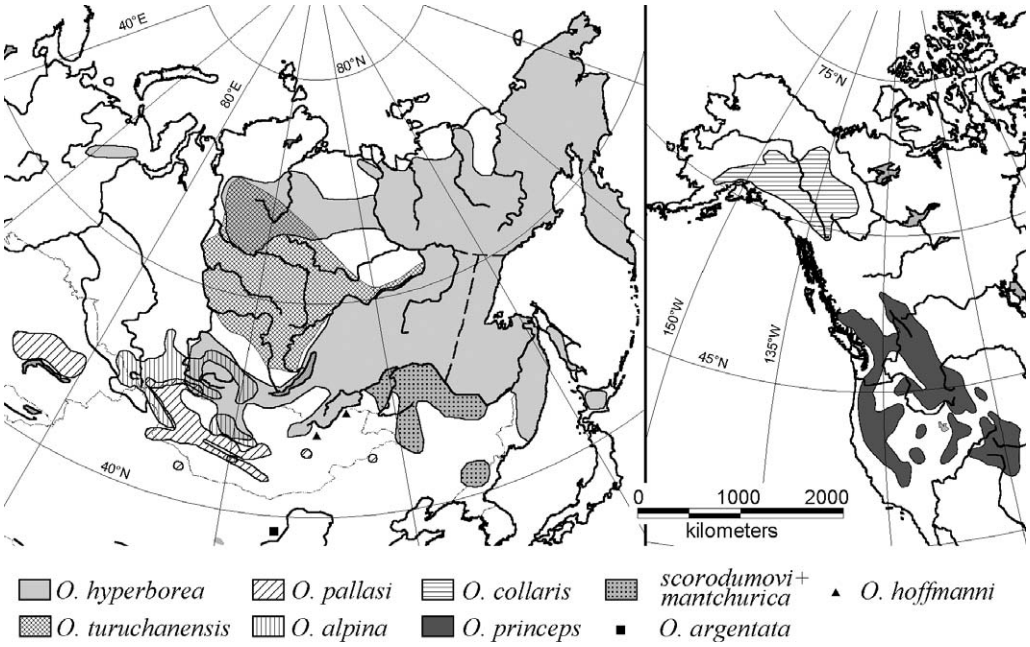

Fig. 1.—Schematic geographic distribution of taxa from the subgenus *Pika*. Dotted line indicates the supposed border between the ranges of acoustic races of *Ochotona hyperborea*. Range of *O. collaris* is drawn after MacDonald and Jones (1987), *O. princeps* after Smith et al. (1990).

Comparative analyses of vocalization in pikas (Lissovsky 2005) argued for the existence of 4 taxa of equal rank, namely *O. alpina*, *O. hyperborea*, *O. turuchanensis*, and *O. scorodumovi*. Examination of acoustic data suggested that *O. turuchanensis* is related to *O. alpina*, and that *O. scorodumovi* appears to inhabit not only Transbaikalia, but also at least the northern part of the Great Khingan Range (Fig. 1).

Three acoustic races have been described within *O. hyperborea*, differing in the structure of alarm calls and designated the ''northern'' (Asia north of the 60th parallel and Kamchatka), ''eastern'' (Hokkaido, Sakhalin, Primorskii Kray, and region between Zeya and the lower Amur Rivers), and ''southern'' (the remainder of the species range) races (Formozov 1991; Lissovsky 2005; Nikol'sky 1984). It was even proposed that these acoustic races may have attained the status of ''semispecies,'' sensu Mayr (Formozov 1991; Mayr 1940).

The situation is different in *O. pallasi*, for which fewer taxonomic studies have been done. Its distribution consists of 2 major allopatric areas: the nominative subspecies occupies eastern Kazakhstan and *O. p. pricei* Thomas, 1911, lives in Mongolia and adjacent territories. Smith et al. (1990) suggested that *O. p. pricei* may represent a distinct species. Several additional forms have been proposed within *O. pallasi*, representing geographically isolated subspecies: *O. p. hamica* Thomas, 1912, *O. p. sunidica* Ma et al., 1980, and *O. p. helanshanensis* Zheng, 1990.

Of special interest are the taxa *O. argentata* Howell, 1928, and *O. hoffmanni* Formozov et al., 1996. Both were initially described as subspecies of *O. alpina* and subsequently elevated to specific rank by Formozov and coauthors (Formozov and Baklushinskaya 1999; Formozov et al. 1996, 2004). However, these studies provided comparisons with a limited sample of only 1 species—*O. alpina*. Therefore, the taxonomic status of both forms should be considered tentative, because available data are scanty. One of these studies (Formozov et al. 2004) asserted that the type localities of *O. p. helanshanensis* and *O. argentata* are located several kilometers apart and the animals are indistinguishable, thereby synonymizing *helanshanensis* with *argentata* (Hoffmann and Smith 2005).

The history of research on North American pikas is a separate issue. Our study is not aimed at the taxonomy of *O. princeps* and *O. collaris*, but they are of phylogenetic interest as putative members of the subgenus *Pika*. For more detailed discussion, see Hoffmann (1993), Hoffmann and Smith (2005), Smith and Weston (1990), and Weston (1981).

Materials and Methods

Material studied.—The complete list of specimens examined is provided in Appendix I. The specimens used in our study were identified using morphological criteria proposed by Lissovsky (2003).

In 1 specimen sequenced in the work of Yu et al. (GenBank accession AF273009—Yu et al. 2000), abnormally high divergence was observed in the short segment of the cytochrome-*b* (*Cytb*) gene located between the primers L14944 and L15136, which was well beyond the range of variation present within *Ochotona*, including both GenBank data and our study. In particular, this segment possessed several amino acid substitutions not found among other pikas. Thus, we assumed that this 153–base-pair (bp) region contains an error and excluded it from further consideration.

