Chapter 8

Associations between human genetic and craniometric differentiation across North Eurasia: The role of geographic scale

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Abstract

This study sets out to consider the influence of geographical scale on the association between molecular genetic differentiation and craniometric phenotypic differentiation in recent human populations. We employ interpopulation distance measurements for three different anatomical regions of the skull and for three different systems of genetic markers in 30 Eurasian populations. Our original dataset comprises 703 male skulls measured for 21 mid-facial, 15 neurocranial and 6 mandibular measurements, in all cases assessing Mahalanobis distances between populations. Published genetic data of more than 2,000 individuals were summarized by between-population F_{ST} based on allele frequencies of autosomal single nucleotide polymorphisms (SNPs), as well as Cavalli-Sforza distances based on the frequencies of 19 Y-chromosome and 29 mtDNA haplogroups. For different geographical scales of analysis, we used Mantel tests to assess the association of craniometric and genetic inter-population distances for the different cranial regions and genetic markers. Our results show that the level of association between craniometric and genetic distances depends on the part of the skull quantified and on the set of variables employed. In our dataset, this association is much stronger for the mid-face than for the cranial vault. Furthermore, the Mantel test correlation coefficients for the broadest, intercontinental level of analysis are moderate to high, and some are among the highest published so far. They are consistently lower at smaller geographic levels of comparison. Autosomal SNP

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distances exhibit the strongest associations with cranial morphology for almost all anatomical regions and at all geographical levels. Our results are evaluated against the background of previous studies assessing the correlation between craniometric, genetic, and geographic distances, drawing attention to the need for investing much more effort in studying factors affecting the association between genetic and craniometric distances at regional and local geographical levels.

INTRODUCTION

During the last two decades, molecular genetic data have been extensively used to validate the role of craniometric variables as a reliable source of information for reconstructing human population history (Roseman 2004; Harvati and Weaver 2006a; von Cramon-Taubadel 2009a; Evteev and Movsesian 2016; Reyes-Centeno et al. 2017, among others). This endeavor follows a decades-long debate on the evolutionary mechanisms affecting cranial form, particularly the degree of environmental and hereditary effects on cranial dimensions (Boas 1912, 1940; Sparks and Jantz 2002; Relethford 2004b, among others). On theoretical grounds, both biological data sources are expected to reflect the natural history of human populations (Relethford and Harpending 1994). For modern humans, this has been empirically supported by the observation that both molecular genetic diversity and cranial phenotypic diversity within modern human populations decreases from Africa, the continental geographic region of origin in the deep past (e.g., Relethford 2004a; reviewed in Reyes-Centeno 2016). In addition, genetic and cranial diversity between populations, i.e., biological distance, increases as a function of geographical separation between populations, i.e., geographical distance (Ramachandran 2005; Betti et. al. 2010). Methodologically, the approach for validating the utility of craniometric variables is therefore often based on the use of genetic distance data as a "gold standard," where it is employed as a benchmark for establishing the degree of biological variation between human populations. In general, it is thought that the higher the degree of association between craniometric and genetic distances is, the better the former reflects the biological relationship between human populations. In this chapter, we concentrate on this methodological approach for validating the utility of craniometric variables in reconstructing the human past.

Early heuristic studies comparing genetic and craniometric distances at the global level were optimistic in reporting moderate to high correlations between the two types of data (Relethford 2004a; Roseman 2004; Gonzalez-Jose et al. 2004; Harvati and Weaver 2006a, 2006b), which comprised both linear and three-dimensional morphometric variables as well as functional and non-functional regions of the genome. However, a bulk of subsequent studies has shown that the strength of the association between craniometric and genetic distances depends on a number of factors, including the part of the skull studied, morphometric technique

applied, system of genetic markers employed and, importantly, on the geographical scale of comparison, i.e., global (intercontinental), continental, or local (Harvati and Weaver 2006a, b; Smith et al. 2007; Smith 2009; von Cramon-Taubadel 2009a, 2009b, 2011a, 2011b, 2016; Ricaut et al. 2010; Reyes-Centeno et al. 2014, 2015, 2017; Herrera et al. 2014; von Cramon-Taubadel and Lycett 2014; Smith et al. 2016; Evteev and Movsesian 2016; Evteev et al. 2017; Moiseyev, de la Fuente 2017). For example, whereas some studies select parts of the skull with respect to hypotheses on skeletal integration and modularity (e.g., von Cramon-Taubadel 2011), others sample skull regions with respect to hypotheses on their phylogenetic utility (e.g., Harvati and Weaver 2006a, 2006b; Smith 2009; von Cramon-Taubadel 2009). In fact, because of distinct research designs, a wide range of statistical association between phenotypic and genetic variation has also been demonstrated in earlier works using anthropometric traits and genetic markers (Hiernaux 1956; Sanghvi 1956; Friedlander et al. 1971; Rothhammer and Spielman 1972; Spielman 1973; Neel et al. 1974; see also Relethford and Lees 1982 and Jorde 1980 for excellent reviews of previous literature). The relative effect of the study design factors listed above remains to be systematically tested since the great majority of recent studies were carried out at the global level and most of these employ only one system of molecular genetic markers.

The question of which anatomical region of the cranium reflects population history best has been a matter of great interest. It is generally agreed that a) the mandible displays the lowest correlations and, within the cranium, b) the temporal bone performs slightly better, probably due to its mostly chondrocranial embryonic origin (Harvati and Weaver 2006a; Nicholson and Harvati 2006; Smith 2009; Reyes-Centeno et al. 2017). However, results of different studies are not directly comparable due to the lack of uniformity in their research designs. It is also unclear if the trends observed at the global (intercontinental) level are applicable to a lower level of population differentiation, i.e., continental or sub-continental. This study therefore sets out to explore to what degree (i) the selection of craniometric and genomic markers, on the one hand, and (ii) the geographic scale of analysis, on the other, affect the association between genetic differentiation and craniometric interpopulation distances across North Eurasia. We employ measurements of three anatomical regions of the skull and three systems of genetic markers, as well as geographic distances across three geographic analytical scales. Importantly, the vast geographical space of North Eurasia has been underrepresented in previous craniometric-genetic association studies and the present work is thus intended to fill this gap. The results obtained for the study's dataset are evaluated against a background of a large number of correlation coefficients between craniometric, genetic, and geographic distances in the literature. Finally, we discuss the implications of our study in the context of a broader debate on the evolution of cranial form in modern humans.

MATERIALS AND METHODS

The cranial sample employed in this study consists of 703 male skulls from 30 Eurasian populations (Table 1) measured by one of the authors (AE; see Evteev et al. 2014 for the intraobserver error test) using a set of standard calipers according to a protocol including 21 mid-facial, 15 neurocranial and 6 mandibular measurements (see Appendix, Table S1, at the end of this chapter). Missing data were imputed by mean substitution with respect to each population, except in cases where an entire cranial region was missing. For example, mandibles were present only in some of the samples (see Table 1 for details of sample sizes). Raw cranial measurements used in this study are available on request. Matrices of Mahalanobis distances were calculated for every set of groups/variables separately for every particular analysis. Each analysis was conducted once using the raw craniometric variables and again using size-standardized variables, calculated by dividing each measurement by the geometric mean of all measurements, per individual (Darroch and Mosimann 1985).

