

# Maternal Genetic Legacy of the Eastern Adriatic Island of Krk – An Interplay of Evolutionary Forces and Island’s Historical Events in Shaping the Genetic Structure of Contemporary Island Population

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## ABSTRACT

*This study presents genetic diversity and structure of contemporary Krk islanders revealed by high-resolution mitochondrial DNA analysis on a sample of 132 unrelated autochthonous adults from seven different settlements and regions of the island. Relatively high level of haplogroup and haplotype diversity in the overall island sample is an indicator of numerous migrations and gene flows throughout the history. Expectedly, the results show the highest frequency of haplogroup H (33.3%), yet this value is much lower compared to different Croatian and other European mainland populations. An interesting finding refers to highly elevated frequencies of some haplogroups, otherwise rare in Croatia and most of the Europe, such as I (11.3%) and W (7.6%) in Krk population, especially pronounced in some settlements. At the level of settlements, many of the major European haplogroups were found to be absent from their mtDNA gene pools, whereas several others show a pronounced deviation from an average. Overall, our results suggest a tangled interplay of different evolutionary forces, such as founder effects and a few strong bottlenecks, presumably due to epidemics, which have occurred in various periods of the island’s history. Cultural customs, such as frequent endogamy in some regions of the island during past centuries, have additionally shaped its genetic structure into the observed present-day diversity patterns.*

**Key words:** *Island of Krk, genetic isolate, mitochondrial DNA, founder effect, bottleneck, endogamy*

## Introduction

With its surface of 405.78 km<sup>2</sup> (together with its neighboring island of Cres), Krk is the largest island of the Adriatic archipelago, located in the northernmost part of the Adriatic in the Kvarner bay (Figure 1). The climate is mostly Mediterranean. In its interior, the island hides fertile valleys and forests, while fresh water is available from two natural lakes and many pools in the

woods surrounding the town of Dobrinj. The vicinity of the mainland, good climatatic conditions, well-indented coastline and abundance of fresh water have made this island an ideal territory for human inhabitation since prehistoric times.

The oldest archaeological evidence for human presence on Krk is found in Vogranska cave in the vicinity of

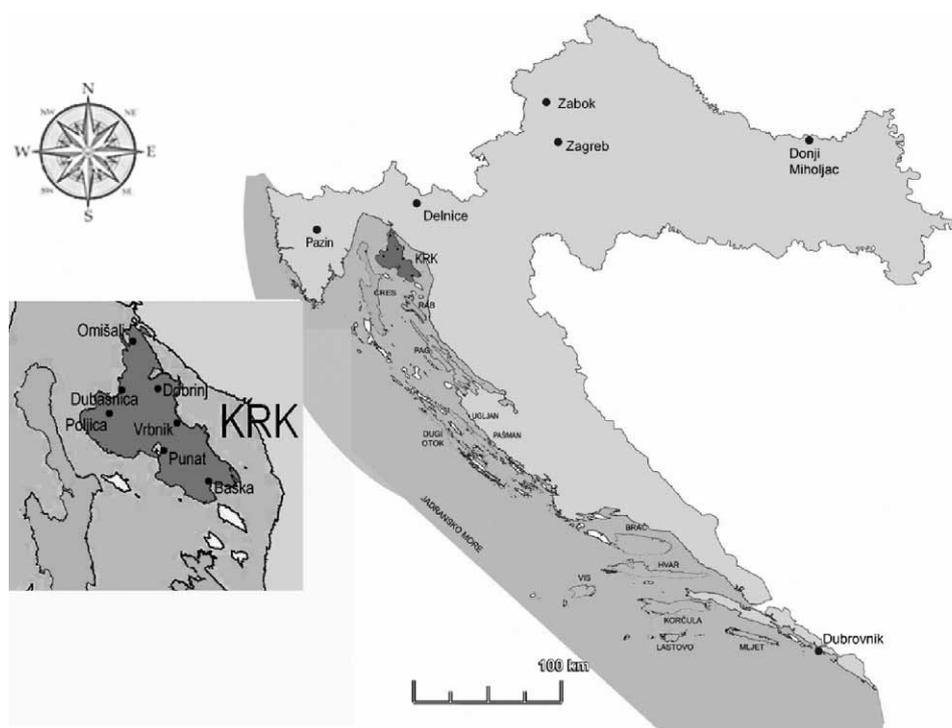


Fig. 1. Geographic position of the island of Krk with its investigated settlements, as well as position of other Croatian mainland and island populations used for comparison.

Baška<sup>1</sup>. Other remains of the first settlements dating from the Neolithic, Bronze and Iron Ages are found around Vrbnik, Garica, Baška and the village of Polje. In the last millennium B.C., the first historically recorded peoples in this Adriatic region were Illyrian tribes Japodi and later Liburni: well-known sailors and pirates who made their living from seafare and trade<sup>2</sup>. The most likely Liburnian settlements on the island of Krk were the towns of Krk and Omišalj. In the next centuries the island of Krk comes under the rule of the Roman Empire when major settlements, the towns Krk (Curicum, Curicta) and Fulfinium (near Omišalj) were built on the locations of the earlier Liburnian settlements<sup>3</sup>.