Among the sequences taken from the work of Niu et al. (2004), 2 turned out to be identical with previously published ones. Moreover, the identical sequences belonged to representatives of different species from different localities (sensu

Lissovsky 2003). These matching sequences belonged to *O. hyperborea* from Magadan (AF176582) and *O. scorodumovi* from Ergun, Inner Mongolia, China (AY056603). The 2nd matching pair was *O. alpina* from the Altai Mountains. (AF273009), containing the above mentioned error, and *O. scorodumovi* from Yichun, Heilongjiang, China (AY056605). Because the specimens of *O. scorodumovi* listed above were referred to *O. hyperborea* and *O. alpina*, respectively, we assumed an error in the data provided by Niu et al. (2004) and refrained from using any of their data in our analyses.

Molecular protocols.—Total genomic DNA from ethanol-preserved tissue was extracted using a Chelex-based method called DryRelease (Hajibabaei et al. 2005; Ivanova et al. 2003). Some recalcitrant tissues and dry skins were extracted using Wizard SV96 Genomic DNA Purification System (Promega, Madison, Wisconsin) following manufacturer instructions, or by another homemade approach called Silitom (Hajibabaei et al. 2005).

Each polymerase chain reaction had a total volume of 12.5 μl and contained 2.0 μl of template (see Hajibabaei et al. [2005] for details). The 762-bp fragment of *Cytb* was amplified using universal primers CB1-5′, L14841 of Kocher et al. (1989) and CB3-3′, H15560 of Palumbi (1996). If amplification of full-length product failed, a shorter product of 472 bp was amplified using the universal primer set (mcb398 and mcb869) of Verma and Singh (2003). For cytochrome-*c* oxidase I subunit (COI) amplification of pikas we used a combination of existing vertebrate primers VF1 and VR1 (named FishR1 in Ward et al. [2005]) and a set of their degenerate modifications (Ivanova et al. 2006) adapted for recovery of mammalian COI. In cases where we were not able to recover full-length product, the RonM primer of Pfunder et al. (2004) was used in combination with C_VR1di to amplify a 470-bp product. Polymerase chain reaction products were separated on a 2% agarose gel.

Unpurified polymerase chain reaction products were directly used for sequencing (Hajibabaei et al. 2005) with BigDye terminator version 3.1 cycle sequencing kit (Applied Biosystems, Foster City, California). VF1d and VR1d primers were used for sequencing the COI polymerase chain reaction products generated with primer cocktails. Bidirectional sequences were assembled in SeqScape version 2.1.1 (Applied Biosystems) and manually edited.

Phylogenetic analyses.—The tree-building algorithms employed in this study were maximum parsimony and maximum likelihood. All analyses were performed for each of the 2 genes separately because of lack of sequences of 1 of the genes in several taxa. In cases when specimens had identical gene sequences, only 1 such sequence was retained for analyses. Base frequency stationarity was evaluated using a chi-square test implemented in PAUP*, beta-test version 4.0b10 (Swofford 1998), with all sites included in analysis and with constant sites excluded in order to increase the sensitivity of the method.

Unweighted maximum-parsimony analysis employing heuristic search with simple stepwise sequences addition and tree-bisection-reconnection branch swapping was performed in PAUP*. Nodal support for maximum parsimony was assessed in the same program from 500 nonparametric bootstrap replicates.

Table 1.—Model parameters of DNA evolution of 2 genes (cytochrome-*c* oxidase I subunit [COI] and cytochrome *b* [*Cytb*]) in pikas, including substitution models (see text for details), base frequencies (A, T, G, and C), substitution rates (R), and gamma shape parameter (alpha).

Gene	COI			*Cytb*		
Codon position	1st	2nd	3rd	1st	2nd	3rd
Substitution model	GTR+Γ	HKY	GTR+Γ	GTR+Γ	HKY	GTR+Γ
A	0.25	0.15	0.35	0.26	0.21	0.34
T	0.18	0.43	0.25	0.24	0.39	0.17
G	0.31	0.14	0.07	0.25	0.14	0.03
C	0.26	0.28	0.33	0.25	0.26	0.46
$R_{[T-C]}$	93.83	49.05	22.46	88.91	31.86	22.67
$R_{[T-A]}$	0.01	0.48	2.51	2.26	9.07	3.62
$R_{[T-G]}$	0.01	0.48	5.29	0.01	9.07	9.36
$R_{[C-A]}$	2.64	0.48	0.49	1.22	9.07	0.94
$R_{[C-G]}$	0.01	0.48	3.22	2.23	9.07	3.32
$R_{[A-G]}$	3.49	49.05	66.03	5.37	31.87	60.09
alpha	0.1	—	3.69	0.17	—	3.81

Maximum-likelihood analysis was performed in Treefinder (Jobb 2005; www.treefinder.de). The maximum-likelihood model of DNA evolution was estimated separately for each of the 3 codon positions. The type of substitution model was chosen on the basis of a hierarchical likelihood-ratio test in Modeltest 3.06 (Posada and Crandall 1998). For the purpose of estimating parameters of the substitution model, the Reconstruct Phylogeny algorithm of Treefinder was started with the ''Optimum'' option for values of all parameters other than base frequencies, for which the ''Empirical'' option was used. Maximum-likelihood models of DNA evolution had a similar structure for both genes (Table 1). The 1st and 3rd codon positions are explained by the general time-reversible model with zero proportion of invariable sites and continuous gamma-distributed rates across sites (Lanave et al. 1984; Rodriguez et al. 1990), whereas the 2nd codon position is explained by the model of Hasegawa et al. (1985). A maximum-likelihood search was conducted with different models of substitutions for 3 codon positions, estimated at the previous step. Maximum-likelihood bootstrap support was based on 500 replicates with the same model parameters as in the tree search.

The analyses were done using only specimens with lengths of sequenced fragments exceeding 600 bp. Specimens with shorter sequences were used only to assess their position on the tree built using neighbor-joining analyses with the Kimura 2-parameter model (Kimura 1980). Neighbor-joining was bootstrapped 500 times in PAUP*.

Trees were rooted with *O. dauurica* (Pallas, 1776) and *O. rufescens* (Gray, 1842). The external position of these taxa relative to the subgenus *Pika* was shown by Yu et al. (2000) and Niu et al. (2004).