Cranial samples were matched with molecular genetic data based on ethno-linguistic affinities and geographical origin. In total, we analyzed genetic data for three types of loci: autosomal single nucleotide polymorphisms (SNPs), mitochondrial DNA (mtDNA), and Y-chromosome DNA. First, the autosomal data were collected from two SNP chip array sources for published data of 26 Eurasian populations, comprising 1450 individuals in total (Tables S2, S3, Appendix). Data for the Adygeans were used for the Shapsugi cranial sample. Genetic variation between populations for SNP allele frequencies was calculated by between-population F_{ST} (Weir and Cockerham 1984) using the software 4P (Benazzo et al. 2015). Inter-population F_{ST} measures have been found to be highly correlated with Mahalanobis distances for craniometric variables (Reyes-Centeno et al. 2017). Second, we used haplogroup frequencies for the Y-chromosome and mtDNA data (Evteev et al. 2017), compiled from numerous studies (Table S4, Appendix) carried out using very divergent methodological approaches and styles of publishing of raw material (full mitochondrial genomes, or HVSI and II sequences, or frequencies of haplogroups). Thus, the only possible way of compiling these into a single dataset was to employ haplogroup frequencies. The Y-chromosome data for the Ulchi include samples of the Nanai. In total, we used frequencies of 19 Y-chromosome haplogroups and 29 mtDNA haplogroups to calculate Cavalli-Sforza distances (Cavalli-Sforza and Edwards 1967) for each system of genetic markers. In all cases, we compiled distance matrices representing inter-population genetic variation for the different genetic markers (Tables S6–S9, Supplementry online material). Table 1 lists details of the availability of different types of genetic markers for different cranial population samples. In most cases, all three molecular data types could be compiled.

Geographic distances between centroids of origin of all populations (Tables S10–S11, Supplementary online material) were calculated as great-circle distances (using the Haversine formula in: http://www.movable-type.co.uk/scripts/latlong.html), ignoring possible water and mountain barriers. In order to compare our results to previous studies, the strength of association between the matrices of craniometric, genetic, and geographic distances was assessed using Mantel tests (Smouse and Sokal 1986). These were carried out in PAST (Hammer et al. 2011) by setting the similarity measure as "User distance" universally for all matrices and testing for significance via 9999 permutations of the matrix values. Results are reported as Pearson *r* correlation values with one-tailed *p* significance values. In addition, we employed Dow-Cheverud tests (Dow and Cheverud 1985) to assess which of the subsets of the variables was statistically more associated with genomic markers in comparison to other cranial subsets. Dow-Cheverud tests were conducted in R using a script coded by M. W. Grabowski and C. C. Roseman.

In order to test the role of the geographical level of comparison (see Fig. 1), we used three areal divisions: intercontinental, continental, and local. First, the main dataset (30 populations, intercontinental level) was divided into two subsets: "West Eurasia" (17 populations, continental level) and "East Eurasia" (12 populations, continental level). These two are based on the separation of Europe and Asia as distinct continents and corresponds with analytical sub-divisions of previous morphological and genetic studies (e.g., Howells 1989; Hanihara 2000; Reich et al. 2012; Fu et al. 2013). As the origin and degree of admixture in the Saami is not completely clear (see Tambets et al. 2004), this population was not included in any of the two subsets. The latter were further divided into

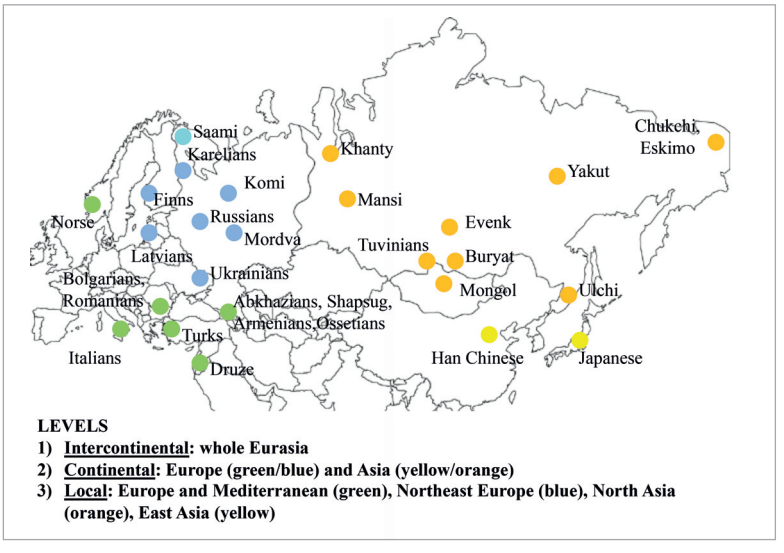

Fig. 1.
Geographic locations of the studied groups.

Sample	Genetic data availability[1]	Sample size (facial skeleton)	Sample size (neurocranium)	Sample size (mandible)	Collection[2]
Abkhazian	abc	15	15	0	RIMA
Armenian	abc	26	26	0	RIMA
Bulgarian	abc	15	14	7	RIMA
Buryat	abc	19	19	17	MAE
Chukchi	ac	31	30	14	RIMA
Druze	abc	21	20	0	MAE
Eskimo (Siberian Yupik)	abc	20	19	16	RIMA
Evenk	bc	15	15	8	RIMA / MAE
Finn	abc	21	21	11	RIMA /MAE
Han	abc	20	19	0	RIMA /NHM
Italian	abc	18	18	0	RIMA
Japanese	abc	26	26	23	RIMA / MDH
Karelian	abc	51	43	36	MAE
Khanty	bc	21	21	11	RIMA
Komi	abc	28	28	27	MAE
Latvian	bc	21	20	14	RIMA
Mansi	abc	16	16	0	RIMA
Mongol	abc	18	18	0	MAE
Mordovian	abc	28	25	25	RIMA
Norse	abc	18	16	8	NHM
Ossetian	abc	26	26	0	RIMA
Romanian	abc	32	22	32	FRI
Russian	abc	64	64	60	RIMA
Saami	bc	27	27	24	MAE
Shapsug	abc	15	15	0	RIMA
Turk	abc	11	11	9	RIMA
Tuvinian	abc	26	26	0	RIMA
Ukrainian	abc	12	12	0	RIMA
Ulchi	abc	22	21	17	RIMA / MAE
Yakut	abc	20	20	15	RIMA / MAE

Total number of samples	**30**	**30**	**19**
Total number of individuals	**703**	**673-683**	**374**

1 a: autosomal SNP data is present, b: Y-chromosome data is present, c: mtDNA data is present

2 Abbreviations: RIMA – Research Institute and Museum of Anthropology, Moscow State University; MAE - Museum of Anthropology and Ethnography (the Kunstkamera), Saint-Petersburg; NHM - Natural History Museum, London; FRI - Francisc Rainer Institute, Bucharest; MDH - Musée de l'Homme, Paris.

Sub-continent/Region
West Eurasia/ Europe-Mediterranean
West Eurasia/Europe-Mediterranean
West Eurasia/Europe-Mediterranean
East Eurasia/North Asia
East Eurasia/North Asia
West Eurasia/Europe-Mediterranean
East Eurasia/North Asia
East Eurasia/North Asia
West Eurasia/Northeast Europe
East Eurasia/East Asia
West Eurasia/Europe-Mediterranean
East Eurasia/East Asia
West Eurasia/ Northeast Europe
East Eurasia/North Asia
West Eurasia/Northeast Europe
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West Eurasia/Northeast Europe
West Eurasia/Europe-Mediterranean
West Eurasia/Europe-Mediterranean
East Eurasia/North Asia
West Eurasia/Northeast Europe
East Eurasia/North Asia
East Eurasia/North Asia

Table 1.
Cranial sample populations, genomic data matching, sample sizes, provenance, and geography.

