Extreme Climate, Rather Than Population History, Explains Mid-Facial Morphology of Northern Asians

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ABSTRACT   Previous studies have examined mid-facial cold adaptation among either widely dispersed and genetically very diverse groups of humans isolated for tens of thousands of years, or among very closely related groups spread over climatically different regions. Here we present a study of one East Asian and seven North Asian populations in which we examine the evidence for convergent adaptations of the mid-face to a very cold climate. Our findings indicate that mid-facial morphology is strongly associated with climatic variables that contrast the temperate climate of East Asians and the very cold and dry climate of North Asians. This is also the case when either maxillary or nasal cavity measurements are considered alone. The association remains significant when mtDNA distances among populations are taken into account. The morphological contrasts between populations are consistent with physiological predictions and prior studies of mid-facial cold adaptation in more temperate regions, but among North Asians there appear to be some previously undescribed morphological features that might be considered as adaptive to extreme cold. To investigate this further, analyses of the seven North Asian populations alone suggest that mid-facial morphology remains strongly associated with climate, particularly winter precipitation, contrasting coastal Arctic and continental climates. However, the residual covariation among North Asian mid-facial morphology and climate when genetic distances are considered, is not significant. These findings point to modern adaptations to extreme climate that might be relevant to our understanding of the mid-facial morphology of fossil hominins that lived during glaciations. Am J Phys Anthropol 000:000–000, 2013.   © 2013 Wiley Periodicals, Inc.

The global dispersion of anatomically modern humans during the Late Pleistocene has meant that some groups have had to adapt to temperate and then circumpolar habitats very different from those of their tropical ancestors. It is believed that survival in cold or extremely cold climates required functional adaptation of the upper airways, where inspired air is conditioned (Franciscus, 1995). For more than a century, how the upper airway and particularly the nasal region adapts to climatic variations has been the focus of research with many studies clearly demonstrating climate-dependent differences. Briefly, with increasingly cold climate the nasal region is said to adapt morphologically and functionally. Thus, the nasal aperture becomes relatively narrow, as expressed by the nasal index. It also narrows relative to the nasal cavity that follows it. This narrowing increases turbulence and so, mixing in the stream of inspired air (Thompson and Buxton, 1923; Davies, 1932; Weiner, 1954; Leon, 1975; Crognier, 1981; Froment and Hiernaux, 1984; Franciscus and Long, 1991; Ohki et al., 1991; Churchill et al., 2004; Doorly et al., 2008; Hubbe et al., 2009); the nares come to face downwards to better dissipate the air stream (Carey and Steegmann, 1981; Churchill et al., 2004; Doorly et al., 2009); the internal part of the nasal cavity lengthens sagittally to increase air conditioning ability (Olsson and Bende, 1985; Keck

et al., 2000; Noback et al., 2011; Holton et al., 2012); and the surface/volume ratio increases ("tight" cavity) to provide greater contact between air and the mucosa and to decrease the velocity of the airstream (Churchill et al.,

2004; Yokley, 2006, 2009; Doorly et al., 2008; Holton et al., 2013). Furthermore, the external nose protrudes more (Carey and Steegmann, 1981; Franciscus, 1995) and in consequence it is hypothesized that the nasal cavity increases in size in cold-adapted groups (Charles, 1930; Wolpoff, 1968; Shea, 1977; Lushchik, 1992; Yokley and Franciscus, 2005; Doorly et al., 2008; Noback et al., 2011; Holton et al., 2012, 2013).

In traditional societies, exposure to extremes of outside temperature is unavoidable while protection of the upper airways is much more difficult than protection of the body (Davies, 1932; Levin and Potapov, 1964; Shea, 1977; Yokley, 2006). Thus, conditioning of inspired air is vital in certain climates, but it is also costly. To avoid damage to the lungs and to ensure adequate gas exchange, inspired air must be warmer than $30°C$ and nearly saturated with water vapor before it reaches the bronchi. When breathing $0°C$ air 25% of total body heat production goes into air conditioning together with up to 1 l of water per day to humidify it and keep the mucosa moist (Webb, 1951; Webster, 1952; Proctor and Andersen, 1982). Desiccated nasal mucosa cannot effectively fight bacteria and this often occurs when the mucosa encounters very cold or dry air (Franciscus, 1995; Yokley, 2006). Thus, direct natural selection for adequate air conditioning capacity among human populations is plausible.