Results

Base frequencies did not deviate from stationarity across taxa (COI: $\chi^2 = 63.14$, $d.f. = 111$, $P > 0.99$ with constant sites excluded and $\chi^2 = 31.75$, $d.f. = 111$, $P > 0.99$ with all sites

Table 2.—P-distances and range of variation (in parentheses) within selected groups of pikas (*Ochotona*).[a]

Group	COI	*Cytb*
O. alpina from East Altai	0.22% (0–0.6)	0.01% (0–0.14)
O. turuchanensis from Putorana Plateau	0.2% (0–0.5)	0%
O. hyperborea from Putorana Plateau	0.04% (0–0.47)	0.14% (0–0.42)
O. alpina	0.32% (0–0.76)	0.19% (0–1.11)
O. turuchanensis	0.25% (0–0.61)	0%
O. hyperborea	2.3% (0–3.64)	2.41% (0–5.29)
O. hyperborea, northern clade	1.67% (0–2.28)	1.23% (0–2.78)
O. hyperborea, southern clade	0.68% (0.30–1.07)	1.07% (0.30–1.95)
O. "*scorodumovi*"	0.61% (0.15–0.91)	1.05%

[a] COI = cytochrome-*c* oxidase I subunit; *Cytb* = cytochrome *b*.

included; *Cytb*: $\chi^2 = 43.32$, $d.f. = 75$, $P > 0.99$ with constant sites excluded and $\chi^2 = 14.34$, $d.f. = 75$, $P > 0.99$ with all sites included; Table 1). Both genes displayed variation within the samples (Table 2). We observed no instances of molecular DNA introgression between recognized species in our samples.

The topology of all trees obtained using different algorithms and inferred from different genes was similar (Figs. 2 and 3). Within the "*alpina–hyperborea*" group, 4 monophyletic taxa persisted on all trees and had strong bootstrap support. *O. alpina*, *O. turuchanensis*, *O. hyperborea*, and *O. scorodumovi* comprised 1 clade, which received strong support with *Cytb* data. Additionally, *O. alpina* and *O. turuchanensis* also formed a persistent clade. The clade containing *O. hyperborea* and *O. scorodumovi* had strong bootstrap support on the *Cytb* tree, but not on the COI tree.

Ochotona pallasi, *O. princeps*, and *O. collaris* formed an outgroup to the 4 taxa mentioned above. The clade containing *O. princeps* and *O. collaris* received strong bootstrap support on most trees. The group "*pallasi*" (including *O. p. pallasi*, *O. p. pricei*, *O. p. sunidica*, and *O. argentata* [= *O. p. helanshanensis*]) seemed to be a sister group to the "*alpina–hyperborea*" complex, but without strong bootstrap support (Fig. 3).

Within *O. hyperborea* several groups could be traced. The 1st group included specimens from the northern part (HYPER2–14) and the 2nd included specimens from the southern part (HYPER15–23) part of the species range. The northern clade did not receive support from some of the analyses (Figs. 2 and 3); however, the pikas from the northeastern part of the range and the form from the Putorana Plateau contained therein did receive consistent strong support. The specimen from Hokkaido (HYPER1) was placed as sister group to the remaining representatives of *O. hyperborea*. P-distance of COI sequences between the northern and southern clades was 2.78% ($SD = 0.2$, 2.44–2.90). P-distance of *Cytb* sequences between the specimen from Hokkaido and the remaining forms was 4.53% ($SD = 0.38$, 3.86–5.29), whereas the sequences of this gene in the northern and southern clades were 2.90% divergent ($SD = 0.32$, 2.37–3.60).

Discussion

Phylogenetic affinities.—The results of our study are concordant with previous ideas of phylogeny of this subgenus as regards the well-recognized "large" taxa. Possibly the most unusual conclusion inferred from the analyses concerns the phylogenetic affinities of the form *O. scorodumovi*. According to the commonly accepted view, largely based on morphology (Hoffmann 1993; Ognev 1940; Smith et al. 1990; Sokolov et al. 1994) it is a subspecies of *O. alpina*. In contrast, results of our study suggest that this taxon is closer to *O. hyperborea* than to *O. alpina*.

Ochotona hoffmanni turned out to be the sister taxon to *O. scorodumovi*, which seems consistent with the geographic proximity of their ranges. However, this conclusion is preliminary because it is based only on the sequence of a short fragment of a single gene.

Our study revealed close affinities of *O. turuchanensis* to *O. alpina*, which is concordant with previous conclusions (Formozov et al. 1999; Lissovsky 2005). The very low level of sequence divergence between the 2 species implies quite recent separation of *O. turuchanensis*. At the same time, strict monophyly of this taxon in our sample indicates its genetic distinction.

Our genetic analyses provided interesting results for the "*pallasi*" group. Clearly *O. p. pallasi* (PALLASI2), *O. p. pricei* (PALLASI3–7), *O. p. sunidica* (PALLASI1), and *O. argentata* (syn. *helanshanensis*) form a monophyletic group. The phylogenetic affinities of *O. argentata* were previously uncertain. This taxon was considered a subspecies of *O. alpina* by many earlier workers (Ellerman and Morrison-Scott 1951; Erbajeva 1988; Hoffmann 1993; Smith et al. 1990). A recent molecular study (Yu et al. 2000) showed the proximity of *O. argentata* (syn. *helanshanensis*) to *O. p. sunidica*. Formozov et al. (2004) considered *O. argentata* to be a separate species, but compared it only with *O. alpina*. Finally, we suggest, based on the results of our study, that *O. argentata* belongs to the "*pallasi*" group; moreover, it seems to be an internal branch of *O. pallasi* sensu lato.

Ochotona princeps and *O. collaris* grouped together as sister taxa, but the divergence of the 2 species turned out to be deeper than that of *O. alpina* and *O. hyperborea* (Fig. 3).

Taxonomy.—From our point of view, it is best to identify the ranks of taxa of the "species group" (in nomenclatorial sense) by similarities in all available data, not by DNA distances alone. The entire body of different types of data accumulated for pikas, especially the *alpina-hyperborea* group, allows us to present several taxonomic hypotheses.

The supposed specific rank of *O. scorodumovi* made on the basis of acoustics and morphology (Lissovsky 2003, 2005) is completely supported by genetic data. The high degree of genetic differences, unique acoustic repertoire, and biogeography argue for recognizing *O. scorodumovi* as a distinct species. The taxonomic composition and valid name for this species awaits a more thorough revision.