two parts each according to the previously shown ecogeographic differences across those geographical levels (Evteev et al. 2014, 2017). The West Eurasian set was divided into a "Europe-Mediterranean" subset (10 populations, local level), including populations from South and West Europe, the Mediterranean, and the Caucasus, as well as into a "Northeast Europe" (7 populations, local level) subset. The East Eurasian set was divided into "North Asia" (10 populations, local level) and "East Asia" (2 populations, local level). The justification for such a division was the climate-morphology associations demonstrated in previous studies (Evteev et al. 2014, 2017) and separating the populations into presumably cold-adapted and non-cold-adapted. For instance, the Norse were included in the "Europe-Mediterranean" subset because, despite formally representing North Europe, they did not display a particularly strong climatic signal in their craniofacial morphology. Since only two populations were included in the "East Asia" subset, this level was not analyzed further. In total, 6 geographical scales and 3 hierarchical geographic levels of population differentiation were considered. The Karelian sample was excluded from the Mantel tests involving mtDNA matrices in the "West Eurasia" and "North Europe" datasets since it was identified as a genetic outlier. In most analyses, samples genotyped through the Affymetrix array (referred as Affymetrix dataset hereafter) comprising 50786 autosomal SNPs were employed. However, analysis of the Northeast Europe level employed data from the Illumina array (Illumina dataset hereafter), which comprised 114109 markers from 6 populations. The inclusion of both the Affymetrix and Illumina datasets for this particular level increased the number of population samples available for analysis (Tables S2, S3, Appendix). The two datasets provide very similar patterns of interpopulation distances (Mantel Pearson correlation: $r = 0.98$, two-tailed $p = 0.04$ after 1000 permutations) and were thus used interchangeably.

In order to test how the level of genetic or morphological differentiation within a geographical scale affects our Mantel test results, we evaluated the association between the mean Mantel correlation coefficients (Table 1) within a region and either mean autosomal F_{ST} or mean Mahalanobis distances (mid-face) within a region, quantified with the Spearman rank correlation coefficient (r).

In order to compare our results to previous analyses, a database containing about two hundred correlation coefficients between craniometric and anthropometric, as well as genetic distances in humans and nonhuman primates, published to date was compiled (Table S12, Supplementary online material). Ninety-six of these coefficients, calculated for worldwide (or intercontinental) modern human cranial samples using Mantel tests (Gonzalez-Jose et al. 2004; Roseman 2004; Harvati and Weaver 2006a, 2006b; Smith et al. 2007; Smith 2009; von Cramon-Taubadel 2009a, 2009b, 2011a, 2011b, 2016; Reyes-Centeno et al. 2017; Smith et al. 2016), were selected to be employed as source of comparison for our results.

A similar database containing more than eighty correlation coefficients between craniometric (anthropometric) and geographic distances, as well as latitude and longitude, in humans was also compiled (Table S13, Supplementary online material). Twenty eight of these coefficients were calculated for worldwide (or intercontinental) modern human cranial samples and geographic distances using Mantel tests (Relethford 2004b; Gonzalez-Jose et al. 2001; Smith et al. 2007; Hubbe et al. 2009, 2010, 2011; Betti et al. 2010; von Cramon-Taubadel 2011b, 2016; Noback and Harvati 2015; Reyes-Centeno et al. 2015) were selected to be compared with our results alongside with six coefficients (Rothhammer and Silva 1990; Lalueza Fox et al. 1996; Fabra and Demarchi 2011; Maley 2011; Weisensee 2013; Hubbe et al. 2014) for samples at lower geographic levels (continental, inter-continental, or local).

RESULTS

Associations at the intercontinental (North Eurasian) level.

Table 2 presents the results of all matrix correlations calculated for different cranial anatomical regions, genetic markers, and geographic distances across the different analytical scales and using the raw dataset. Results are similar when using size-standardized craniometric variables (Table S5, Appendix). All the coefficients at the intercontinental level are moderate to high (Fig. 2). But the strength of the association is clearly different between different systems of genetic markers and different anatomical regions (see Figs. 2 and 3). Correlations with the autosomal SNP data demonstrate the strongest associations, while they are weakest for the Y-chromosome data. Considering the lower levels of population differentiation, the autosomal SNP matrices are consistently more

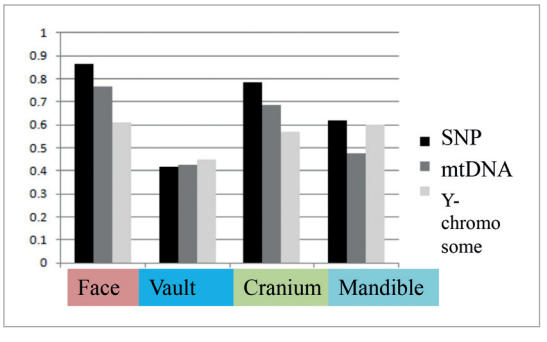

Fig. 2.
Correlations between the matrices of craniometric and genetic distances at the intercontinental analytical level.

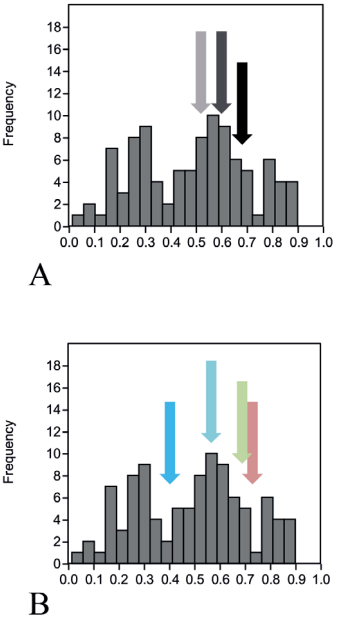

Fig. 3.
Mean coefficients obtained in the present study (intercontinental level) against the distribution of 96 coefficients published previously.
A) Different systems of genetic markers (arrows: SNP – black, mtDNA dark grey, Y-chromosome – light grey);
B) Different skull anatomical regions (arrows: face – pink, cranium – green, mandible – light blue, vault – deep blue).

Table 2.
Correlations[1] between the matrices of craniometric, genetic and geographic distances.

Analytical scale	Skull region[2]	SNP	mtDNA	Y-chromosome	Geography
Intercontinental	*North Eurasia*				
	Mid-face	**0.865*****	**0.767*****	**0.61*****	**0.76*****
	Vault	**0.416*****	**0.428*****	**0.448*****	**0.36*****
	Cranium	**0.783*****	**0.685*****	**0.57*****	**0.66*****
	Mandible	**0.617*****	**0.474*****	**0.6*****	**0.58*****
	mean	0.67	0.589	0.557	0.59
Continental	*East Eurasia*				
	Mid-face	**0.426***	0.25	**0.5****	**0.39***
	Vault	0.08	0.19	**0.34***	**0.36***
	Cranium	**0.36***	**0.3***	**0.52****	**0.44****
	Mandible	-0.03	-0.2	0.55	0.03
	mean	0.209	0.135	0.478	0.305
	West Eurasia				
	Mid-face	**0.54*****	0.17	**0.39*****	**0.27****
	Vault	**0.16***	0.12	0.02	0.21
	Cranium	**0.29***	0.15	0.19	**0.27***
	Mandible	**0.69****	0.003	**0.47***	**0.49*****
	mean	0.42	0.111	0.268	0.31
Local	*North Asia*				
	Mid-face	**0.685****	**0.56****	0.19	**0.5****
	Vault	0.22	0.24	-0.18	**0.44***
	Cranium	**0.55***	**0.45****	-0.005	**0.53*****
	Mandible	-0.17	-0.22	-0.1	-0.21
	mean	0.321	0.258	-0.024	0.315
	Europe-Mediterranean				
	Mid-face	**0.35***	0.1	0.21	0.25
	Vault	0.21	0.12	-0.03	0.04
	Cranium	0.2	0.15	0.08	0.11
	mean	0.253	0.123	0.087	0.133
	North Europe				
	Mid-face	0.17	-0.11	0.39	0.27
	Vault	0.2	0.81	0.17	0.18
	Cranium	0.12	0.53	0.26	0.18
	Mandible	-0.31	0.54	0.06	-0.12
	mean	0.045	0.443	0.22	0.128

1 Values are Pearson r correlation values; bold type indicates statistical significance after 9999 permutations (Mantel test): one-tailed * $p<0.05$; ** $p<0.01$; *** $p<0.001$.
2 Number of variables in anatomical region: mid-face = 21; vault = 15; cranium (mid-face and vault) = 36; mandible = 6.

associated with the craniometric distance matrices at all levels while the uni-parental markers display various patterns (Table 2; Figs. 5 and 6). The facial skeleton is the part of the cranium exhibiting the highest correlations with genetic distances in all the geographical scales studied (Table 2; Figs. 3, 5 and 6). The mandible displays on average higher coefficients compared to the vault. However, due to small sample sizes, the results for this bone are typically not statistically significant. Within the cranium subsets, the mid-face was significantly more associated with genomic distances than the vault at the highest, intercontintental scale (Dow-Cheverud $r = 0.512$, $p = <0.001$).