That selective pressures could apply to the respiratory system in general is evidenced by several prior studies. For example, childhood mortality in a wide range of modern circumpolar populations is strongly and significantly correlated with mean January temperature and one of the main causes of death is respiratory disease (Young and Makinen, 2010; see also Rüttimann and Loesch, 2012). Additionally, from twin studies it is known that the air conditioning capacity of the nasal cavity has a strong genetic component (Sahin-Yilmaz et al., 2007) and so, is potentially amenable to selection. Further, several recent studies have demonstrated that, in general, the face and particularly the maxilla are among the cranial regions least correlated with neutral genetic distances and among those most correlated with climate (Roseman, 2004; Harvati and Weaver, 2006a; von Cramon-Taubadel, 2009a,b; Smith, 2009). However, a direct climatic influence on mid-facial development cannot be excluded (Steegmann and Platner, 1968; Rae et al., 2006).

Cranial adaptation to cold is an important issue in human evolution because our sister taxon, the Neanderthals, shows many peculiarities of mid-facial and nasal form that have been attributed to cold adaptation (Coon, 1962; Franciscus, 1995, 2003; Schwartz and Tattersall, 1996; Hawks et al., 2000; Harvati and Weaver, 2006b; Holton and Franciscus, 2008; Schwartz et al., 2008; Rae et al., 2011). However, not all of these are consistent with what is observed among modern humans (Carey and Steegmann, 1981; Franciscus, 1995; Rae et al., 2011), or in experimental or wild animals living in cold environments (Steegmann and Platner, 1968; Rae et al., 2006; Márquez and Laitman, 2008), which has led to debate over this explanation. Alternatively, cold adaptation in modern humans may have different manifestations from cold adaptations in Neanderthals, but this cannot readily be tested. A third possibility is that extreme cold may demand additional adaptive anatomical responses to those frequently described between tropical and colder temperate climates. However, many studies that consider adaptation to extreme cold have only included Inuits (Shea, 1977; Harvati and Weaver, 2006a; Noback et al., 2011) sometimes with Buryats or Mongolians (Roseman, 2004; von Cramon-Taubadel, 2009a), as representatives of people from extremely cold climates. Nonetheless the presence of even one such sample in the analysis usually strongly affects the outcome; for instance, Harvati and Weaver (2006a) note that the association between climate and morphology is no longer significant after exclusion of the Inuit sample.

Most previous studies have examined, either diverse aspects of cranial form, or anatomically restricted components of the upper airway. Very few studies have examined the whole upper airway (e.g., Franciscus, 1995; Noback et al., 2011), as we do here, and only a few prior studies have considered internal nasal measurements (Charles, 1930; Lushchik, 1992; Yokley, 2009; Butaric et al., 2010; Holton et al., 2012, 2013). Thus, we comprehensively examine internal and external aspects of nasal and mid-facial morphology to assess covariation with different climatic variables.

Our aim is to assess the extent to which covariations are explained by climate or genetic relatedness. We investigate the relative importance of different climatic variables in driving specific convergent adaptive changes of the mid-face. To these ends, our analyses include groups that have previously been described as cold adapted but not in terms of the detailed morphology of the mid-face (Alexeeva, 1986; Kozlov and Vershubsky, 1998; Leonard and Crawford, 2002; Alexeeva, 2005; Alexeeva et al., 2008). Many previous studies of cold adaptation of the nasal region have considered European, North African and Near Eastern groups as cold-adapted, comparing them with sub-Saharan tropical groups (Crognier, 1981; Franciscus, 1995; Butaric et al., 2010). These studies are therefore unable to directly address the impact of extreme cold. In consequence, how extreme cold impacts on facial morphology remains controversial. Thus, some previous studies have examined cold adaptation in the cranium among either widely dispersed and genetically very diverse groups of humanity that have been isolated for tens of thousands of years (Harvati and Weaver, 2006a; Noback et al., 2011) or very closely related groups (Wolpoff, 1968; Shea, 1977; Hernandez et al., 1997). In the former it is difficult to control for isolation by distance and in the latter to extrapolate to the whole species. Thus, the present study examines possible cold adaptation among populations with intermediate degrees of genetic relatedness and limited geographic spread (see Materials and Methods for details).

