

INTROGRESSION: IN A CONTACT ZONE OF TWO CLOSELY RELATED SPECIES? NOT NECESSARILY

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Introgressive hybridization, also known as introgression, is the gene flow from one species into the gene pool of another, by the repeated backcrossing of an interspecific hybrid with one of its parent species. Several recent studies have uncovered genetic evidence for hybridization and introgression in different animal groups (e.g. Bierne, *et al.*, 2003; Kokshoorn and Gittenberger, 2012; Keller, *et al.*, 2013; Morii, *et al.*, 2015; Wenne, *et al.*, 2016) although the introgressive hybridization is most often cryptic and only revealed from studies that combine nuclear and mitochondrial DNA data. It is expected to occur across hybrid zones, in sympatry or at least parapatry, and between closely related species (e.g. Katoh and Ribí, 1996). However, hybrids may occur sometimes between phylogenetically distant species, whose reproductive isolating mechanisms, inevitably effective during speciation process, later have been lost (Falniowski, *et al.*, 1993).

Hauffenia Pollonera, 1898 and *Kerkia* Radoman, 1978 are two genera of minute (shell diameter about 1 mm) valvatoïd-shelled snails. They both belong to the family Hydrobiidae, but not represent sister clade relationships, thus are rather distantly related phylogenetically. They inhabit caves and other subterranean waters in the Balkans. Rysiewska *et al.* (in press) reported introgression of the 'Hauffenia' mtDNA type from central Slovenia into two different clades of *Kerkia*, one from Ljubač in central Croatia, and another from Podgrade in southern Croatia. Two latter populations are about 150 km apart and belong to the *Kerkia* lineage considering the three nuclear loci. Their mtDNA was most similar to *Hauffenia erythropomatia* (Hauffen, 1856) from the cave Babja luknja in Slovenia, about 210 km and 360 km from Ljubač and Podgrade, respectively. The introduced 'Hauffenia' mtDNA type and the closest *H. erythropomatia* COI differed by 0.8% only.

The tendency of mtDNA to cross interspecific barriers is somewhat counterintuitive as it could give rise to hybrid dysfunction due to the key function of enzymes involved in the oxidative-phosphorylation process. Besides through recombination and horizontal gene transfer, such crossing can happen through hybridization, when F1 hybrids backcross with one or both parental species and foreign

genetic material is integrated into the genomes of either parent. Introgressive hybridization obscures species boundaries. Hence, the study of interspecific gene flow is fundamental to understand the molecular mechanisms of speciation and species delimitation, how species maintain their biological integrity despite exchanging genes and the role of adaptation in the process of genetic introgression (Arnold, 2006). Gene flow between closely related taxa may be a product of a neutral event that has no effect on an individual's phenotype or fitness, or adaptive consequences of hybridization and gene exchange may occur (Arnold, 2006; Abbott *et al.*, 2013). The interspecific mtDNA gene flow via hybridization has been documented mainly in the contact zones (e.g. Morii *et al.*, 2015; Harrison and Larson, 2014; Wenne *et al.*, 2016) and between closely related taxa. Several hundred kilometers, as well as high level of phylogenetic distance between populations of *Kerkia* and *Hauffenia* can therefore cast doubt on the adequacy of postulating the introgression as a cause for similarity in the COI gene.

Possible explanations would be that either pseudogene *would* have been *amplified* in *Kerkia* from Podgrade and Ljubač, or strong natural selection would act similarly upon populations involved. The lack of stop codons and indels in the COI sequences, as well as their identical length, both contradict the anticipated pseudogenes. Meanwhile the presence of the *Hauffenia*- and *Kerkia*-type haplotypes in Ljubač population rejects the selection theory. Considering the fact that *Kerkia* and *Hauffenia* are still living in sympatry in some places (e.g. cave Krška jama, although without introgression), such a situation with the subsequent hybridization might well existed also in the past. Later, the transfer of the "new" introduced mtDNA to other *Kerkia* populations and its subsequent loss in some of them might occur – possibly as a result of natural selection or genetic drift.

As already stated above, hybridization between distantly related taxa may sometimes occur (e.g. Falniowski, *et al.*, 1993). Huge geographical distance among the populations listed above is harder to comprehend. It might simply be overestimated due to the undersampling. Little or no information is available on the abundance and *distribution*

of the interstitial (wells, gravel bars) and troglotic (caves) microgastropods as limited accessibility coupled with tininess makes their sampling extremely challenging. Mainly, collections consist exclusively of the empty shells and therefore the vast majority of the subterranean snails are known only from their shell morphology. Sampling is highly weather-dependent; the best time is after heavy rains following a prolonged dry period. Usually several repeat visits to the site are required to obtain at least some living specimens. Apart from the undersampling, degradation of water resources in the Balkans might have contributed to the extensive fragmentation of species ranges, increasing the distances among our taxa. Animals adapted to subterranean environments are thought to be highly geographically isolated due to their limited tolerance of physical conditions on the surface as well as limited dispersal ability. However, such isolation is not necessarily the case, and several records of unexpectedly high levels of gene flow between springs, also the ones theoretically isolated, are known. Moreover, the distribution of the interstitial fauna might be much more continuous than already recorded, due to data deficiency. Anyway, a recent contact between *Hauffenia erythropomatia* and *Kerkia* from Podgrađe and Ljubač is unlikely. So the introgressed mtDNA probably represents a remnant of past hybridization and may reflect ancestral continuous distribution of the studied taxa.

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