One of the most significant periods in history with strong impact on genetic legacy of the Krk islanders was the arrival of Slavic tribes (Croats) between the 6<sup>th</sup> and the 8<sup>th</sup> centuries. Newcomers were mainly cattle-breeders and farmers and they occupied rural island regions, while indigenous Roman descendants retreated to fortified towns, such as the town of Krk (Vecla). Toponyms of settlements and other locations on the Krk island clearly point to the stratification of ethnic groups that inhabited this island over the course of history. Three major historical periods could be emphasised; pre-Romanic, Romanic and Slavic<sup>4</sup>. The oldest Slavic settlements on the island are Dobrinj, Omišalj, Vrbnik and Baška<sup>4,5</sup>. After the fall of the Western Roman Empire in the year 476, the whole area of Kvarner bay and Dalmatia came under the rule of the Byzantine Empire and later of Venice. In 1118 duke Dujam, the ancestor of the Frankopan family comes into

possession of the Krk island. This wealthy and powerful family reigned over the island in the next few centuries<sup>6</sup>. In the middle of the 15<sup>th</sup> century it inhabited the western part of the island named Dubašnica and Poljica, fertile but unoccupied land, with groups of immigrants from the hinterland of the Velebit mountain. They were called Vlachs or Morlachs. These new families formed new settlements on the island. They were mostly of Slavic origin, including also some families speaking the Romanian language, incomprehensible to local indigenous islanders<sup>6-10</sup>.

The island fell again under the Venetian rule in 1480 until its demise in 1797. After a short French rule, the Habsburg Monarchy reigned over the island until 1918.

Only in the 20<sup>th</sup> century, after the unstable period of wars and Italian occupation, the island of Krk finally becomes fully integrated as a part of Croatian territory.

The history of this island was turbulent not only because of many migratory waves but also due to occasional economic crises, wars and outbreaks of epidemics that struck the islanders. The very first appearance of plague on Krk in 1348 coincided with its first occurrence in Europe. This serious disease appeared again in several recurrent epidemics during the Middle Ages. In the middle of the 19<sup>th</sup> century the epidemic of cholera spread from Venice and Adriatic coastal region all the way to Krk island<sup>11</sup>. Its consequences were devastating for the Krk populations, as were of the Spanish influenza in the beginning of the 20<sup>th</sup> century<sup>12</sup>. A specific way of settlement building with narrow streets facilitated the spreading of these lethal diseases among the population. The western

part of the island with the youngest settlements was composed of dispersed villages, so its inhabitants mostly evaded these epidemics. However, this region was infected by malaria from the earliest times in the history of the island, due to natural lakes and swamps present there. Malaria was the cause of high mortality until the early 20<sup>th</sup> century when it was finally eradicated<sup>13</sup>.

The above mentioned leads to the assumption that many evolutionary forces and historical events left their imprints in shaping the genetic structure and diversity of contemporary Krk population. Island isolates are generally among the most suitable populations for theoretical analyses of microevolutionary processes and population differentiation<sup>14–18</sup>. Analyses of mtDNA in such isolated populations proved to be very informative in microevolutionary studies<sup>19–21</sup>. Genetic diversity of mitochondrial DNA (mtDNA) in the Krk population was previously studied on the basic level of haplogroup resolution<sup>20,22,23</sup>. In this study we continue our research on maternal genetic legacy using the high resolution analysis and complete sequencing of some intriguing mtDNA lineages found on Krk. Our aim was to resolve phylogenetic affiliation of mtDNA lineages of Krk islanders, not only at the level of the whole island, but also at the level of island regions or settlements.

## Materials and Methods

Blood samples were taken from randomly chosen 132 autochthonous unrelated adult individuals from seven settlements or regions of the island of Krk – 20 from Omišalj, 17 from Dobrinj, 19 from Dubašnica, 20 from Poljice, 19 from Vrbnik, 16 from Punat and 21 from Baška. All participants gave their informed consent. Genomic DNA was extracted from whole blood using the »salting out« procedure<sup>24</sup>. The hypervariable segment I (HVS-I) of the control region of mtDNA was PCR amplified, purified and sequenced on Applied Biosystems 3730xl DNA Analyzer using the Big Dye Terminator kit (Applied Biosystems, Warrington, UK). Haplogroup and subhaplogroup affiliation was determined through the combined usage of RFLP method and sequencing based on SNP polymorphisms in HVS I and II as well as in coding region of mitochondrial genome. Sequences were aligned and analyzed according to rCRS (NC\_012920), by using ChromasPro software (Technelysium Pty Ltd, Tewantin QLD, Australia). Haplogroup nomenclature was determined as previously described by Van Oven & Kayser<sup>25</sup>. In construction of phylogenetic networks both reduced median and median joining algorithms were applied as implemented in the program Network 4.502 (Fluxus Engineering Web site). According to the position in mitochondrial genome and the impact on network construction, different molecular weights were assigned to observed substitutions<sup>26,27</sup>. Genetic distances among the studied island and intra-island population, were calculated using Arlequin 3.5 software<sup>28</sup>. Placing the investigated populations in comparative context was performed using the Primer 6.0. software<sup>29</sup>, based on haplogroup frequen-