In order to further describe how mid-facial and nasal morphologies vary among peoples from very cold continental and Arctic regions we present a study of several North Asian populations who live in very cold rather than moderate climates and one from a temperate climate. This focus allows us to assess directly if associations between extreme climate and morphology parallel or differ from what has been previously described for more temperate versus tropical climates. Further, by assessing morphological adaptation in relation to neutral genetic distances we are able to explore the extent to which neutral evolution, rather than adaptation underlies what we observe.

MATERIAL AND METHODS
Sample

To control for sexual dimorphism, we sampled only males from seven related populations (Alexeev and

TABLE 1. The sample of crania and climatic data for their regions of origin

| Group	Language family	Sample size	Location[a]	Collection		T_{min}[e]	T_{max}	P_{min}	P_{max}	VP_{min}	VP_{max}
				MSU[b]	MAE[c]						
Evenks	Manchu-Tungus (Northern branch)	13[d]	52–58°N; 109–116°E	7	6	−29.83	14.86	5.48	94.24	0.24	11.70
Ulch	Manchu-Tungus (Southern branch)	17	52–53°N; 137–141°E	8	9	−24.54	15.22	15.04	88.06	0.55	14.05
Buryats (Kyakhta, Eastern)	Mongolian (Northern branch)	19	50–51.5°N; 104–109°E	0	19	−23.12	17.63	4.98	107.02	0.58	13.02
Mongols (Ulan Bator, Eastern)	Mongolian (Central cluster)	18	46.5–48.5°N; 104–108°E	1	17	−21.05	17.34	0.92	70.35	0.74	11.92
Yakuts	Turkish (specific; many Mongolian and Paleoasian words)	17	61–65°N; 112–135°E	3	14	−38.93	16.76	7.90	49.73	0.20	11.98
Inuit (Naukan)	Eskimo–Aleut	20	65.5–66.5°N; 169–170°W	20	0	−26.11	11.42	20.54	55.58	0.97	9.85
Khanty (Northern)	Ugrian (Ob-Ugric branch)	21	65–67°N; 64–70°E	21	0	−22.66	14.16	17.55	62.81	0.96	11.81
East Asia (Northern Han and Koreans)	Sino-Tibetan (Han); language isolate (Korean)	14[f]	38–46°N; 123–134°E	14	0	−15.20	21.37	8.01	185.65	1.26	20.04
Total		139		74	65						

[a] Approximate latitude and longitude; see Material and Methods section for details.
[b] Anuchin Institute and Museum of Anthropology of Lomonosov Moscow State University (MSU).
[c] Peter the Great Museum of Anthropology and Ethnography, the Kunstkamera (MAE), St Petersburg, Russia.
[d] Sample size is the same for all variables.
[e] T_{min}: mean temperature of the coldest month, °C; T_{max}: mean temperature of the warmest month, °C; P_{min}: mean precipitation of the driest month, mm per month; P_{max}: mean precipitation of the wettest month, mm per month; VP_{min}: lowest monthly vapor pressure, hPa; VP_{max}: highest monthly vapor pressure, hPa.
[f] Including 10 Han and 4 Koreans.

Gohman, 1984; 125 skulls; Table 1; Fig. 1a) from Siberia, the Far East and Arctic, some of which (Yakuts, Ulch, Evenks, Khanty) have never been studied in relation to craniofacial cold adaptation. These samples were collected during archaeological excavations of burial grounds that date from the beginning of the18th century to the beginning of the 20th century (Alexeev and Gohman, 1984). For comparison, we accessed a sample of East Asians (northern Chinese and Korean peoples; 14 skulls; Table 1), who have inhabited a temperate climatic zone for many thousands of years. These skulls of East Asian peoples were collected during autopsies at the end of the 19th century in Vladivostok (see Fig.1a). For most of the skulls sex was attributed using known sexually dimorphic cranial features (see White and Folkens, 2000). In a few cases the postcranial skeleton was also used for sex diagnosis (some Evenks) while for a few individuals sex was known, e.g., from archaeological field data (Inuit, some Yakuts) or records (East Asians). We avoided skulls with intermediate expression of dimorphic features. Full details of the collections from which skulls were accessed and of their catalogue numbers are given in Supporting Information Table S1.

