Phylogeography of water louse *Asellus aquaticus* (L.) (Crustacea: Isopoda) in Europe

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Water louse, *Asellus aquaticus* (Linnaeus, 1758) is an ubiquitous isopod crustacean – widely distributed all over the Europe, in a variety of freshwater to brackish habitats – feeding on detritus. Thus, it appears to be a remarkable model organism for phylogeographic research. Despite the fact, that the most of the species range seems to be inhabited by morphologically uniform populations of the nominotypical subspecies *A. aquaticus aquaticus* Linnaeus, 1758, a few endemic populations, spatially restricted mostly to the southern Europe, were described as other subspecies or forms. The previous studies revealed deep genetic subdivisions within the morphospecies *A. aquaticus*, suggesting the presence of putative cryptic species.

The current study concerns phylogenetic relationships within the morphospecies *A. aquaticus* covering almost the entire range of the taxon – from the British Isles and Scandinavia in the north, to the Mediterranean and Black Sea coasts, and Asia Minor to the south. The main goal of the research was to explore and embed the population genetic structure into paleo-geographical context, using DNA molecular data from three loci: one mitochondrial – cytochrome oxidase subunit I gene (*CO1*), and two nuclear – *28S rRNA* gene (*28S*) and internal transcribed spacer II (*ITS2*), and bioinformatic tools. The presence of putative cryptic species was demonstrated, including the time frame for their divergence. The historical and present-day demography, migration patterns and occurrence of possible glacial refugia for particular lineages were illustrated.

The mitochondrial DNA-based phylogenetic and species delimitation approaches showed that *A. aquaticus* morphospecies most probably originated in the Pannonian part of the Paratethys Sea and is a conglomerate of genetically distinct lineages, most of which diverged during the Late Miocene and Pliocene (*ca.* 8-2.5 Ma). Currently, they have narrow ranges in southern Europe, including the recently described endemic *Asellus kosswigi* Verovnik, Prevorčnik & Jugović, 2009 from the north-western Dinaric Karst (for which other lineages are paraphyletic). On the other hand, one lineage is widely distributed in Europe and seems to correspond to the nominotypical subspecies *A. a. aquaticus*, for which a recent population expansion was revealed, both in demographic and spatial terms. It probably emerged and initially diversified in the Dinaric Western Balkans in the Middle/Late Pliocene (*ca.* 4-2.5 Ma) with several subclades surviving and diversifying through the Pleistocene glaciations (since *ca.* 2.5 Ma). This taxon is characterized by the greatest colonisation potential, exhibiting the ability of wide range dispersal, possibly derived also by anthropogenic vectors and/or ectozoochory. In spite of the general absence of spatial genetic structure within *A. a. aquaticus*, the coalescent approach revealed two different phylogeographic stories involved in its diversification. Firstly, for the proglacial cluster group – widely distributed in areas close to the glacier margins (north of the Alps, Sudetes, Carpathians) and in the Pannonian Basin – which is relatively younger and composed of many closely related individuals. It originated in Pleistocene and lasted continuously through the Last Glacial Maximum (25-17 kya) in numerous high latitude refugia. This was probably due to the vast network of proglacial lakes and rivers, which played a crucial role in the maintenance of genetic diversity, population growth, and high dispersal rate. These findings are confirmed by trace fossils from the proglacial lacustrine sediments, discovered in northern Europe. Conversely, the periglacial cluster group – spatially restricted mainly to the northern Balkans, Pontic Region, and also the Pannonian Basin – is older and more divergent. It apparently retained a relatively stable population size during the glacial interglacial cycles, without signs for expansion. These results contradict the previous assumption of glacial refugia for the taxon located at lower latitudes.

The mitochondrial lineages are not reciprocally monophyletic with respect to the nuclear markers. This phylogenetic pattern can be interpreted predominantly as a result of incomplete lineage sorting, potentially indicating an ongoing speciation process, but also as an effect of introgression caused by secondary contact of formerly peripatric or allopatric populations.

The current research enriched the knowledge about the past natural processes as well as the more recent anthropogenic influences, which shape the extant population genetic structure of modern European biota. The evolutionary history of *A. aquaticus* revealed unexpected patterns and is an important lesson when making predictions for other aquatic taxa. Reasonably, the data can be used in comparative studies, including cryptic species, invasive species, and the effects of climatic changes on living organisms. The results underline the relevance of species delimitation when using water louse in environmental or ecological studies and, in more practical context, as a bioindicator in water quality assessments. Moreover, the outcomes of the research suggest that we should stop perceiving the proglacial habitats as inhospitable, lifeless ice deserts.