A complete revision of the pikas inhabiting eastern Transbaikalia and northeastern China is needed. Currently the only specimens available in collections outside China are from the Chinese Eastern Railway pass across the Great Khingan Mountains. Unfortunately, the Chinese collections appear to lack specimens from that particular locality, which is the type

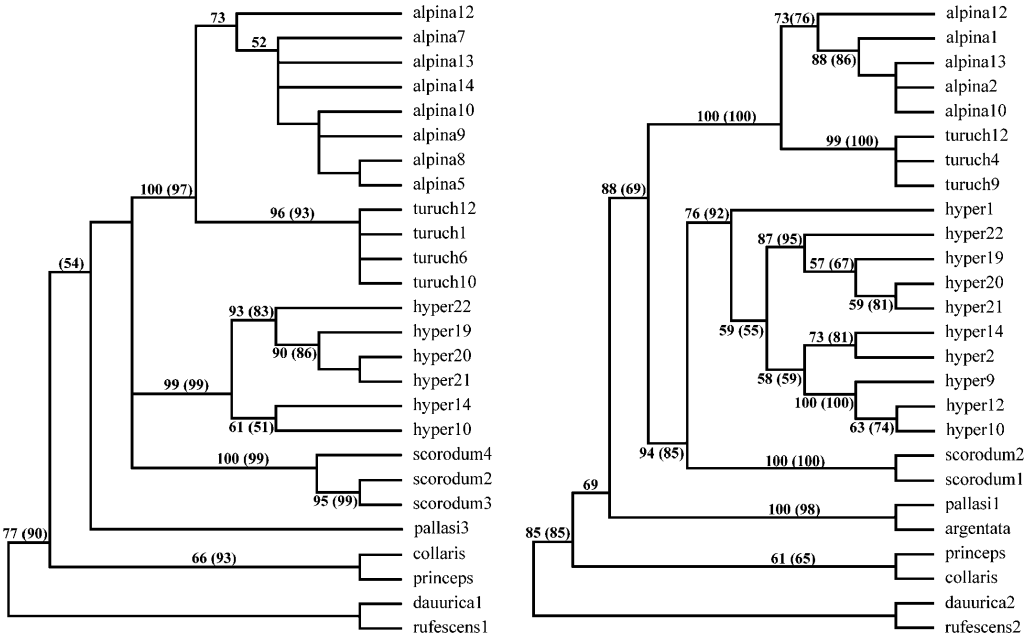

Fig. 2.—Topology of trees obtained using maximum likelihood and maximum parsimony for cytochrome-*c* oxidase I subunit (left) and cytochrome *b*. Numbers on branches indicate bootstrap support for maximum likelihood (in parentheses) and maximum parsimony. Bootstrap values less than 50 are not shown. For explanations of taxa labels, refer to Appendix I.

locality of taxon *mantchurica*. As a result, the comparison of typical *mantchurica* with other pikas inhabiting northeastern China remains to be made. In previous studies (e.g., Sokolov et al. 1994) it was assumed a priori that China is inhabited by *mantchurica*, whereas the areas north of the Argun' River are inhabited by the form *scorodumovi*. Our results show typical *O. scorodumovi* from Transbaikalia and the specimen from northern Manchuria with similar haplotypes, their genetic distances being well within the range of intraspecific variation in other species (Fig. 3). This suggests that at least northern Manchuria is inhabited by *O. scorodumovi*. This conclusion is corroborated by the results of acoustic analyses (Lissovsky 2005). The question of whether *mantchurica* and *scorodumovi* are conspecific remains open until further comparative studies are done including type material from both taxa. If their conspecificity is confirmed, the name *O. mantchurica* Thomas, 1909, would have priority over *O. scorodumovi* Skalon, 1935, as the senior synonym. We lacked material of the race *coreana* Allen and Andrews, 1913, in our study. This unstudied taxon, isolated in the Changbai Mountains on the border of China and Korea, is also probably a relative of Manchurian pikas.

Our results are compatible with hypotheses about the distinctiveness of *O. hoffmanni*. The uniqueness of this taxon was established previously only by comparison with *O. alpina* (Formozov and Baklushinskaya 1999; Formozov et al. 1996). Based on the results of our study, it would be worthwhile to provide additional comparisions of this taxon with *O. scorodumovi*.

Our results also provide additional support for the taxonomic status of *O. turuchanensis*. Recognition at the species level was proposed on the basis of morphology, ecology, and bioacoustics (Lissovsky 2003, 2004a, 2004b, 2005). The degree of morphological divergence in *O. turuchanensis* is such that most researchers (e.g., Hoffmann 1993; Naumov 1934; Ognev 1940; Smith et al. 1990; Sokolov et al. 1994) did not consider it closely related to *O. alpina*. They also did not distinguish it from *O. hyperborea*, with which it lives sympatrically in some areas (Lissovsky 2003). It should be noted that the similarity of nuclear DNA between *O. turuchanensis* and *O. alpina* is lower than that of mitochondrial genes. A study conducted using random amplified polymorphic DNA methods (Lissovskaya and Formozov 1999) indicated that genetic distance between *O. turuchanensis* and *O. alpina* is 1.44 times greater than that between the most divergent subspecies of *O. hyperborea*. Ecological differences between *O. turuchanensis* and *O. alpina* are significant. *O. alpina* is a typical inhabitant of rocky talus slopes in the alpine belt (Sokolov et al. 1994) and penetrates into the taiga only along rocky outcrops, whereas *O. turuchanensis* is confined to plain taiga of central Siberia, preferring hilltops with buttes even if they are covered with soil (Lissovsky 2004a) and attaining maximal population densities on slopes with abundant eluvium (Lissovsky 2004b). Our study of mitochondrial DNA supports the previous data. The monophyly of *O. turuchanensis* and its position relative to *O. alpina* suggest equal ranks for these taxa.

It appears that *O. turuchanensis* represents a case of a young species with rapid morphological divergence, which is rarely found in mammals. A similar case is exemplified by the polar bear (*Ursus maritimus*—Talbot and Shields 1996), which is thought to have diverged from a population of the brown bear (*Ursus arctos*) in the Middle Pleistocene, but the degree of its morphological and ecological differentiation is considerable.