Study design factors affecting the association between craniometric and genetic distances at worldwide and intercontinental levels.

Based on our systematic literature review, we found that almost all correlation coefficients published previously (Table S12, Supplementary online material) which can be directly compared with those obtained in the present study were undertaken using worldwide or intercontinental cranial samples, employing geometric morphometric techniques and Mantel tests. Thus, only these geographic levels are considered in this section. However, several systems of genetic markers were used in previous studies and a variety of approaches to sampling of cranial variables were employed. The anatomical regions defined by different authors are numerous and differ with regard to their study design, using, for example, functional anatomical regions or developmental modules. The aggregated categories "braincase," "face," "cranium" and "mandible" are analyzed further. The single anatomical regions for which at least five coefficients were published by at least two authors were considered separately and include the following categories: "basicranium," "neurocranium," "temporal," "vault," "face" and "upper face." The genetic marker systems employed in the literature include: autosomal short-tandem repeats (i.e., STRs or microsatellites), mtDNA from coding regions, "classic" polymorphisms such as blood group or protein markers, and autosomal SNPs.

The mean coefficients for different cranial regions and genetic marker systems in the reviewed literature are presented in Fig. 4a and 4b, respectively, with the inclusion of our original results. An exceptionally high mean was obtained for the vault and, surprisingly, the lowest coefficients were for the neurocranium, which is practically synonymous to the vault. The means of other anatomical regions vary in a relatively narrow range from $r = 0.31$ (mandible) to $r = 0.56$ (cranium). Generalized anatomical regions—cranium, braincase and facial—display slightly higher mean coefficients compared to the others, including the temporal bone and the basicranium, that are argued to contain more phylogenetic information (Lockwood et al. 2004; Harvati and Weaver 2006b; von Cramon-Taubadel 2009a; Reyes-Centeno et al. 2017). The coefficients for the cranium and braincase obtained in the present study for North Eurasia

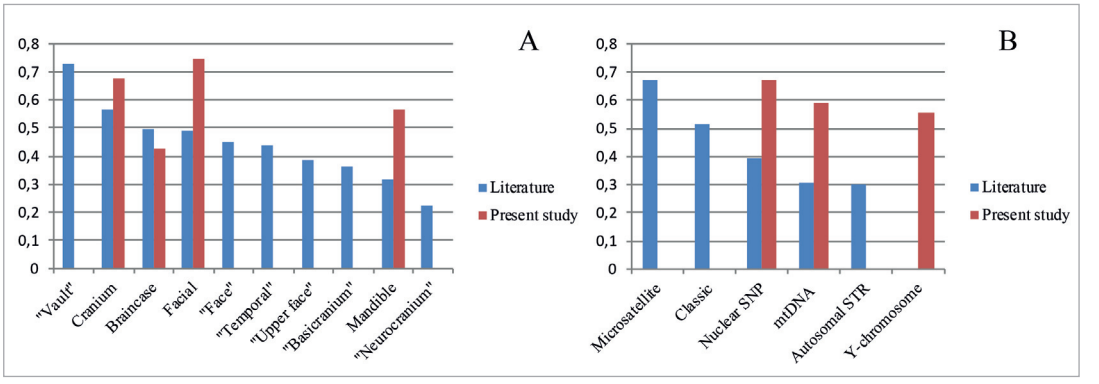

Fig. 4.
Mean correlation coefficients for different cranial anatomical regions and modules (a) and genetic marker systems (b). Reference literature consists of 96 studies. STR I – values published by various authors (Roseman 2004; Harvati and Weaver 2006a, 2006b von Cramon-Taubadel 2009a, 2009b, 2011a); STR II – values from Smith et al. 2007, 2016; Smith 2009.

are very close to the means of respective cranial regions while the coefficients for the facial skeleton and mandible are substantially higher than average (Fig. 4a). An interesting picture is observed for the means of the genetic marker systems (Fig. 4b). For instance, coefficients for the same sets of STRs can vary widely, likely because of a difference in cranial sample composition between different studies: compare STR-I and STR-II (Fig. 4b). The coefficients obtained in the present study for all three systems are about as high as the mean for previous studies using microsatellites. Notably, "classic" (i.e., serological) and uniparenatal markers at the worldwide level do not perform substantially worse than high-throughput nuclear markers.

Geographic distances.

The mean correlation coefficients between geographic and craniometric distances for the four cranial anatomical regions obtained in the present study is almost as high as the means for the autosomal genetic distances (i.e., $r = 0.59$ and $r = 0.67$, respectively; Table 2). It is also substantially higher than the mean ($r = 0.41$) of the 28 coefficients published previously (Table S13, Supplementary online material). The mean calculated across the five lower geographic levels and three cranial anatomical regions (except the mandible), $r = 0.3$, is slightly less than the value for the six analyses of continental, regional, or local levels found in the literature ($r = 0.44$). Importantly, our results show strong associations between geographical distances and the autosomal F_{ST} for some regions (North Eurasia – 0.95; East Eurasia – 0.83; North Asia – 0.82; Northeast Europe – 0.78) but not others (West Eurasia – 0.57; Europe-Mediterranean – 0.66).

Associations at the continental and local levels.

In general, a substantial drop in the strength of association between the cranial metrics, on the one hand, and genetic markers or geography, on

the other hand, is observed in the continental data subsets compared to the full North Eurasia (intercontinental) dataset (Table 2; Figs. 5 and 6). The same pattern is observed in the sub-continental levels compared to the continental ones, with the exception of North Asia, where correlation values in some cases increase. As evidenced in the summary of results in Table 2, autosomal SNP distances display the highest correlations with craniometric distances compared to other systems of genetic markers. Likewise, the mid-facial set of measurements consistently displays the highest correlations with genetic distances. Therefore, the two following aspects are considered below in more detail: the association of the mid-facial craniometric distances with various genetic and geographic distances (Fig. 5), and the association of autosomal SNP distances with various craniometric distances (Fig. 6).

