

## Comparative Phylogeographic Patterns of Several Vertebrates in the East Palearctic

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**Abstract**—An overview of our own and literature molecular phylogenetic studies on intraspecies variability in widely distributed Asian fishes, amphibians, birds, and mammals is presented. In many cases, the populations from the southeastern parts of the species ranges demonstrate distinct sets of haplotypes and increased variability. This means that such populations might have experienced isolation in refuges and that eastern Asia might have served as a hotspot in the speciation process for many Asian animals.

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Molecular phylogenetics (and its subdiscipline, comparative phylogeography) offers opportunities for understanding the evolutionary history of not only particular species, but also of their complexes. This overview provides some our own and the published data on the phylogeography of species of fish, amphibians, birds, and mammals that were widely distributed in the Palearctic.

The group of species of freshwater fish of sculpins of the *Cottus poecilopus* complex is distributed over all of the north Palearctic. The endemic of southern Primorye, sculpin *Cottus volki* was separated as an independent species on the basis of several morphological differences; however, it is considered that it belongs to this complex. It forms a cluster on the phylogenetic tree constructed on the basis of complete sequences of the control region of mtDNA that is separate from other members of the complex, as a sister group close to the tree root [1]. Its basal position on the tree is supported by the presence in *Cottus volki* of several ancestral characters [2]. This suggests that it was isolated from the main trunk of the group in the Pliocene or early Pleistocene.

The siberian salamander *Salamandrella keyserlingii* is distributed over a vast territory in northern Asia, from the Urals to Chukotka and north of Hokkaido. The species is monotypic; although morphologists have found some insignificant distinctions in the salamanders from Primorye, they do not distinguish even a subspecies. However, the haplotypes of the mitochondrial gene of cytochrome b (*cyt b*) in salamanders from Primorye drastically differ from those of the remaining part of the range from the Urals to Sakhalin. The divergence level reaches 10%, which is comparable to differences between definite species and

even genera in other groups of amphibians. Based on these genetic and some morphological differences, the species status of salamanders from Primorskii and Khabarovsk regions, viz., the Schrenck newt *Salamandrella schrenckii*, was proven [3]. This discovery demonstrates once again the possibilities of using modern molecular genetics for fauna inventory.

*S. schrenckii* has high intraspecies and intrapopulation variability. As well, haplotypes of its mitochondrial DNA have some specific features that permitted the suggestion that the population from the Primorye passed a shorter evolutionary route from its predecessors and acted as an ancestor to the remaining populations. The genetic homogeneity of the Siberian salamander throughout the range can be explained by the rather rapid dispersal of individuals to the west and to the north. The subdivision of the haplotypes of *S. schrenckii* into “northern” and “southern” forms, which differ by 3.2%, was found. A unique replacement of isoleucine by valine at codon 119, which is conserved in the Hynobiidae family, in all haplotypes of the “northern” cluster and only part of the haplotypes of the “southern” cluster indicates the origin of the “northern” form of *S. schrenckii* on the basis of the “southern” form. As well, only the “northern” cluster exhibits signs of demographic expansion [4].

The genus *Onychodactylus*, clawed newts, is distributed less widely than oriental salamanders and both species of the genus are endemic to eastern Asia. On the phylogenetic tree constructed from complete sequences of gene *cyt b*, haplotypes of newts *Onychodactylus fischeri* from Primorye differ from the remaining *Onychodactylus* by 14.9% (p-distance). The divergence level of Korean and Chinese newts of *Onychodactylus japonicus* is 10.3%, that of Korean from

Chinese is 8.4%, and Korean between themselves, 2.1%. The population from Primorye turned out to be exactly at the base of the entire tree of the genus, which suggests its separation from the trunk as early as in the early Miocene during the separation of mountain systems accompanying the formation of the Sea of Japan [5]. Molecular-genetic data suggest the presence of several cryptic species within *O. fischeri* in the motherland.