An unusually high level of intraspecific genetic differentiation was observed in *O. hyperborea*. It is tempting to propose

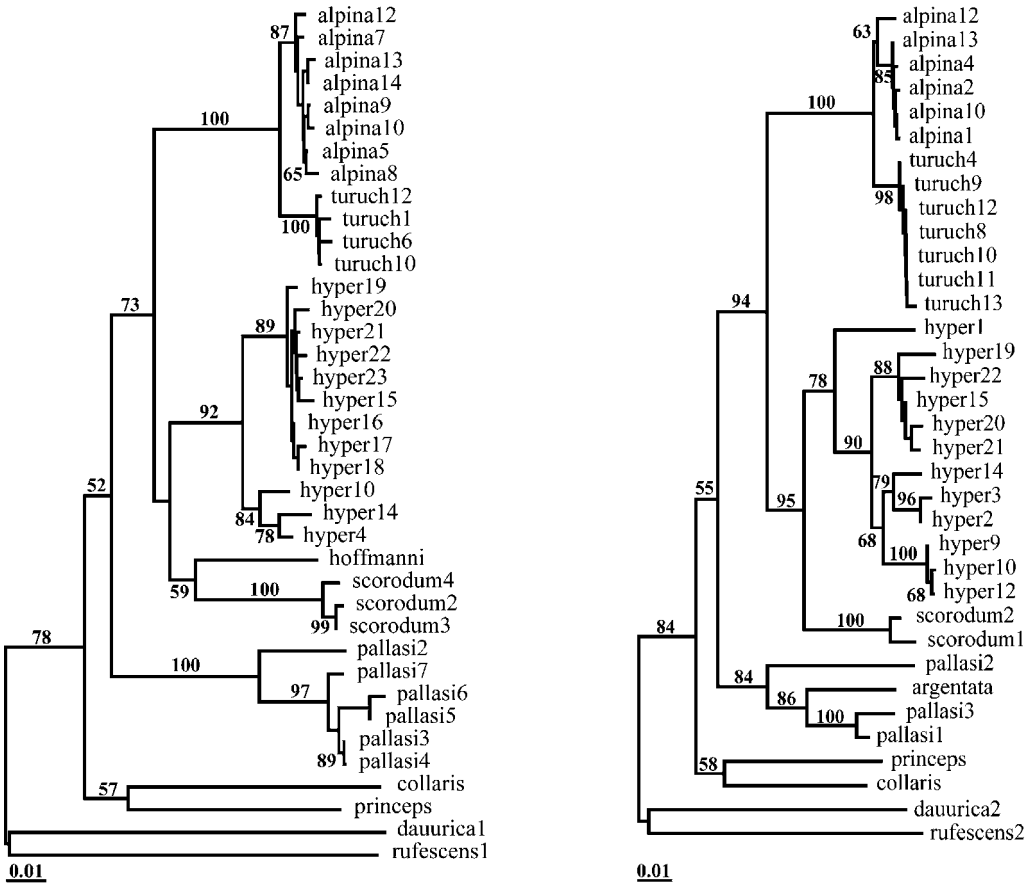

Fig. 3.—Neighbor-joining trees constructed using the Kimura 2-parameter model for cytochrome-*c* oxidase I subunit (left) and cytochrome *b*. Numbers on branches indicate bootstrap support; values less than 50 are not shown. For explanations of taxa labels, refer to Appendix I.

splitting *O. hyperborea* into 2 or 3 taxa, but this appears premature. Arguing against it are features such as the structure of karyotypes (Formozov et al. 1999; Hayata and Shimba 1969; Vorontsov and Ivanitskaya 1973), morphometric characters and structure of skull sutures (Lissovsky 2003), and the uniform and unique structure of the acoustic repertoire (Lissovsky 2005) in all populations of *O. hyperborea*, all of which support the integrity of this species.

The structure of genetic variation reflects, from our point of view, the history of range fragmentation in *O. hyperborea*, but not yet speciation events. The northern clade did not receive strong bootstrap support in most of the analyses, as opposed to the groups it contains: northeastern Asia and the Putorana Plateau. On the other hand, the southern clade enjoyed strong bootstrap support, as well as a lower level of intragroup differentiation (Table 2). Examination of these data suggests that northern and southern clades diverged 1st, parts of the northern clade diverged shortly afterwards, and pikas from the southern clade descended in a single genetic line, which spread widely only recently.

Given the available data, we regard *O. hyperborea* as a single species, consisting of well-defined geographic races. As opposed to the *O. alpina–O. turuchanensis* species complex, which is morphologically divergent but genetically similar, *O. hyperborea* comprises a number of genetically distant groupings with minimal morphological and behavioral differences. Nevertheless, the question of taxonomic and evolutionary relationships between the clades and their subdivisions, as well as the possibilities of current or past hybridization among them are definitely worth additional genetic and ecological study. It is particularly important to do more research on *O. h. yesoensis*, using larger sample sizes and additional genetic markers. The confirmation of the existence of a basal haplotype on Hokkaido could shed light on the phylogeography of the whole "*alpina–hyperborea*" group.

It is important to note that the northern and southern clades revealed by our analyses, as well as the taxon from Hokkaido, are generally concordant with the acoustic races of *O. hyperborea*. Formozov (1991) proposed according these acoustic races the status of semispecies. However, the content of these semispecies differed essentially from the groupings revealed in our study. The suggestion to raise the status of acoustic races was proposed mainly with respect to northern and southern races and was largely based on the confusion of *O. hyperborea* with *O. turuchanensis*. Additionally, our genetic findings suggest an early divergence of the eastern (Hokkaido) race, despite the fact that it is the least distinguishable acoustically (Lissovsky 2005). It is interesting that, according to Formozov (1991), pikas from the upper Zeya River belong to the eastern acoustic race, although our study has shown their

close affinities with the southern clade. This discrepancy is mitigated in part by the fact that Formozov (1991) suggested the occurrence of hybridization of the 2 acoustic races in the upper Zeya Basin.