**TABLE 1**  
FREQUENCIES AND HAPLOTYPES OF (SUB)HAPLOGROUPS IN THE KRK POPULATION (IN PERCENTAGES)

(Sub)hg	HVS-I (-16000)	N	%
A4	223-290-311-319-362	1	0.76
H*	168	1	0.76
H*	362	1	0.76
H*	239-356	3	2.27
H*	241-311	1	0.76
H*	93-291	1	0.76
H*	93-309	1	0.76
H*	CRS	2	1.52
H1	CRS	6	4.55
H13	CRS	2	1.52
H3	CRS	3	2.27
H5	304	12	9.09
H6	362	7	5.30
H6	189-362	1	0.76
H6	362-287	1	0.76
H7	221	1	0.76
H7	221-311	1	0.76
HV	311	6	4.55
I5a	129-148-223	2	1.52
I5a	129-148-223-391	6	4.55
I1a	129-172-223-311-391	6	4.55
I5a	93-129-148-223-391	1	0.76
J1c	69-126-224	1	0.76
J1c	69-126-261	1	0.76
J1c	69-126-309	1	0.76
J1c	69-126-366	2	1.52
J1c	69-92-126-261	7	5.30
K1	224-311	8	6.06
K1a	224-245-311	1	0.76
T1a	126-163-186-189-294	1	0.76
T2a	126-294-296-324-362	2	1.52
T2b	126-289-294-296-304-360	1	0.76
T2b	126-294-296-304	2	1.52
T2b	126-294-304-344	1	0.76
U2e	51-129C-189-362	2	1.52
U4	79-356	4	3.03
U5	192-270	1	0.76
U5a	256-270	3	2.27
U5a1	189-192-256-270-304-399	1	0.76
U5b1	136-192-256-270	2	1.52
U5b1	182-189-192-270	3	2.27
U5b1	189-270-278	4	3.03
U5b1	93-182-189-192-270	1	0.76
V	298	6	4.55
V	169-298	1	0.76
W3	223-270	1	0.76
W3	223-292	3	2.27
W6	192-223-292-325	5	3.79
W6	93-223-292-325	1	0.76

TABLE 2  
FREQUENCIES OF (SUB)HAPLOGROUPS IN 7 DIFFERENT SETTLEMENTS AND REGIONS OF THE KRK ISLAND (IN PERCENTAGES)

	N	H1	H3	H5	H6	H7	H13	H*	H	HV	J1c	J	T1a	T2a	T2b	T	K1	K1a	K	U2e	U4	U5a	U5a	U5b	U5b	U	V	I1a	I5a	I	A4	W3	W6	W			
	tot.																																				
Omišalj	20		15					10	25	25	25	25	10	5	15	10						10			5	15	10	5	5	10							
Dobrinj	17		11.8			11.8		17.6	29.4	17.6	17.6	17.6	5.9											11.8	11.8	5.9	29.4	35.3									
Dubašnica	19	5.3		5.3	10.5	36.8	10.5	5.3	5.3								21.1	5.3	26.3		5.3				5.3			5.3	5.3						10.5	10.5	
Poljica	20	15					5	5	25	20	5	5	5	5	5	5	15	15	5			5			10	15								5	5		
Vrbnik	19	10.5						5.3	31.6																26.3	26.3	5.3	21.1	21.1							15.8	15.8
Punat	16							25					12.5	12.5	6.3	6.3								6.3	12.5	18.8	6.3	12.5	12.5	6.3							
Baška	21			52.4				4.8	57.1								4.8	19							23.8						19					19	
Krk total	132	4.5	2.3	9.1	6.8	1.5	1.5	7.6	33.3	4.5	9.1	9.1	0.8	1.5	3	5.3	6.1	0.8	6.8	1.5	3	2.3	0.8	0.8	7.6	15.9	5.3	4.5	6.8	11.3	0.8	3	4.5	7.6			

cies of the Principal Component Analysis (PCA plot) or based on genetic distances (Fst) visualized as the dendrogram of genetic distances. Complete sequencing of the chosen samples was performed using the methodology described by Taylor and Rieder in 1998<sup>30</sup>.