While mtDNA distances exhibit higher correlations compared to the Y-chromosome at the intercontinental level, the opposite is true in 4 out

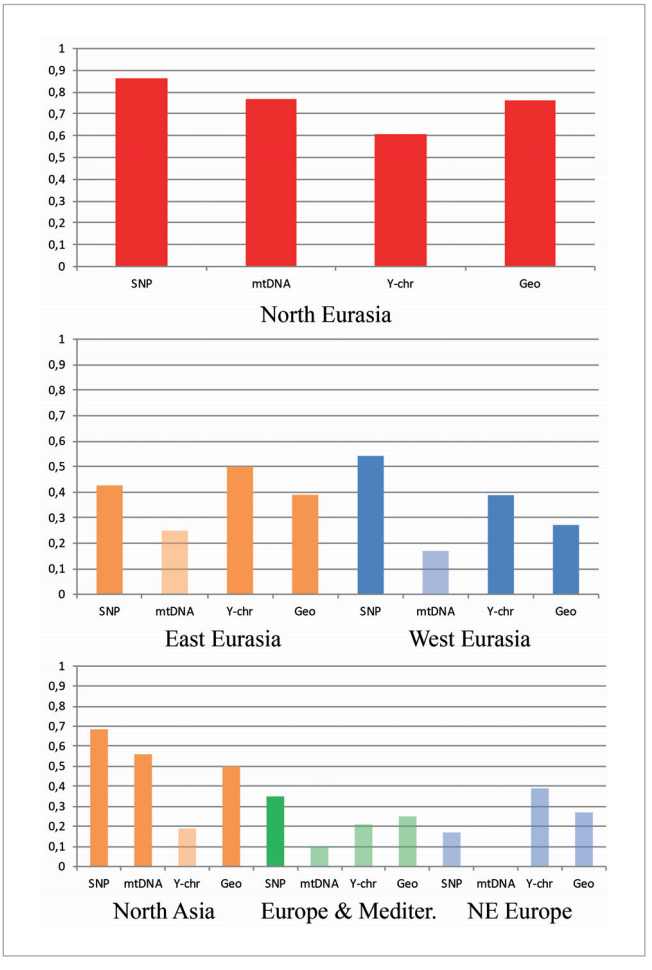

Fig. 5.
The associations between the mid-facial variables, various systems of genetic markers, and geographic distances. Y-axis on all plots corresponds to Pearson *r* correlation coefficients following Mantel tests. Statistically insignificant coefficients ($p \geq 0.05$) are depicted as transparent bars.

of 5 subsets at lower levels (Fig. 5). Coefficients for the mid-facial metrics (Fig. 6) are typically much higher compared to the vault. The results for the mandible are highly variable, ranging from negative to moderately high positive correlations (though not significant in most cases). The cranium in all geographical subsets displays slightly lower associations compared to the mid-face alone.

The results of the Dow-Cheverud tests for the continental scales show that the difference between the mid-face and vault at this level only applies to West Eurasia (Dow-Cheverud $r = 0.326$, $p = 0.004$) but not to East Eurasia (Dow-Cheverud $r = 0.305$, $p = 0.074$). At the regional scales, the mid-face was significantly more associated with genomic variation only at the North Asian scale (Dow-Cheverud $r = 0.393$, $p = 0.045$).

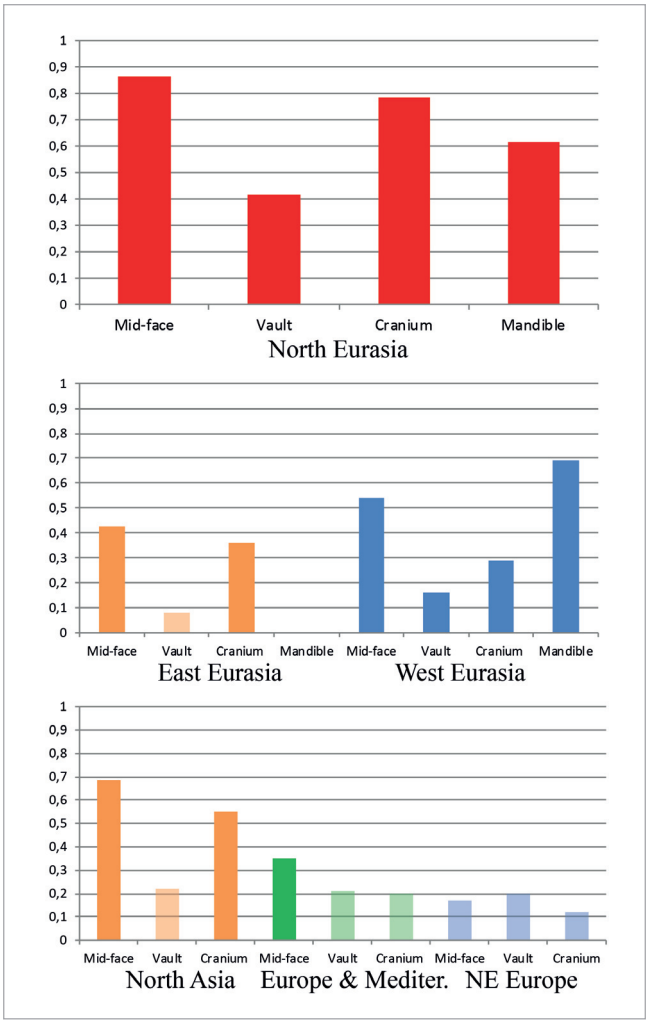

Fig. 6.
The associations between autosomal SNP markers and various anatomical regions of the skull. Y-axis on all plots corresponds to Pearson *r* correlation coefficients following Mantel tests. Statistically insignificant coefficients ($p \geq 0.05$) are depicted as translucent bars.

DISCUSSION

The values of the Mantel test coefficients obtained in this study for the intercontinental (North Eurasian) level are moderate to high, which is fully consistent with previous findings at the global level. Some of the coefficients are among the highest published so far. At this level, all the systems of genetic markers employed, as well as geographic distances, display similar results. However, autosomal SNP distances exhibit the strongest associations with cranial morphology in almost all geographical scales and at all levels. This is a predictable result considering that the mode of inheritance of SNPs and cranial morphological traits is similar: numerous loci spread throughout the genome, no sex linkage, relatively low mutation rate, etc. (Lynch 1989; Weaver 2011; Aime et al. 2015). Local variation of the association of cranial morphology with uniparental markers can, in turn, potentially reveal interesting stories about population history when considered against a "background" of autosomal data. For instance, in 4 out of 6 geographical scales Y-chromosome distances are more correlated with cranial morphology than mtDNA distances. We hypothesize that this result might be due, at least in part, to sex-biased migration patterns in different regions of Eurasia. Thus, this and other demographic factors may account for the differential association of craniometric diversity and sex-inherited genetic diversity. In order to further test these inferences using craniometrics, sampling crania of the female sex for the same populations would be necessary. In our opinion, simultaneous use of different systems of genetic markers in craniometric-genetic association studies can provide the most detailed picture of population history, as has been advocated in previous work (Herrera et al. 2014; Evteev and Movsesian 2016). Nevertheless, if only one type of markers is to be used, for instance as a control for population history or phylogeny, the preference, according to our results, should be given to autosomal data.

The results of our study confirm finds of previous works showing that the level of association between craniometric and genetic distances depends on the part of the skull quantified and on the set of variables employed. In general, this association is higher for the mid-face than for the cranial vault in all geographical levels across North Eurasia, as observed by the absolute Mantel test correlation values. The Dow-Cheverud test further showed that this difference is significant at the intercontinental scale, as well as at the West Eurasia and North Asia scales. This is despite the well-established associations of facial shape with climatic conditions in Eurasia (see Evteev et al. 2017 for a review). Importantly, previous work (Howells 1989; Betti et al. 2009) arrived at very similar conclusions for large worldwide datasets. The higher correlations observed for mid-facial traits compared to the vault are not completely unexpected since a number of studies show that the vault is a rather volatile structure which can change rapidly under the influence of a number of factors (Alexeeva 1968; Relethford 2004b). Thus, the mid-

facial region is often considered the most important area for ancestry assessment in forensic studies (e.g., Hefner 2009; Scholts et al. 2009). However, the analysis of coefficients published previously demonstrates that the strength of the association is basically identical for the face and braincase, at least at the worldwide level (but see Betti et al. 2009). Thus, the higher coefficients for the mid-facial skeleton might be specific for North Eurasia, suggesting that the cranial features that are most informative of population history or phylogeny might be found in different parts of the skull for different geographical regions.