We can suggest only preliminary conclusions concerning the taxonomy of the "*pallasi*" group because we lack information on intragroup variation. Close relationships were shown to exist between *O. p. pricei* and *O. p. sunidica*. The level of divergence is concordant with intrapopulation levels of other taxa. Additionally, profound genetic divergence was shown to exist between the nominal taxon and *O. p. pricei*. Furthermore, *O. argentata* also seems to be an internal branch, relative to *O. pallasi* sensu lato. Thus, considering the magnitude of intraspecific divergences even within the taxonomically compact "*alpina–hyperborea*" group, we can only suggest that the "*pallasi*" group comprises 3 well-defined taxa: *O.* (*p.*) *pallasi, O.* (*p.*) *pricei*, and *O.* (*p.*) *argentata*. *O. p. hamica* included as a subspecies by Hoffmann and Smith (2005) was absent in our study. The taxonomic rank of these taxa should remain tentative, until more thorough studies are carried out.

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APPENDIX I

The list of specimens used in analysis. Information is in the following order: locality, decimal latitude, and decimal longitude from specimen label; length of cytochrome-*c* oxidase I subunit fragment recovered and used in the study and sequence reference in parentheses (NCBI GenBank accessions and BOLD process identification numbers); length of cytochrome-*b* fragment recovered and used in the study and sequence reference in parentheses (GenBank accessions); and tissue source or publication. Tissue source: ZMMU indicates original sequences recovered from collection specimens deposited in the Zoological Museum of Moscow State University, Moscow, Russia. Coordinates are provided only for the specimens sequenced in this study.

Ochotona alpina.—ALPINA1: China, Xinjiang, Altay Mountains, Buhasi, —, 565 (AF273009), Yu et al. (2000); ALPINA2: Russia, southeastern Altay Mountains, Yuzhno-Chuyskiy Range, upper Taldura River, 49.93°N, 87.88°E, 657 (NCBI DQ347414, BOLD ABPS031-04), 719 (DQ335509), ZMMU S-160836 liver; ALPINA3: Russia, southeastern Altay Mountains, Yuzhno-Chuyskiy Range, upper Taldura River, 49.93°N, 87.88°E, 657 (NCBI DQ347418, BOLD ABPS032-04), 719 (DQ335510), ZMMU S-160837 liver; ALPINA4: Russia, southeastern Altay Mountains, Yuzhno-Chuyskiy Range, upper Taldura River, 49.93°N, 87.88°E, 606 (NCBI DQ347417, BOLD ABPS030-04), 674 (DQ335508), ZMMU S-160852 liver; ALPINA5: Russia, southeastern Altay Mountains, Yuzhno-Chuyskiy Range, upper Taldura River, 49.93°N, 87.88°E, 657 (NCBI DQ347419, BOLD ABPS033-04), 719 (DQ335511), ZMMU S-161351 liver; ALPINA6: Russia, southeastern Altay Mountains, Yuzhno-Chuyskiy Range, upper Taldura River, 49.93°N, 87.88°E, 657 (NCBI DQ347420, BOLD ABPS034-04), 719 (DQ335512), ZMMU S-161352 liver; ALPINA7: Russia, southeastern Altay Mountains, Yuzhno-Chuyskiy Range, upper Taldura River, 49.93°N, 87.88°E, 657 (NCBI DQ347421, BOLD ABPS035-04), 719 (DQ335513), ZMMU S-161354 liver; ALPINA8: Russia, southeastern Altay Mountains, Yuzhno-Chuyskiy Range, upper Taldura River, 49.93°N, 87.88°E, 657 (NCBI DQ347422, BOLD ABPS036-04), 719 (DQ335514), ZMMU S-161355 liver; ALPINA9: Russia, southeastern Altay Mountains, Yuzhno-Chuyskiy Range, upper Taldura River, 49.93°N, 87.88°E, 657 (NCBI DQ347423, BOLD ABPS037-04), 719 (DQ335515), ZMMU S-161356 liver; ALPINA10: Russia, southeastern Altay Mountains, Yuzhno-Chuyskiy Range, upper Taldura River, 49.93°N, 87.88°E, 657 (NCBI DQ347424, BOLD ABPS038-04), 719 (DQ335516), ZMMU S-161357 liver; ALPINA11: Russia, southeastern Altay Mountains, Yuzhno-Chuyskiy Range, upper Taldura River, 49.93°N, 87.88°E, 657 (NCBI DQ347413, BOLD ABPS039-04), 719 (DQ335517), ZMMU S-161358 liver; ALPINA12: Russia, Krasnoyarskiy Kray, Ermakovskiy District, Oyskiy Range, 52.85°N,

93.00°E, 657 (NCBI DQ347415, BOLD ABPS001-04), 719 (DQ335482), ZMMU S-167265 liver; ALPINA13: Russia, Altayskiy Kray, Charishskiy District, Tigiretskiy Range, upper Inya River, 51.00°N, 83.57°E, 657 (NCBI DQ347416, BOLD ABPS006-04), 719 (DQ335487), ZMMU S-171510 liver; ALPINA14: Russia, Tuva, Mongun-Taiginsky District, Tsagan-Shibetu Mountains foothills, 50.38°N, 90.56°E, 606 (NCBI DQ347425, BOLD ABPS096-05), —, ZMMU S-168615 skin.

Ochotona argentata.—ARGENTATA: China, Ningxia, Mountain Helan, —, 719 (AF272996), Yu et al. (2000).

Ochotona collaris.—COLLARIS: unknown, 657 (NCBI NC003033), 719 (NC003033), Lin et al. (2002).

Ochotona dauurica.—DAUURICA1: Russia, Chita Region, Krasnokamenskiy District, near Krasnokamensk, 50.07°N, 117.87°E, 657 (NCBI DQ347426, BOLD ABPS041-04), 680 (DQ335519), ZMMU S-175916 liver; DAUURICA2: China, Shanxi, Youyu, —, 719 (AF273000), Yu et al. (2000).

Ochotona hoffmanni.—HOFFMANNI (paratype): Mongolia, Khenteyskiy Aymak, upper Kerulen River, Delger-Haan, 47.20°N, 109.00°E, 421 (NCBI DQ347427, BOLD ABPS083-05), —, ZMMU S-145149 skin.