All Siberian groups represent roughly the same general North-Eastern Asiatic craniofacial morphology (Woo and Morant, 1934; Alexeev and Gohman, 1984; Hanihara, 2000; Maddux, 2011), live in neighboring regions and have been comprehensively investigated in terms of historical and cultural relationships (Alexeev and Gohman, 1984). The East Asian sample presents generally similar craniofacial morphology to the Siberian and Arctic groups in this study (Woo and Morant, 1934; Alexeev and Gohman, 1984; Hanihara, 2000; Maddux, 2011). This is important since many authors have noted that functional adaptation is most effectively assessed among populations within the same major branch of modern humans (Thompson and Buxton, 1923; Davies, 1932; Hubbe et al., 2009).
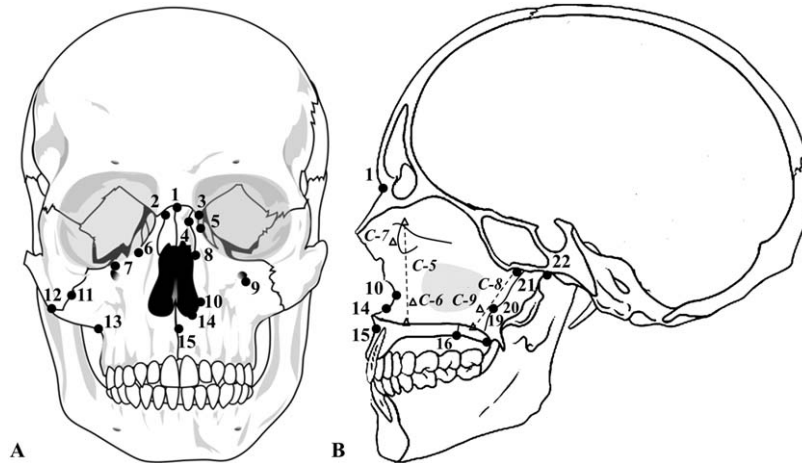
Measurements

Twenty-two landmarks (Supporting Information Table S2, Fig. 2) were used to take 33 measurements (Table 2) from each cranium. All measurements were undertaken by the same person (AE, Table 1) using as appropriate, sliding, spreading or coordinate calipers as well as specially adapted calipers with oblique jaws for internal
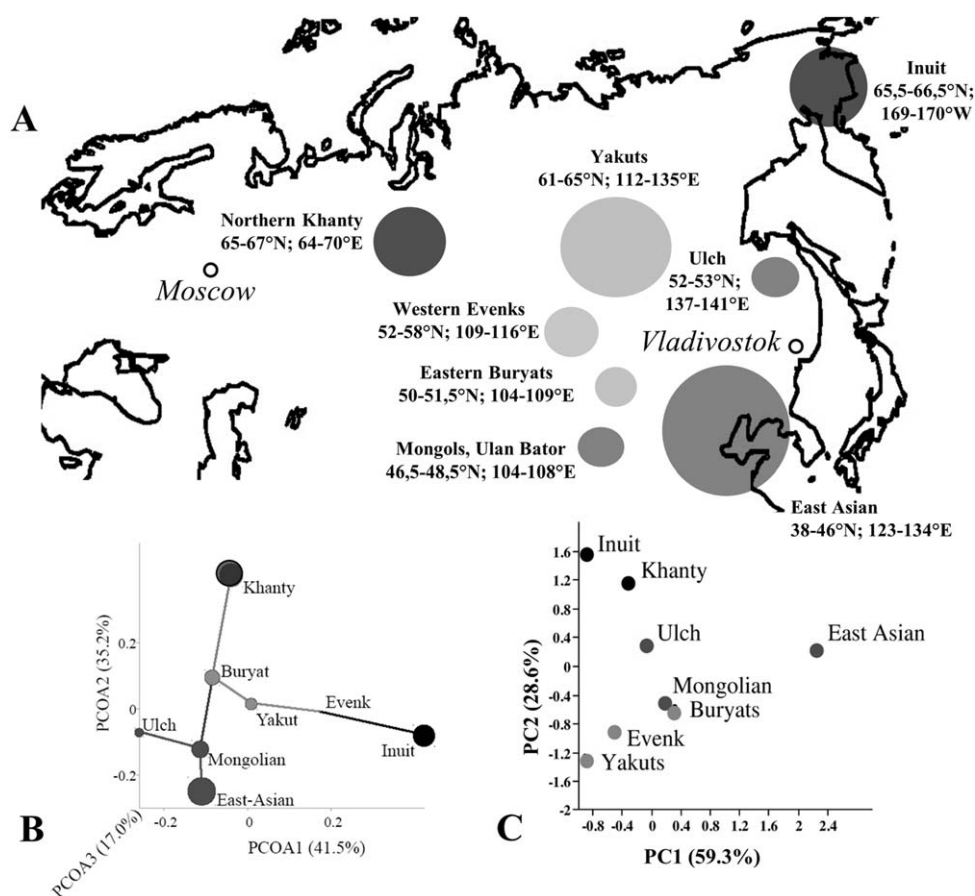
Fig. 1. Geographic locations of the studied groups with their genetic and climatic distances. **A**. Geographic locations of the studied groups. Positions and sizes of the circles approximately indicate the region used for each population to estimate climatic variables (Table 1). Shadings of circles correspond to shades in 1b and 1c to facilitate reading of these in terms of geography. **B**. Genetic distances between the groups. Principal coordinates and minimum spanning tree of distances from frequencies of the 20 main Eurasian mtDNA haplogroups (Table 3). First three PCos shown as a bubble-plot where the size of the points represents scores on the 3rd principal coordinate. Numbers in brackets are % total variance explained by each PCo. **C**. Climatic distances between the groups. PCA using six climatic variables (Table 1 and Supporting Information Table S4). Data from http://climexp.kn-mi.nl. Numbers in brackets are % total variance explained by each PC.