### Results

The high-resolution mitochondrial DNA analysis of a sample of 132 adult Krk inhabitants revealed at least 26 different subhaplogroups and 49 haplotypes. Their frequencies and distribution in the populations sampled by us at the level of the whole island and seven island settlements are presented in Table 1 and 2, and visualized in Figure 2. Expectedly, haplogroup (hg) H is the most prevalent clade in the whole sample with a total frequency of 33.3%. Hg H is by far the predominant European haplogroup. Certain clades of this widely dispersed haplogroup proved to be molecular signals of peopling of Europe after the Last Glacial Maximum<sup>31–34</sup>. However, its frequency on the Krk island is significantly lower than among average European or Croatian mainland populations<sup>35–37</sup>. The majority of subhaplogroups belongs to H5 and H6 clades and a substantial portion of them belongs to so far unclassified branches denoted as H\*. This means that they do not belong to any of the in this study tested clades, neither to H1-H15 nor to H19-20. Haplogroup U is the second largest haplogroup on this island (15.9%, together with K 22.7%) represented by numerous lineages, mostly from U5b1 branch. The diversity of hg J (9.1%) is limited only to several lineages in J1c subhaplogroup, while its sister's clade T (5.3%) shows a greater variability of observed subhaplogroups. Within haplogroup K (6.8%) the majority belongs to ancestral K1 lineage, not divided into K1a, K1b or K1c clades, found only on the islands of Krk and Cres in the total Croatian sample<sup>38</sup>. Haplogroup V (5.3%) represents a rather substantial part of maternal genetic variation on this island. Together with HV (4.5%), the two are usually found at lower frequencies in genetically open European populations<sup>36,37,39</sup>. MtDNA haplogroups that derive directly from the superclade N (N1a, N1b, I, W, are X) are relatively rare in Europe and do not usually exceed the level of 5%<sup>35</sup>. In the Krk sample, probably due to the effect of genetic drift, including founder effect(s), N1a, N1b and haplogroup X were found to be completely absent, at least in our sample. The finding of haplogroup A4, a Northern Asian haplogroup<sup>40</sup>, only on this particular island in the total Croatian sample (although at a very low frequency) is a molecular signal of long-distance migratory events in the peopling of this region<sup>20,22,38</sup>. Some interesting findings include highly elevated frequencies of otherwise rare haplogroups, such as I (11.3%) and W (7.6%) in the overall Krk population, especially pronounced at the level of some settlements.

At the level of settlements (Table 2), many of the major European haplogroups were absent from their respective mtDNA gene pools. For example, haplogroup H is present in most of the settlements with only two or three

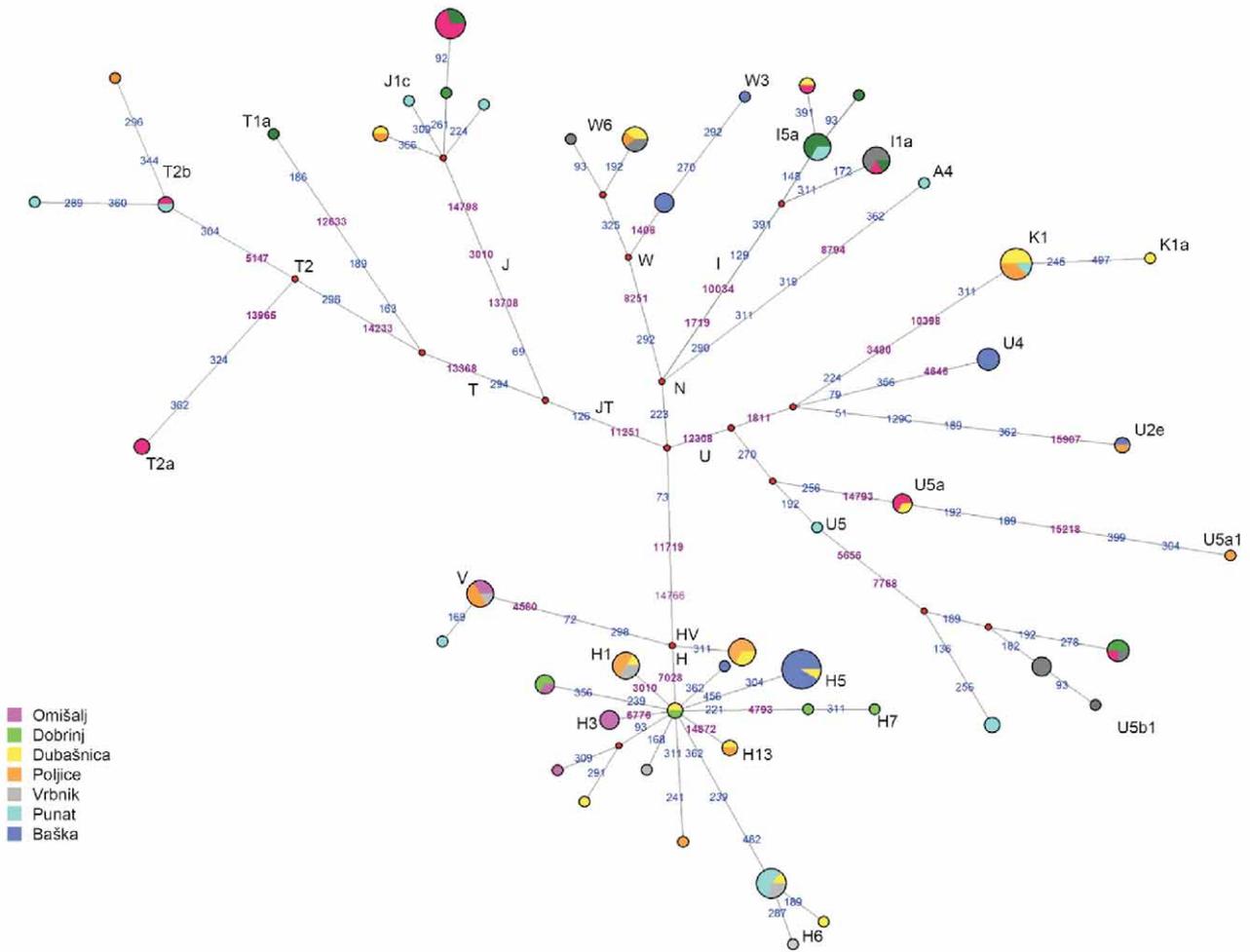


Fig. 2. Reduced-Median-Joining network of mtDNA haplogroups in 7 island regions and settlements. The node size is proportional to the number of samples. HVS-I mutations are shown in italic (–16 000).