Ochotona hyperborea.—HYPER1 (*O. h. yesoensis*): Japan, Hokkaido Island, —, 719 (AB053257); HYPER2: Russia, Magadan Region, vicinity of Magadan, —, 591 (AF176582); HYPER3: Russia, Yakutia, Verkhoyanskiy District, Adycha River, 67.90°N, 135.49°E, 421 (NCBI DQ347448, BOLD ABPS093-05), 344 (DQ335524), ZMMU S-160607 skin; HYPER4: Russia, Yakutia, Verkhoyanskiy District, Adycha River, 67.90°N, 135.49°E, 421 (NCBI DQ347447, BOLD ABPS092-05), —, ZMMU S-160605 skin; HYPER5: Russia, Krasnoyarskiy Kray, Taymirskiy Autonomous District (AD), vicinity of Talnakh, 69.43°N, 88.77°E, 656 (NCBI DQ347434, BOLD ABPS012-04), —, ZMMU S-162962 liver; HYPER6: Russia, Krasnoyarskiy Kray, Taymirskiy AD, Glubokoe Lake, 69.32°N, 89.98°E, 657 (NCBI DQ347428, BOLD ABPS011-04), 719 (DQ335492), ZMMU S-162963 liver; HYPER7: Russia, Krasnoyarskiy Kray, Taymirskiy AD, Kutaramakan Lake, 68.78°N, 91.87°E, 421 (NCBI DQ347440, BOLD ABPS025-04), 719 (DQ335503), ZMMU S-164008 liver; HYPER8: Russia, Krasnoyarskiy Kray, Taymirskiy AD, Kutaramakan Lake, 68.78°N, 91.87°E, 657 (NCBI DQ347439, BOLD ABPS024-04), 719 (DQ335502), ZMMU S-164009 liver; HYPER9: Russia, Krasnoyarskiy Kray, Taymirskiy AD, Kutaramakan Lake, 68.78°N, 91.87°E, 657 (NCBI DQ347441, BOLD ABPS026-04), 719 (DQ335504), ZMMU S-164010 liver; HYPER10: Russia, Krasnoyarskiy Kray, Taymirskiy AD, Kutaramakan Lake, 68.78°N, 91.87°E, 657 (NCBI DQ347436, BOLD ABPS020-04), 719 (DQ335499), ZMMU S-164021 liver; HYPER11: Russia, Krasnoyarskiy Kray, Taymirskiy AD, Kutaramakan Lake, 68.78°N, 91.87°E, 657 (NCBI DQ347438, BOLD ABPS022-04), —, ZMMU S-164025 liver; HYPER12: Russia, Krasnoyarskiy Kray, Taymirskiy AD, Kutaramakan Lake, 68.78°N, 91.87°E, 606 (NCBI DQ347435, BOLD ABPS019-04), 719 (DQ335498), ZMMU S-164026 liver; HYPER13: Russia, Krasnoyarskiy Kray, Taymirskiy AD, Kutaramakan Lake, 68.78°N, 91.87°E, 657 (NCBI DQ347437, BOLD ABPS021-04), 385 (DQ335500), ZMMU S-164027 liver; HYPER14 (topotype): Russia, North of the Chukotka peninsula, vicinity of Pereval'naya Mountain at upper Kattevyaem River, 66.73°N, 171.98°E, 657 (NCBI DQ347433, BOLD ABPS008-04), 719 (DQ335489), ZMMU S-173145 liver; HYPER15: Russia, Amur Region, Zeyskiy District, Zeyskiy Zapovednik, 54.05°N, 126.92°E, 378 (NCBI DQ347445, BOLD ABPS089-05), 325 (DQ335523), ZMMU S-150671 skin; HYPER16: Russia, Yakutia, Neryungri District, Nagorny, 55.97°N, 124.94°E, 421 (NCBI DQ347446, BOLD ABPS090-05), —, ZMMU S-150683 skin; HYPER17: Russia, Tuva, Erzin District, Upper Naryn River, 50.22°N, 96.31°E, 421 (NCBI DQ347442, BOLD ABPS056-05), —, ZMMU S-46656 skin; HYPER18: Mongolia, Ara-Hangay Aymak, Bulgan, Urd-Tamrin-Gol River, 47.32°N, 101.10°E, 421 (NCBI DQ347444, BOLD ABPS080-05), —, ZMMU S-125772 skin; HYPER19: Russia, Krasnoyarskiy Kray, Ermakovskiy District, Kulumis Range, 52.97°N, 92.93°E, 657 (NCBI DQ347429, BOLD ABPS002-04), 674 (DQ335483), ZMMU S-167267 liver; HYPER20: Russia, Krasnoyarskiy Kray, Partizanskiy District, railway station Krol, 54.67°N, 93.50°E, 657 (NCBI DQ347430, BOLD ABPS003-04), 719 (DQ335484), ZMMU S-167268 liver; HYPER21: Russia, Krasnoyarskiy Kray, Kuraginskiy District, East Sayan Mountains, Nichka River, 54.15°N, 93.98°E, 657 (NCBI DQ347432, BOLD ABPS005-04), 719 (DQ335486), ZMMU S-170400 liver; HYPER22: Russia, Buryatia, Ulan-Burgasi Range, 34th km along the highway Ulan-Ude–Ust'-Barguzin, 51.98°N, 107.75°E, 657 (NCBI DQ347431, BOLD ABPS004-04), 719 (DQ335485), ZMMU S-169107 liver; HYPER23: Russia, Buryatia, Severo-Baykalsky District, Barguzinsky Zapovednik, Shumiliha River, 54.10°N, 109.58°E, 402 (NCBI DQ347443, BOLD ABPS076-05), —, ZMMU S-116195 skin.