Fig. 2. Landmarks used in this study. Numbered landmarks (Supporting Information Table S2) are indicated with dots. Some measurements of the internal nasal cavity do not use anatomical landmarks but rather measure e.g., the narrowest point (Table 2). Points between which these measurements are taken are shown as triangles and are labelled according to the definition of measurements in Table 2. Two such measurements are also shown as dotted lines.

nasal structures. Measurements (Fig. 2, Table 2) were chosen to broadly sample the different functional components of the external nose and nasal cavity, previously considered relevant to cold adaptation (Bunak, 1960; Moss and Young, 1960; Chierici et al., 1973; Enlow, 1975; Cheverud, 1982; Mooney and Siegel, 1986; Anton, 1989; Keck et al., 2000; Mlynski et al., 2001; Churchill et al., 2004; Depew et al., 2005; von Cramon-Taubadel, 2009a,b; Holton et al., 2010; Maddux et al., 2011). All measurements were used in the analyses of covariation between mid-facial morphology and climate. Additionally, subsets of variables that focus on specific anatomical and functional regions (the nasal bones—six variables; "premaxilla"—nine variables; the maxilla—nine variables; the nasal cavity—nine variables, the choanae—four variables; see Table 2) were used to assess how these anatomical regions relate to climate (Maddux et al., 2011). Note that this subdivision resulted in some variables being present in more than one subset, which means that the findings from each subset are not necessarily independent of each other (see Table 2 for details of subsets).

An assessment of measurement error was carried out in which five Inuit crania were repeatedly measured five times on 5 different days. Permutational MANOVA (Anderson, 2005) using Euclidean distances confirms that the variation among replicates is negligible compared with the significant variation among individuals ($P = 0.0001$). That errors are small relative to differences between specimens is also readily appreciated from Supporting Information Figure S1, which presents a plot of the first two principal components of the PCA based on all replicates and shows tight clusters of replicates and well separated individuals. Thus, it is unlikely that our findings are influenced by measurement error.

Climatic variables

We tabulated climatic data (Table 1) from the population sampling locations. The variables are mean temperature of the coldest month (°C), mean temperature of the warmest month (°C), mean precipitation of the driest month (mm/month), mean precipitation of the wettest month (mm/month), lowest monthly vapor pressure (hPa), and highest monthly vapor pressure (hPa). We used the KNMI Climate Explorer compiled by van Oldenborgh (available at: http://climexp.knmi.nl; last accessed 17 January, 2013) to retrieve observations from the CRU TS3 database with a resolution of 0.5 degrees, for the years 1901 to 2006.