Turning back to the analysis of literature data, our review sheds light on three primary points. First, it is clear that the cranium in general displays the strongest association with molecular genetics. The same applies to the generalized anatomical regions—face and neurocranium—compared to single bones or smaller units. The morphology of the temporal bone and basicranium do not appear more "phylogenetically relevant" than other modules. According to the same literature analysis, the lowest coefficients among all parts of the skull are typically obtained for the mandible. In the present study, the form of the mandible can display high correlations with genetic distances but these are highly variable across the geographical scales analyzed and are typically not significant. In this regard, it should be noted that sample composition in our study and others is quite different for the mandible compared to other anatomical regions, as the mandible is typically poorly presented in skull collections. Second, our review of the literature also shows that the use of linear measurements instead of landmark-based data employed in most recent works is not inferior in the strength of correlations with genomic data. This is an important observation from the point of view of studying fragmented cranial material since linear measurements can be more easily collected on fragmentary remains and in a cost-effective manner with a standard sliding caliper, in comparison to relatively costly instrumentation required for landmark data acquisition. Third, the results of some previous studies (e.g., Roseman 2004; Roseman et al. 2010; von Cramon-Taubadel 2014) show that the search for phylogenetically informative structures of the skull based on defining a priori modules might not be productive since "…environmental and genetic variation in individual traits are randomly distributed across regions of the cranium rather than being structured by developmental origin or degree of exposure to strain" (Roseman et al. 2010: 1). The use of linear measurements, which often run across different bones and cranial regions, provides an opportunity to apply a potentially more productive "module-free" approach in the search for phylogenetically important variables (see Betti et al. 2009, 2010; Roseman 2004). Likewise, existing (Roseman 2004; Betti et al. 2010; Roseman et al. 2010; Evteev et al. 2020) and novel (e.g., Rathmann and Reyes-Centeno 2020) "module-free" approaches can additionally offer an exhaustive summary of association between anatomical and molecular genetic variation under a framework that conforms to both quantitative genetics and population genetics theory.

With regard to how geography influences the association of cranial and molecular genetic variation, our results show that the correlation of the geographic distance matrices with craniometric ones is about as high as that of autosomal SNP matrices and less variable than the coefficients for uni-parental markers. This holds true for all anatomical regions and levels of comparison. However, the correlations between geographic and genetic matrices differ substantially in different geographical scales studied. Being very high in some levels, where morphological differentiation is strong and geographic distances are large (North Eurasia, North Asia), our results show that it is only moderate in other levels (West Eurasia, Europe-Mediterranean). Thus, geography can only very cautiously be used as a proxy for genetic distances, especially at local levels.

A less optimistic but important finding of this study is the fact that the strength of morphology-genetic association drops consistently and dramatically when moving from the intercontinental scale to lower geographic levels of comparison. In general, this result is expected as a result of the degree of gene flow, where populations close to each other are more likely to meet and exchange genes in comparison to populations far from each other. As such, gene flow is expected to have the immediate effect of homogenizing genetic structure in geographically proximate populations while its consequences for phenotypic variation may be much less pronounced, and this would affect the strength of association between genetic and craniometric data (Reyes-Centeno et al. 2017). Our results can also be explained by numerous confounding factors, the most apparent of which is the imperfect match between cranial and genetic samples. For example, in recent studies on the subject, genetic and morphometric data rarely come from the same individuals and often are not even from the same ethno-linguistic groups. Nevertheless, a number of studies (Hiernaux 1956; Sanghvi 1956; Friedlander et al. 1971; Rothhammer and Spielman 1972; Spielman 1973; Neel et al. 1974; Jorde, 1980; Relethford and Lees 1982) comparing somatometric variables, serological markers, and geographical distances using partially or completely overlapping samples show that even with such a study design, correlations at local levels are not high, and range from 0.17 to 0.55 (Tables S12–S13, Supplementary online material). Another factor is the inherent partial non-neutrality of cranial morphology which is, compared to neutral genetic markers, less affected by stochastic evolutionary factors like genetic drift, mutations, or founder effects. Even if morphological features are not under a direct influence of environmental factors, the need for making a functional structure makes their regulatory and protein-coding genes much more restricted in variation compared to a set of neutral genetic loci (see Lockwood et al. 2004; Weaver 2014). Interestingly, our results show that the strength of morphology-genetic association in North Asia is almost as high as that at the global level. This pattern can be explained by the fact that North Asian populations are extremely diverse in terms of cranial morphology and genetics simulta-

neously due to the large distances between the populations, their low population sizes, and relative isolation (Debets 1951; Jorde 1980).

Overall, our results provide a pattern that appears to be a general rule: a high level of genetic and/or morphological differentiation in a region leads to an increase of morphology-genetic correlations. Across the six regions studied, mean F_{ST} values based on autosomal markers in a region and Mantel test coefficient values between morphological and genetic distances within regions display a Spearman r correlation of 0.94 (p = 0.003). The same value for mean F_{ST} and mean Mahalanobis distance values is 0.71 (p = 0.14). Thus, the larger craniometric and genetic distances are in a region, the more similar picture of population relationship they tend to provide. As such, our results emphasize the need for investing much more effort in studying factors affecting the association between genetic and craniometric distances at different geographical scales. The strength of this association at worldwide or intercontinental levels is well established and is consistently moderate to high almost irrespectively of the variables used or the part of the skull employed. However, this firm observation can be of little practical value since in the great majority of craniometric studies, the researcher is concerned with interpopulation relationships at much lower geographic scales.

As a whole, our study has implications for the way that craniometric data is utilized in studies that aim to reconstruct the human past. We have shown that geographical scale is an important analytical factor affecting the association between genomic and cranial variation. Because the association between molecular genetic and craniometric datasets is not uniform across different geographical scales in Eurasia, studies that reconstruct population affinities or migration patterns need to explicitly consider the evolutionary forces that might differentially act across geographical space (e.g., see Hubbe, this volume, for a review on the effects of population migration events in Eurasia). Further work is also necessary in understanding how mechanisms in the past have influenced patterns of genomic and cranial variation of recent and present-day populations at different geographical scales.

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APPENDIX. SUPPLEMENTARY TABLES S1–S5.

Table S1.
List of skull anatomical regions analyzed and craniometric variables.

Cranial region	Code*	Name
mid-face	57/WNB	Simotic chord
mid-face	-/SIS	Simotic subtense
mid-face	56 (2)/-	Total lateral length of the nasalia
mid-face	50/-	Maxillofrontal (interorbital) breadth
mid-face		Nasal height from infranasion
mid-face	54/ NLB	Nasal breadth
mid-face	Premaxilla-4 (Evteev et al. 2017)	Frontal process height
mid-face	Premaxilla-6 (Evteev et al. 2017)	Height of the superior part of the piriform aperture
mid-face	Premaxilla-8 (Evteev et al. 2017)	Zygoorbitale subtense
mid-face	-/SSS	Zygomaxillary subtense
mid-face	45(3)/-	Zygoorbitale chord
mid-face	≈46/ZMB	Zygomaxillary chord
mid-face	Maxilla-3 (Evteev et al. 2017)	Oblique "cheek height"
mid-face	Maxilla-4 (Evteev et al. 2017)	Lateral length of the body of the maxilla
mid-face	Maxilla-5 (Evteev et al. 2017)	Length of the palate from subspinale
mid-face	Maxilla-6 (Evteev et al. 2017)	Internal breadth of the palate
mid-face	Cavity-2 (Evteev et al. 2017)	Inferior anterior breadth of the nasal cavity
mid-face	Cavity-3 (Evteev et al. 2017)	Posterior height of the nasal cavity
mid-face	Cavity-4 (Evteev et al. 2017)	Inferior posterior breadth of the nasal cavity
mid-face	59/-	Morphological height of the choanae
mid-face	≈ 59(1)/-	Choanae breadth

* Martin 1928 / Howells 1989.
** Nomenclature of the Pearson's Biometrics School.