Ochotona pallasi.—PALLASI1 (*O. p. sunidica*): China, Inner Mongolia, Dongwuqi, —, 719 (AF272990), Yu et al. (2000); PALLASI2 (*O. p. pallasi*): Kazakhstan, Taldi-Kurgan Region, S Shubartau foothills, 78.53°N, 46.83°E, 354 (NCBI DQ347458, BOLD ABPS086-05), 317 (DQ335522), ZMMU S-148337 skin; PALLASI3 (*O. p. pricei*): Russia, Tuva, Mongun-Taiginsky District, sur. of Mugur-Aksi Village, 50.32°N, 90.33°E, 657 (NCBI DQ347453, BOLD ABPS047-04), 391 (DQ335520), ZMMU S-168612 muscle; PALLASI4 (*O. p. pricei*): Russia, Gorniy Altay Republic, Kosh-Agachskiy District, Tashanta Village vicinity, 49.73°N, 89.19°E, 421 (NCBI DQ347452, BOLD ABPS091-05), —, ZMMU S-151829 skin; PALLASI5 (*O. p. pricei*): Mongolia, Bayan-Hongor Aymak, East of Mongolian Altay, 6 km SE from Bayan-Under, 47.79°N, 98.65°E, 421 (NCBI DQ347455, BOLD ABPS078-05), —, ZMMU S-117014 skin; PALLASI6 (*O. p. pricei*): Mongolia, Kobdo Aymak, Djungar Gobi, Baitag-Bogdo-Nuruu, 45.24°N, 90.99°E, 296 (NCBI DQ347456, BOLD ABPS082-05), —, ZMMU S-139660 skin; PALLASI7 (*O. p. pricei*): Mongolia, Bayan-Hongor Aymak, South Khangay, Dzag, 46.95°N, 99.15°E, 421 (NCBI DQ347454, BOLD ABPS057-05), —, ZMMU S-50495 skin.

Ochotona princeps.—PRINCEPS: unknown, 657 (NCBI AJ537415), 719 (AJ537415).

Ochotona rufescens.—RUFESCENS1: Iran, Khorasan Province, Quchan, Batkhor, 37.11°N, 58.78°E, 655 (NCBI DQ347459, BOLD ABPS098-05), —, ZMMU S-178636 liver; RUFESCENS2: laboratory strain, 719 (AJ132206).

Ochotona "*scorodumovi*."—SCORODUM1: China, Helongjing, Wudalianchi, —, 719 (AF272994), Yu et al. (2000); SCORODUM2: Russia, Chita Region, Sretenskiy District, vicinity of Ust'-Chernaya Village, right bank of Shilka River, 52.94°N, 119.09°E, 657 (NCBI DQ347449, BOLD ABPS040-04), 683 (DQ335518), ZMMU S-175365 liver; SCORODUM3: Russia, Chita Region, Mogochinskiy District, vicinity of Anikino Village, 53.42°N, 120.37°E, 657 (NCBI DQ347450, BOLD ABPS097-05), —, ZMMU S-175369 skin; SCORODUM4 (topotype): Russia, Chita Region, Krasnokamensky District, vicinity of Kaylastuy, 49.83°N, 118.25°E, 657 (NCBI DQ347451, BOLD ABPS102-05), —, ZMMU S-178619 liver.

Ochotona turuchanensis.—TURUCH1: Russia, Krasnoyarskiy Kray, Taymirskiy AD, Glubokoe Lake, 69.32°N, 89.98°E, 657 (NCBI DQ347465, BOLD ABPS010-04), 391 (DQ335491), ZMMU S-162965 liver; TURUCH2: Russia, Krasnoyarskiy Kray, Taymirskiy AD, Glubokoe Lake, 69.32°N, 89.98°E, —, 719 (DQ335493), ZMMU

S-162967 liver; TURUCH3: Russia, Krasnoyarskiy Kray, Taymirskiy AD, Glubokoe Lake, 69.32°N, 89.98°E, —, 719 (DQ335497), ZMMU S-162971 liver; TURUCH4: Russia, Krasnoyarskiy Kray, Taymirskiy AD, Glubokoe Lake, 69.32°N, 89.98°E, —, 694 (DQ335496), ZMMU S-162975 liver; TURUCH5: Russia, Krasnoyarskiy Kray, Taymirskiy AD, Glubokoe Lake, 69.32°N, 89.98°E, 657 (NCBI DQ347462, BOLD ABPS015-04), 719 (DQ335495), ZMMU S-162976 liver; TURUCH6: Russia, Krasnoyarskiy Kray, Taymirskiy AD, Glubokoe Lake, 69.32°N, 89.98°E, 657 (NCBI DQ347466, BOLD ABPS014-04), 719 (DQ335494), ZMMU S-162977 liver; TURUCH7: Russia, Krasnoyarskiy Kray, Taymirskiy AD, Glubokoe Lake, 69.32°N, 89.98°E, 657 (NCBI DQ347464, BOLD ABPS009-04), 719 (DQ335490), ZMMU S-163474 liver; TURUCH8: Russia, Krasnoyarskiy Kray, Taymirskiy AD, Kutaramakan Lake, 68.78°N, 91.87°E, 657 (NCBI DQ347467, BOLD ABPS028-04), 391 (DQ335506), ZMMU S-164007 liver; TURUCH9: Russia, Krasnoyarskiy Kray, Taymirskiy AD, Kutaramakan Lake, 68.78°N, 91.87°E, 654 (NCBI DQ347460, BOLD ABPS023-04), 719 (DQ335501), ZMMU S-164015 liver; TURUCH10: Russia, Krasnoyarskiy Kray, Taymirskiy AD, Kutaramakan Lake, 68.78°N, 91.87°E, 657 (NCBI DQ347461, BOLD ABPS027-04), 479 (DQ335505), ZMMU S-164019 liver; TURUCH11: Russia, Krasnoyarskiy Kray, Taymirskiy AD, Kutaramakan Lake, 68.78°N, 91.87°E, 652 (NCBI DQ347468, BOLD ABPS029-04), 675 (DQ335507), ZMMU S-164022 liver; TURUCH12: Russia, Irkutsk Region, Zhigalovskiy District, vicinity of Dalnyaya Zakora Village, 54.69°N, 104.62°E, 657 (NCBI DQ347463, BOLD ABPS007-04), 719 (DQ335488), ZMMU S-171587 liver; TURUCH13: Russia, Irkutsk Region, Ust-Kutsky District, vicinity of Ust-Kut, 56.69°N, 105.72°E, —, 391 (DQ335525), ZMMU S-165402 skin.