These variables have been shown to be correlated with many morphological and physiological features (Alexeeva, 1986; Leonard and Crawford, 2002), including craniofacial morphology in native Siberian and Arctic populations (Davies, 1932; Carey and Steegmann, 1981; Crognier, 1981; Harvati and Weaver, 2006a; von Cramon-Taubadel, 2009a,b; Hubbe et al., 2009; Noback et al., 2011). We used the monthly values rather than annual averages because seasonality is strongly pronounced in northern Asia.

Because it is crucial that climatic data relate to the same locations from which we sampled populations, we used locality information from the collection, recording longitude and latitude. Data from local meteorological stations were then interpolated to obtain representative values for population sample areas (see Fig. 1). Specific population areas (e.g., Western Evenks, Eastern Buryats or Northern Khanty) are more relevant than provenances of each skull because several of these populations tend to be migratory within their regions.

Genetic data

As a measure of population relatedness, genetic distances based on mtDNA were calculated among the populations (Table 3; Fig. 1b). This is more reliable than using geographical distances as a proxy for genetic difference. These distances were computed according to the formula of Cavalli-Sforza and Edwards (1967) based on frequencies of the 20 main Eurasian mtDNA haplogroups (A, B, C, D, E, F, G, HV, I, J, K, L, M—including Q and pre-Z, N—including S-, R, T, U, W, Y, Z) for Evenks ($N = 71$; Starikovskaya et al., 2005), Ulchi ($N = 87$; Starikovskaya et al., 2005), Buryats ($N = 116$; Derenko et al., 2003; Starikovskaya et al., 2005), Mongolians ($N = 47$; Jin et al., 2009), Yakuts

TABLE 2. Dimensions of the mid-face and nose

Variable name	Name of the variable	Landmarks between which the variable is measured
Nasal-1	Simotic chord	4–4
Nasal-2	Simotic subtense	Subtense to the chord 4–4
Nasal-3	Upper breadth of the nasalia	2–2
Nasal-4	Upper protrusion of the nasalia	Subtense to the chord 2–2
Nasal-5	Upper length of the nasalia, midline	1-shortest line connecting 4–4
Nasal-6	Upper length of the nasalia, lateral	2–5
Premaxilla-1	Zygoorbitale subtense	Subtense to the chord 7–7
Premaxilla-2	Frontal process breadth	5–5 minus 4–4[a]
Premaxilla-3	Frontal process protrusion	Subtense from 4 to the chord 5–5
Premaxilla-4	Frontal process height	3–6
Premaxilla-5	Piriform aperture margin protrusion	Subtense from 10 to the chord 11–11
Premaxilla-6	Zygomaxillary subtense	Subtense from 15 to the chord 12–12
Premaxilla-7	"Premaxilla" height	2–14
Premaxilla-8	Piriforme aperture breadth	10–10
Premaxilla-9	Height of the inferior part of the piriform aperture	10–14
Maxilla-1	Zygoorbitale chord	7–7
Maxilla-2	Anterior breadth of the maxilla	11–11 minus 10–10
Maxilla-3	Zygomaxillary chord	12–12 minus nasal breadth (nasolaterale-nasolaterale)
Maxilla-4	Lateral zygomatic process height	11–12
Maxilla-5	Medial zygomatic process height	7–13
Maxilla-6 (cavity-2)[b]	Medial length of the body of the maxilla	10–20
Maxilla-7	Length of the palatal process of the maxilla	15–16
Maxilla-8	Breadth of the palatal process of the maxilla	17–17
Maxilla-9	Lateral length of the body of the maxilla	9–18
Cavity-1	Superior length of the nasal cavity	8–21 minus Premaxilla-1
Cavity-2 (maxilla-6)	Medial length of the nasal cavity	10–20
Cavity-3 (maxilla-7 + choanae-1)	Inferior length of the nasal cavity	15–19
Cavity-4 (choanae-3)	Choanae breadth	20–20
Cavity-5	Anterior height of the nasal cavity	The point where *sutura lacrimomaxillaris* intersects with the root of *concha nasalis media*—the most distant point on the floor of the nasal cavity
Cavity-6	Inferior anterior breadth of the nasal cavity	Maximal distance between the lateral walls of the nasal cavity below *crista conchalis* immediately after piriform aperture margin but before *hiatus maxillaris*
Cavity-7	Superior anterior breadth of the nasal cavity	Maximal distance between the lateral walls of the nasal cavity between *crista conchalis* and *crista ethmoidalis* immediately after piriform aperture margin but before *sulcus lacrimalis*
Cavity-8 (choanae-4)	Posterior height of the nasal cavity	21—the most distant point on the floor of the nasal cavity
Cavity-9	Inferior posterior breadth of the nasal cavity	Maximal distance between the lateral walls of the nasal cavity below *crista conchalis* anterior to choanae but posterior to *hiatus maxillaris*
Choanae-1	Length of *lamina horizontalis* of the palatine bone	16–19
Choanae-2	Morphological height of the choanae	19–22
Choanae-3 (cavity-4)	Breadth of the choanae	20–20
Choanae-4 (cavity-8)	Functional height of the choanae	21—The most distant point on the floor of the nasal cavity