low-frequency lineages. The town of Baška is not an exception in its general mtDNA variation pattern, but it is evident that one particular lineage of subhaplogroup H5 is present in more than 50% of the sample. A somewhat greater diversity of lineages is observed in Dubašnica and Poljica regions, the youngest island settlements with a higher influx of newcomers during the recent period of the island's history. These regions also exhibit a high variety of haplotypes, as it is seen from the network of all observed haplotypes (Figure 2). Some otherwise rare haplogroups, such as K1, HV and W6, are present mainly in this part of the island and can be considered as an example of recent gene flows from the mainland. The greatest deviation from the average population is demonstrated by a high frequency of haplogroup I in the region of Dobrinj, where its frequency exceeds 35%. There are several different lineages of haplogroup I, mainly present in the northwestern part of the island, where early Slavic influences are reflected in linguistic variants and toponyms. The complete sequences of two distinct I subhaplogroups are presented in Figures 3. and 4. Elevated fre-

quencies of the subhaplogroups of W clade are present mostly in the town of Baška (W3) and in Vrbnik, Dubašnica and Poljica (W6) while they are absent in the rest of the island.

To place the population of the Krk island in the context of the genetic landscape of the Eastern Adriatic as well as of the Croatian mainland, we made an interpopulation comparison with a number of other populations from different geographic regions of Croatia by comparing subhaplogroup frequencies through the PCA analysis (Figure 5). It is evident that all investigated island populations are to a smaller or greater extent isolated in comparison to the Croatian mainland. The island of Krk is presented as one of the Kvarner islands. The outlying position of this island population in comparison to other Eastern Adriatic islands is due to H5, W and I haplogroups. Also the overall population of this island is positioned closely to the mainland and it shows a relatively high index of genetic diversity of 0.9705 among Eastern Adriatic islands (data not shown)<sup>38</sup>.

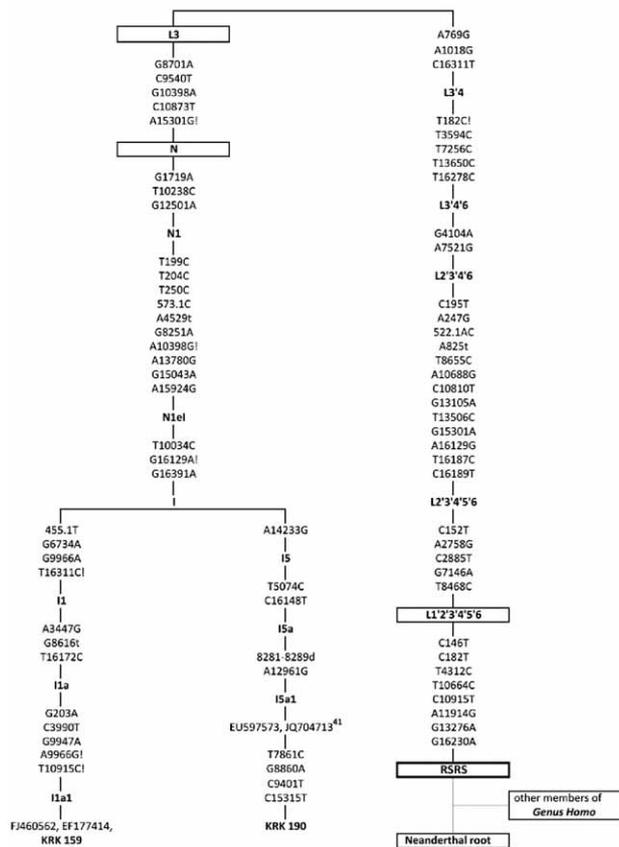


Fig. 3. Maximum parsimony phylogenetic tree for two I1a1 and I5a1 samples from Omišalj and Dobrinj, respectively. The tree is rooted in the Reconstructed Sapiens Reference Sequence (RSRS), as recently described in Behar et al 2012<sup>41</sup>. Scoring mutation in mtDNA genomic sequence relative to RSRS, allows to present them, contrary to rCRS-based scoring, in an evolutionary correct way – from ancestral towards derived character states. All mutations are shown on branches; they are transitions unless a base change is indicated by a small letter and deletions have a »d« prefix. Recurrent mutations are indicated by exclamation mark.

In order to estimate the relationship among seven different regions and settlements and to place them into a context of intra-island substructuring we performed the PCA analysis of the sampled island populations (Figure 6). The greatest outlying position exhibits Baška, the southernmost island settlement, mainly due to H5 and W3 and U4 haplogroups. A clear outlying position is observed for the Poljica and Dubašnica regions with many dispersed villages, founded in the 15<sup>th</sup> century, mainly by cattle breeders and farmers. Punat, Vrbnik, Omišalj and Dobrinj, old islands settlements with Slavic and pre-Slavic influences form the third cluster on PCA plot.