Description	Source
Distance between the closest points of two nasomaxillary sutures	Martin 1928; Howells 1989
Subtense to simotic chord	Howells 1989
Infranasion – nasomaxillare	Martin 1928; Evteev et al. 2017
Maxillofrontale-maxillofrontale	Martin 1928; Evteev et al. 2017
Infranasion-nariale	Evteev et al. 2017
Alare-alare (nasolaterale-nasolaterale)	Martin 1928; Howells 1989
Maxillofrontale - the point of intersection of the inferior orbital margin and the tangent line to the lower margin of the sulcus lacrimalis	Evteev et al. 2017
Nasomaxillare - conchale	Evteev et al. 2017
Subtense to the chord between left and right zygoorbitale	Evteev et al. 2017
Subtense from tubspinale to the chord between left and right zygomaxillare	Howells 1989
Zygoorbitale - zygoorbitale	Martin 1928
Zygomaxillare- zygomaxillare	Martin 1928
Sum of the distances from the middle of the zygomaxillary suture to zygoorbitale and zygomaxillare	Evteev et al. 2017
Distance from sphenomaxillare superior to the most inferior point of the foramen infraorbitale	Evteev et al. 2017
Subspinale-staphylion	Evteev et al. 2017
Distance between left and right palatomaxillare laterale	Evteev et al. 2017
Maximal distance between the lateral walls of the nasal cavity below crista conchalis immediately after piriform aperture margin but before hiatus maxillaris	Evteev et al. 2017
From the point where the pterygopalatine suture intersects with the margin of the vomer to the most distant point on the floor of the nasal cavity	Evteev et al. 2017
Maximal distance between the lateral walls of the nasal cavity below crista conchalis anterior to choanae but posterior to hiatus maxillaris	Evteev et al. 2017
Staphylion - hormion	Martin 1928
Distance between the points of intersection of the pterygopalatine suture and crista conchalis	Martin 1928; Evteev et al. 2017

cont. ⟶

Table S1. cont.

Cranial region	Code*	Name
neurocranium	1/GOL	Maximum cranial length
neurocranium	8/XCB	Maximum cranial breadth
neurocranium	17/BBH	Basion–bregma height
neurocranium	5/BNL	Cranial base length
neurocranium	9/M9	Minimum frontal breadth
neurocranium	11/AUB	Biauricular breadth
neurocranium	29/FRC	Nasion-bregma chord
neurocranium	Sub. Nβ (Biometrics**)	Frontal subtense
neurocranium	30/PAC	Bregma-lambda chord
neurocranium		Parietal subtense
neurocranium	31/OCC	Lambda-opisthion chord
neurocranium		Occipital subtense
neurocranium	26/M26	Sagittal frontal arc
neurocranium	27/M27	Saggital parietal arc
neurocranium	28/M28	Saggital occipital arc
mandible	71a/-	Minimum width of the ramus
mandible	65/-	Condylar breadth
mandible	66/-	Bigonial breadth
mandible	67/-	Anterior breadth
mandible	69/-	Symphyseal height
mandible	69(3)/-	Corpus width of the mandible

* Martin 1928 / Howells 1989.
** Nomenclature of the Pearson's Biometrics School.

Description	Source
Glabella – opisthocranion	Martin 1928
Eurion-eurion	Martin 1928
Basion–bregma	Martin 1928
Basion-nasion	Martin 1928
Frontotemporale-frontotemporale	Martin 1928
Auriculare - auriculare	Martin 1928
Nasion-bregma	Martin 1928
Subtense to the nasion-bregma chord	Alekseev and Debets 1964
Bregma-lambda	Martin 1928
Subtense to the bregma-lambda chord	Alekseev and Debets 1964
Lambda-opisthion	Martin 1928
Subtense to the lambda-opisthion chord	Alekseev and Debets 1964
Arc from nasion to bregma	Martin 1928
Arc from bregma to lambda	Martin 1928
Arc from lambda to opisthion	Martin 1928
Minimum width of the ramus	Martin 1928
Maximum breadth between the mandibular condyles	Martin 1928
Maximum breadth between the mandibular angles	Martin 1928
Maximum breadth between the mental foramina	Martin 1928
Height of the mandibular symphysis in the mid-sagittal plane	Martin 1928
Maximum width of the mandibular body at the level of the mental foramen	Martin 1928

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Table S2.
List of genomic populations and sample sizes for Affymetrix dataset (50786 SNPs), paired with cranial populations.

Genetic Population (Affymetrix)	N	References	Cranial Population Match
Abkhasian	9	Lazaridis et al. 2014	Abkhazian
Adygei	17	Lazaridis et al. 2014	Shapsug
Armenian	10	Lazaridis et al. 2014	Armenian
Armenian_WGA	3	Lazaridis et al. 2014	Armenian
Bulgaria_POPRES	2	Nelson et al. 2008	Bulgarian
Bulgarian	10	Lazaridis et al. 2014	Bulgarian
Buryat	25	Xing et al. 2010	Buryat
CHB(Han_Chinese_in_Beijing_China)	84	Altschuler et al. 2010	Han (North China)
Han_NChina	10	Lazaridis et al. 2014	Han (North China)
Chukchi	20	Lazaridis et al. 2014	Chukchi
Druze	39	Lazaridis et al. 2014	Druze
Eskimo_Naukan	13	Lazaridis et al. 2014	Eskimo (Siberian Yupik)
Finland_POPRES	2	Nelson et al. 2008	Finn
Finnish	104	Auton et al. 2015	Finn
TSI(Tuscans_italy)	88	Altschuler et al. 2010	Italian
Italian_Bergamo	12	Lazaridis et al. 2014	Italian
Italian_South	1	Lazaridis et al. 2014	Italian
Italian_Tuscan	8	Lazaridis et al. 2014	Italian
Italy	213	Nelson et al. 2008	Italian
Japan_POPRES	68	Nelson et al. 2008	Japanese
Japanese	29	Lazaridis et al. 2014	Japanese
Japanese	13	Xing et al. 2009	Japanese
JPT(Japanese_in_Tokio)	91	Altschuler et al. 2010	Japanese
Mansi	8	Lazaridis et al. 2014	Mansi
Mongola	6	Lazaridis et al. 2014	Mongol
Mongola	2	López-Herráez et al. 2009	Mongol
Mordovian	10	Lazaridis et al. 2014	Mordovian
North_Ossetian	10	Lazaridis et al. 2014	Ossetian
Norway_POPRES	2	Nelson et al. 2008	Norse
Norwegian	11	Lazaridis et al. 2014	Norse
Romania_POPRES	16	Nelson et al. 2008	Romanian

cont. ⟶

Genetic Population (Affymetrix)	N	References	Cranial Population Match
Russia_POPRES	8	Nelson et al. 2008	Russian
Russian	22	Lazaridis et al. 2014	Russian
Russian	1	López-Herráez et al. 2009	Russian
Turkey_POPRES	7	Nelson et al. 2008	Turk
Turkish	4	Lazaridis et al. 2014	Turk
Turkish_Adana	10	Lazaridis et al. 2014	Turk
Turkish_Aydin	7	Lazaridis et al. 2014	Turk
Turkish_Balikesir	6	Lazaridis et al. 2014	Turk
Turkish_Istanbul	10	Lazaridis et al. 2014	Turk
Turkish_Kayseri	10	Lazaridis et al. 2014	Turk
Turkish_Trabzon	9	Lazaridis et al. 2014	Turk
Tuvinian	10	Lazaridis et al. 2014	Tuvinian
Ukraine_POPRES	2	Nelson et al. 2008	Ukrainian
Ukrainian_East	6	Lazaridis et al. 2014	Ukrainian
Ulchi	25	Lazaridis et al. 2014	Ulchi
Yakut	20	Lazaridis et al. 2014	Yakut
Total number of individuals:	**1093**		

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Table S3.
List of genomic populations and sample sizes for Illumina dataset (114109 SNPs), paired with cranial populations.