The eastern subspecies of carrion crow *Corvus corone orientalis* is distributed from the Yenisei to Kamchatka and Japan. The pattern of phylogeography according to the *cyt b* gene unexpectedly revealed subdivision into two groups of haplotypes. One belongs to the populations of Primorye, Japan, and southern Sakhalin and the other, to the remaining extended range [6]. The average Kimura 2-parametric distance between them is 2.5%. The use of another, more rapidly evolving site of mtDNA, the Control Region, supported and provided detail for this result [7]. Besides of Primorye, the southern part of Khabarovsk krai and Japan, haplotypes of the southeastern cluster were found in a certain proportion in populations of northern Sakhalin and Kamchatka. Only the western cluster corresponds to the model of population expansion. Such a pattern suggests the presence in the past of genetic isolation of the southeastern population, under whose conditions a special genotype formed.

We found a similar pattern of intraspecies differentiation for the magpie *Pica pica*. Over its extended transpalearctic range, populations of the southeastern part belonging to two subspecies, *P. p. jankowskii* and *P. p. sericea*, are distinguished. Their mitochondrial haplotypes form isolated clusters on phylogenetic trees; p-distances of 6.6%, according to the control region, and 5.1%, according to *cyt b* gene, occur [8].

The great spotted woodpecker *Dendrocopos major* is distributed over the entire Palearctic. Two intraspecies groups differing by 3% according to incomplete sequences of three genes, *ND2*, *ND3*, and *cyt b*, for a total of 1365 bp were found. One of them corresponds to populations of Primorye, Sakhalin, and Hokkaido. It is suggested to restore the species status of the subspecies *D. m. japonicus* that unites them, which was initially described as a separate species [9]. Between the studied samples throughout the remaining range, from Khabarovsk to Finland, variation is almost lacking, which suggests rapid dispersal after the melting of glaciers.

The Korean field mouse *Apodemus peninsulae* is widely distributed in the Palearctic. The study of the mitochondrial gene *cyt b* demonstrated that in the population from Primorye, the haplotypic diversity is higher than in the populations of Sakhalin, Korea, and Siberia. The remaining haplotypes can be deduced precisely from the Primorye haplotypes. It has been suggested that the Pleistocene refugium from which the population was distributed to Siberia, north Asia, and Hokkaido was located here [10]. Later using the

same gene, but in more comprehensive material with the method of median networks, it was proven that the initial haplotypes are localized in populations of Primorye, Khabarovsk krai, and Sakhalin. The derivatives of these haplotypes are those of Siberia, Japan, and Korea. A similar pattern was obtained for a closely related species, the striped field mouse *Apodemus agrarius* [11].

The asian chipmunk *Tamias sibiricus*, which is distributed in eastern Asia, also exhibited deep differentiation into two groups of mitochondrial haplotypes corresponding to the geographic grouping of populations. One haplogroup corresponds to the populations of Korea, and the other, to the populations of Primorye, the Magadan oblast, Transbaikalia, and north-eastern China. The distance between them reaches 11.3%, which exceeds the average interspecies level of differences, whereas within the groups it is 1.9% and 1%, respectively. In both clades, population growth was shown using Fs and pairwise distribution tests. The use of a molecular clock suggests the presence of two independent refugia, one in Korea, and the other in the southeast of Russia, which were isolated in the glacial period. Considering the high mobility of the chipmunk, it is of interest to note that within Korea three groups of haplotypes diverged to the same degree as the haplotypes of northeastern China, Magadan oblast, and Transbaikalia are distinguished [12].

In most of the cited examples, the *cyt b* gene of mtDNA was used as the most popular molecular marker, which revealed not only interspecies differences, but also intraspecies structure. The assessment of the time of divergence is still ambiguous because of dissimilar rates of evolution in different lineages and with respect to different genes, as well as due to the absence of convincing calibrations based on paleontological data. Because of the limited size of this paper, we only mention a few of all the publications on the molecular phylogenetics of transpalearctic animals. In many such papers, the absence of phylogeographic structure is shown, which in most cases can be explained by the recent extension of their ranges. The examples listed here, on the contrary, indicate a distinct structuredness, which suggests the existence of common factors that determined the fate of the species. The genetic variability in the southeastern marginal parts of the ranges of these species is increased and the corresponding clusters are near the bases of phylogenetic trees. This may be evidence of the presence here in the past (presumably in the Pliocene or early Pleistocene) of isolates in refugia with subsequent dispersal. The southeastern marginal populations of many transpalearctic animal species thus served as a center of genetic diversity and speciation.

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