Genetic distances (Fst) obtained by the pairwise difference method are presented in Table 3 (Fst distances are placed above diagonal and their corresponding p-values below diagonal). Visual representation of Fst values is shown as a dendrogram of genetic distances between island subpopulations (Figure 7). These results are quite

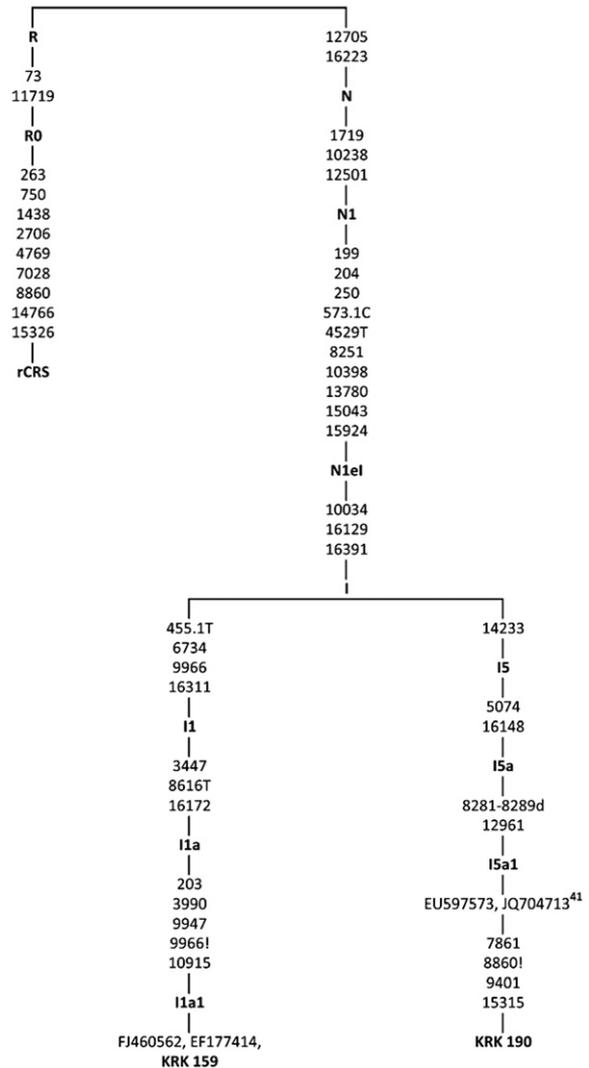


Fig. 4. Maximum parsimony phylogenetic tree for two I1a1 and I5a1 samples from Omišalj and Dobrinj, respectively, rooted in rCRS<sup>42</sup> for comparison with Figure 3. All mutations are shown on branches; they are transitions unless a base change is indicated by a letter and deletions have a »d« prefix. Recurrent mutations are indicated by exclamation mark.

similar to those of the principal component analysis (PCA) (Figure 6) and confirm the existence of isolation at the intra-island level. The most plausible explanation is that genetically closer founders inhabited different settlements in various periods of the island's history, while prolonged practice of endogamy and some strong bottlenecks created differences between investigated subpopulations.

In order to assess plausible similarity between maternal genetic substructure based on high resolution analysis of mtDNA and previously reported analysis of the linguistic features of different settlements carried out in the space of basic vocabulary<sup>43,44</sup>, we compared the dendrogram of genetic (Figure 7) and linguistic distances

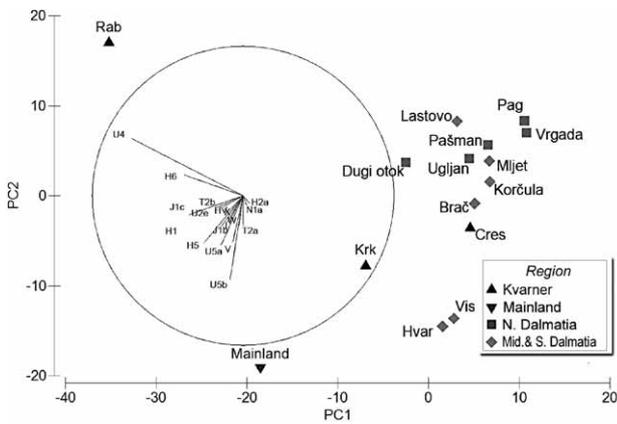


Fig. 5. PCA plot of Krk population (Kvarner region) and other mainland and island populations by Croatian regions. The first two principal components describe 71.4% of variation (45.1 and 26.3, respectively).

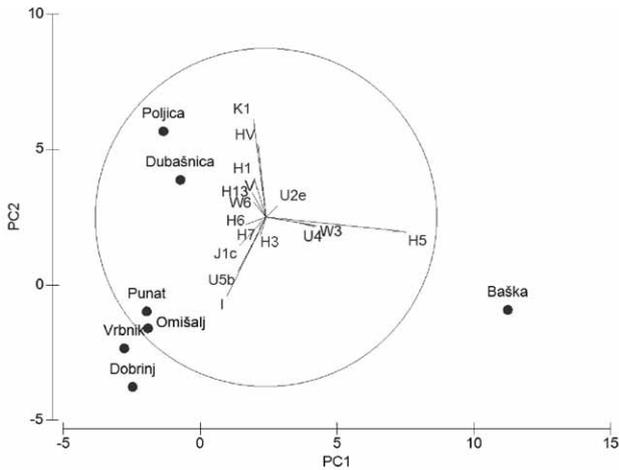


Fig. 6. PCA plot based on frequencies of subhaplogroups in the analysed island regions and settlements. The first two principal components describe 74.5% of variation (50.6 and 23.9, respectively).