Genetic Population (Illumina)	**N**	**References**	**Cranial Population Match**
Finland	157	Leu et al. 2010	Finn
Finnish	100	Auton et al. 2015	Finn
Finnish	2	Hellenthal et al. 2014	Finn
Karelians	15	Yunusbayev et al. 2015	Karelian
Komis	16	Yunusbayev et al. 2015	Komi
Mordovian	15	Yunusbayev et al. 2012	Mordovian
Russian_central and South	32	Yunusbayev et al. 2015	Russian
Ukranian	20	Yunusbayev et al. 2012	Ukrainian
Total number of individuals:	**357**		

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Table S4.
Sample sizes for paired uni-parental genetic data (mitochondrial and Y-Chromosome DNA polymorphisms).

Cranial Population	mtDNA*	Y-chromosome**
Abkhazian	137 (Kutuev 2010)	162 (Kutuev 2010)
Armenian	191 (Richards 2000)	57 (Kutuev 2010)
Bolgarian	855 (Karachanak 2012)	808 (Karachanak 2013)
Buryat	101 (Pakendorf et al. 2003)	81 (Jin et al. 2009)
Chukchi	24 (Starikovskaya et al. 1998)	No data
Druze	622 (Shlush 2008)	109 (Zalloua 2008)
Eskimo (Siberian Yupik)	50 (Raff et al. 2015)	33 (Lell et al. 2002)
Evenk	40 (Pakendorf et al. 2003)	96 (Tambets et al. 2004)
Finn	432 (Meinila 2001; Richards 1996)	316 (Lappalainen 2006; Heinrich 2009)
Han (North Chinese)	322 (Jin et al. 2009)	242 (Jin et al. 2009)
Italian	70 (Rienzo 1991)	347 (Coia 2013; Batini 2015)
Japanese	211 (Jin et al. 2009)	154 (Jin et al. 2009)
Karelian	303 (Lappalainen 2008)	202 (Lappalainen 2006, 2008)
Khanty	209 (Pimenoff et al. 2006)	27 (Pimenoff et al. 2006)
Komi	214 (Osipova 2005)	153 (Mirabal 2009; Trofimova 2015)
Latvian	299 (Pliss 2006)	159 (Pliss 2015)
Mansi	95 (Pimenoff et al. 2006)	25 (Pimenoff et al. 2006)
Mongol	95 (Jin et al. 2009)	65 (Jin et al. 2009)
Mordovian	102 (Bermisheva 2002)	59 (Trofimova 2015)
Norse	74 (Passarino 2002)	1789 (Dupuy 2006; Batini 2015)
Ossetian	162 (Kutuev 2010)	153 (Kutuev 2010)
Romanian	146 (Jankova-Ajanovska 2014)	67 (Bosch 2005)
Russian	306 (Malyarchuk 2004)	183 (Fechner 2008; Malyarchuk 2008; Mirabal 2009)
Saami	637 (Ingman 2007)	189 (Dupuy 2006; Batini 2015)
Shapsug (Adygean)	155 (Kutuev 2010)	154 (Kutuev 2010)
Turk	190 (Quintana-Murci 2004; Jankova-Ajanovska 2014)	20 (Batini 2015)
Ukrainian	680 (Pshenichnov 2013)	154 (Mielnik-Sikorska 2013)
Ulchi	160 (Sukernik et al. 2012)	53 (Lell et al. 2002) (combined with the Nanai)
Yakut	83 (Pakendorf et al. 2003)	155 (Tambets et al. 2004)
Total	**6965**	**6012**

* Polymorphisms: A, B, CZ, D, F, G, HV, H, I, J, K, L, M, N, R, T, U*, U1, U2, U3, U4, U5, U6, U7, U8, V, W, X, Y.
** Polymorphisms: B, C, D, E, F, G, H, I, IJ, J, K, L, N, P, Q, R1a, R1b, R*, T.

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Table S5.
Correlations between the matrices of craniometric, genetic, and geographic distances for size-standardized craniometric variables.

Geographical Scale		SNP		mtDNA		Y-Chromosme		Geography	
		r-value	*p-value*	*r-value*	*p-value*	*r-value*	*p-value*	*r-value*	*p-value*
Eurasia	mid-face	0.904	0.001***	0.789	0.001***	0.589	0.001***	0.800	0.001***
	vault	0.409	0.001***	0.427	0.001***	0.441	0.001***	0.388	0.001***
	cranium	0.805	0.001***	0.700	0.001***	0.570	0.001***	0.693	0.001***
	mandible	0.243	0.031*	0.173	0.105	0.247	0.007**	0.279	0.011*
	mean	0.590		0.522		0.462		0.540	
East Eurasia	mid-face	0.639	0.011*	0.446	0.014*	0.463	0.004**	0.511	0.002**
	vault	0.152	0.377	0.275	0.085	0.413	0.016*	0.421	0.01**
	cranium	0.438	0.028*	0.356	0.050	0.553	0.003**	0.496	0.007**
	mandible	0.141	0.535	0.057	0.793	0.332	0.063	0.145	0.427
	mean	0.342		0.284		0.440		0.393	
West Eurasia	mid-face	0.631	0.001***	0.170	0.262	0.393	0.003**	0.265	0.017*
	vault	0.169	0.280	0.088	0.622	0.028	0.801	0.210	0.092
	cranium	0.318	0.04*	0.123	0.509	0.196	0.104	0.271	0.042*
	mandible	0.849	0.002**	0.165	0.598	0.395	0.048*	0.283	0.031*
	mean	0.492		0.136		0.253		0.257	
North Asia	mid-face	0.765	0.002**	0.676	0.001***	0.222	0.259	0.537	0.001***
	vault	0.207	0.272	0.281	0.098	-0.173	0.385	0.460	0.009**
	cranium	0.576	0.01**	0.507	0.006**	-0.015	0.935	0.587	0.002**
	mandible	-0.245	0.477	-0.146	0.564	-0.053	0.812	-0.075	0.678
	mean	0.326		0.330		-0.005		0.377	
Europe-Mediterranean	mid-face	0.321	0.105	0.085	0.682	0.091	0.638	0.122	0.538
	vault	0.188	0.447	0.081	0.713	-0.033	0.885	0.039	0.887
	cranium	0.221	0.363	0.116	0.630	0.060	0.730	0.121	0.604
	mean	0.264		0.153		0.028		0.165	
Northeast Europe	mid-face	0.139	0.687	-0.117	0.741	0.490	0.055	0.242	0.330
	vault	0.190	0.699	0.790	0.065	0.213	0.417	0.182	0.447
	cranium	0.153	0.695	0.537	0.208	0.292	0.260	0.193	0.456
	mandible	0.002	1.000	0.850	0.049*	0.125	0.786	0.012	0.962
	mean	0.121		0.515		0.280		0.157	

Notes: *r*-values are Pearson correlation coefficients; statistical significance after 1000 permutations: two-tailed *p*-value *<0.05; **<0.01; ***<0.001.