(Figure 8) between different regions and settlements on the Krk island.

The dendrogram of linguistic distances in six investigated island settlements and regions shows the greatest similarity between Omišalj and Vrbnik, both closely related to Dobrinj, which is also one of the oldest Slavic settlements on this island. The remaining settlements form separate clusters. Similarities between Njivice and the rest of Dubašnica region can be explained by their mutual ancestry dating from the 15<sup>th</sup> century. Their local speech represents a modern variant of the local dialect, greatly distant from other dialects on this island. The greatest outlier stands for the population of Baška due to its specific dialectal variants<sup>43,44</sup>. The comparison of these two dendrograms (Figure 7 and 8) shows great similarities, the clusters of Baška, Dubašnica and Poljica and

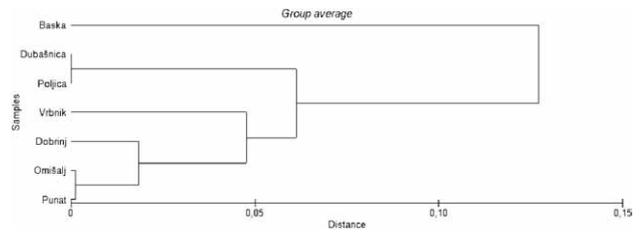


Fig. 7. The dendrogram of genetic distances on the island of Krk based on *Fst* values (group average method).

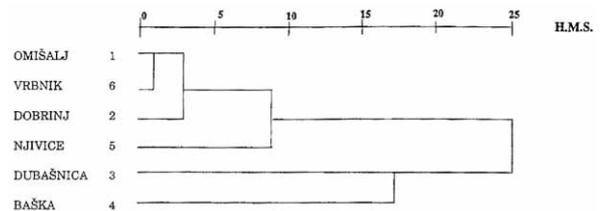


Fig. 8. The dendrogram of linguistic distances on the island of Krk based on HMS values (adopted from Sujoldžić et al. 1993<sup>43</sup>).

other investigated populations in the northwestern part of the Krk island are clearly separated, confirming their different genetic background and various migratory events in the island's history.

## Discussion

The aim of this study was to elucidate matrilineal population substructuring and genetic variability of the Krk island and its settlements shaped by evolutionary forces and certain cultural features. The background of these differences could be traced back to specific migratory waves of ethnically different groups in various periods in the history of the island. Toponyms on the Krk island, of pre-Romanic, Romanic and Slavic origin<sup>4</sup> show stratification of ethnic groups that inhabited this island since prehistoric times. After Illyrians and Romans, Slavic populations had the strongest influence on the genetic structure of the island between the 6<sup>th</sup> and the 8<sup>th</sup> centuries and even more recently in the 15<sup>th</sup> century, during the latest substantial migratory events. Together with their gene pools, the newcomers brought along different dialects of the Croatian language<sup>4,43,45</sup>.

The results of this study show a relatively high diversity of subhaplogroups in the overall island sample and a strong impact of founder effects. The analysis of the genetic structure at the level of seven settlements or regions shows a very high level of intra-island differentiation. Principal component analysis, *Fst* genetic distances and phylogenetic approach point to significant substructuring between different regions and settlements.

Meanwhile, the performed highest resolution structural analysis of some mtDNA genomes allowed us to show that sub-branches of hg I, one of the "anomalously" frequent mtDNA pool haplogroups found on Krk, are

**TABLE 3**  
POPULATION PAIRWISE  $F_{ST}$  DISTANCES (ABOVE DIAGONAL) AMONG ISLAND POPULATIONS AND CORRESPONDING  $p$ -VALUES (BELOW DIAGONAL) GAINED BY PAIRWISE DIFFERENCE METHOD

-	Omišalj	Dobrinj	Dubašnica	Poljica	Vrbnik	Punat	Baška
Omišalj	*	0.018	0.074	0.065	0.086	0.001	0.150
Dobrinj	0.220	*	0.082	0.102	0.039	0.019	0.168
Dubašnica	0.011	0.010	*	0.024	0.046	0.019	0.088
Poljica	0.023	0.006	0.853	*	0.069	0.034	0.101
Vrbnik	0.006	0.100	0.067	0.018	*	0.019	0.137
Punat	0.415	0.207	0.205	0.074	0.200	*	0.119
Baška	0.000	0.000	0.017	0.014	0.001	0.006	*

phylogenetically far apart within the haplogroup (Figure 3). Indeed, while at the level of HVS-based tree (Figure 2) they appear as rather close sister clades, complete sequence data show that they, in fact, differ in 21 nucleotide positions. Taking the coalescence age of hg I as equal to about 23 000 years<sup>41</sup>, one may assume that the two basal branches of hg I – I1 and I5 – separated already around the Last Glacial Maximum – yet their carriers co-inhabit now the same Adriatic island.

According to all preformed genetic analyses the town of Baška represents the greatest outlier. The region of Baška was inhabited by the first waves of Slavic immigrants into the island, as early as in 6<sup>th</sup> or 7<sup>th</sup> century, which is evidenced by the Slavic origin of its name<sup>4,44</sup>. Subsequent migratory flows brought new arrivals from the town of Senj. Their genetic, but also linguistic distance from other Krk settlements is further substantiated by the results of the analysis of their local dialects, that clearly separate Baška from the rest of the island due to its specific speech variants<sup>43,44</sup>. Numerous anthropological investigations, such as the study of HLA variants or hereditary dwarfism, seen only on this part of the island, have confirmed genetic isolation of the Baška region<sup>46,47</sup>. A very strong bottleneck that this population experienced in the middle of the 19<sup>th</sup> century was the epidemic of cholera. At that time 191 families were infected and some of them became extinct<sup>11</sup>, which could be one of the reasons for a lower level of its genetic variability. An elevated frequency of some subhaplogroups such as H5 and W3 and, on the other hand, a complete lack of other (probably lost from the gene pool) could be a sign of the above mentioned events.

Based on the performed analyses – phylogenetic approach, analysis of genetic distances and frequency of observed haplotypes – Omišalj, Vrbnik and Dobrinj on the Northwestern part of the island, as examples of the earliest Slavic settlements, form a joint cluster, separate from other investigated settlements. The linguistic and migrations distances also showed greater similarity and enhanced gene flow between them. The outlying position of the Poljica and Dubašnica regions with many dispersed villages founded and inhabited during the 15<sup>th</sup> century migrations of Slavic and Romanian families from the Velebit hinterland, relative to other island settlements is

clearly evident. Their shared genetic background has been supported not only by the results of the described genetic differentiation and variability, but also by the linguistic analysis, that reveal specific speech variants used in these settlements, but not found elsewhere on the island<sup>43,44</sup>.

It is possible that certain cultural customs, such as endogamy, influenced the formation of the genetic structure of contemporary Krk populations. Autochthonous folklore recorded in many villages suggests the existence of consanguineous marriages, often between first cousins<sup>48–50</sup>. The endogamy on the island was most likely due to financial reasons, because that way the land and other material goods given as dowry were kept in a family<sup>51</sup>. For this reason many of the island settlements have remained genetically closed communities over longer periods. The phylogenetic network of the observed haplotypes confirms the above mentioned custom. The closest settlements often share the greatest proportion of haplotypes, which is especially pronounced in Dubašnica and Poljica, as well as in Baška, genetically and geographically the most isolated settlement. These findings are also substantiated by the previous study of marital migrations on the island that showed a strong tendency to marriages between partners from geographically closer regions<sup>52</sup>.

This study of high resolution mitochondrial DNA analyses provides an insight into the genetic history of the Krk islanders. All presented findings confirm that the tangled interplay of evolutionary forces, especially of founder effects and bottlenecks together with some cultural customs have played a significant part in shaping the genetic structure of the contemporary populations of the island of Krk.

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## **MAJČINSKO GENETIČKO NASLJEĐE ISTOČNOJADRANSKOG OTOKA KRKA – MEĐUIGRA EVOLUCIJSKIH SILA I POVIJESNIH ZBIVANJA U OBLIKOVANJU GENETIČKE STRUKTURE DANAŠNJE OTOČKE POPULACIJE**

### **S A Ž E T A K**

Ovo istraživanje daje uvid u genetičku raznolikost i strukturu populacije današnjih stanovnika otoka Krka, na temelju analize visoke rezolucije mitohondrijske DNA. U istraživanje su uključena 132 odrasla, autohtona ispitanika iz sedam različitih naselja ili područja otoka Krka. Relativno velika raznolikost haplogrupa i haplotipova u ukupnome otočnom uzorku pokazatelj je brojnih migracija i tokova gena tijekom povijesti. U skladu s očekivanjima, rezultati su pokazali najveću učestalost haplogrupe H (33,3 %), ali mnogo manju u usporedbi s drugim, kopnenim populacijama Hrvatske i Europe. Zanimljiv nalaz je povećana učestalost inače rijetkih haplogrupa u Hrvatskoj i većini Europe kao što su I (11,3 %) i W (7,6%) u ukupnoj krčkoj populaciji, naročito izraženih u pojedinim naseljima. Na razini naselja mnoge su glavne europske haplogrupe odsutne iz genske zalihe, dok učestalosti pojedinih haplogrupa pokazuju značajna odstupanja od prosjeka. Sveukupni rezultati upućuju na zamršeno međudjelovanje evolucijskih sila, kao što su učinak utemeljitelja i nekoliko snažnih uskih grla, vjerojatno posljedica epidemija, koja su se zbivala u različitim razdobljima otočne povijesti. Kulturni običaji, kao što je učestala endogamija u pojedinim područjima otoka tijekom proteklih stoljeća, vjerojatno su doprinijeli oblikovanju današnje genetičke raznolikosti i strukture otoka.