[a] Nasal-1 (distance between landmarks 4 on both sides) was being subtracted from Premaxilla-2 (distance between landmarks 5 on both sides) for each specimen.
[b] Where two variable names are given, with the second in brackets this is because the variable can be considered to be part of two anatomical regions and is named accordingly, depending on the analysis in hand.

($N = 83$; Puzyrev et al., 2003), Siberian Inuit ($N = 77$; Starikovskaya et al., 1998), Khanty ($N = 210$; Gubina et al., 2005), Northern Han Chinese ($N = 331$; Kivisild et al., 2002; Yao et al., 2002) and Koreans ($N = 179$; Jin et al., 2009). All these data are from the database of the Human Genetics Laboratory (Vavilov Institute of General Genetics, Russian Academy of Sciences, Moscow, Russia).

We used genetic data that as much as possible match the cranial samples in terms of locality (Fig. 1a, Table 1).

Statistical methods

Raw linear measurements were used to compute population means (Supporting Information Table S3). These and

population climatic data (Table 1) were then standardized by converting all values to z scores with respect to the mean of group means. This has the effect of making all variables of equal weight in subsequent analyses but preserves information about the relative magnitudes of each population mean. Climatic variation was summarized using principal components analysis of standardized climate variables (Fig. 1; Supporting Information Table S4).

In this study we are concerned to know if and how differences among populations relate to climatic variables. Thus, our analyses focus on differences among population means. This is a common approach in studies of mid-facial climatic adaptation (Thompson and Buxton, 1923; Davies, 1932; Weiner, 1954; Wolpoff, 1968; Shea, 1977; Carey and Steegmann, 1981; Crognier, 1981; Froment and Hiernaux, 1984; Franciscus and Long, 1991; Lushchik, 1992; Roseman, 2004; Harvati and Weaver, 2006a; Hubbe et al., 2009; Butaric et al., 2010) with several exceptions (Maddux et al., 2011; Noback et al., 2011). An alternative is to focus instead on variation among individuals. This brings with it the disadvantage that many factors contribute to among-individual variation and climate effects may well be obscured by their effects. Additionally, climate and genetic data are available for populations rather than individuals. To assess the extent of overlap among specimens from diverse populations we carried out a between group PCA (Mitteroecker and Bookstein, 2011) and present a plot of the first two between group PCs from this (Supporting Information Fig. S2 and Table S5). The most distinctive population is from East Asia while Inuit and Khanty are also somewhat distinct.

The magnitude and significance of apparent associations between population mean morphology and climate were assessed in two ways. The first used RV coefficients (a multivariate measure of association; Robert and Escoufier, 1976) based on standardized population mean craniometric and climate data. The second used Mantel tests (Mantel, 1967; Sokal and Rohlf, 1995) applied to matrices of Euclidean distances computed using standardized population means. The morphological matrices used all 33 craniometric variables or subsets (nasal bones, "premaxilla," maxilla, cavity, and choanae—Table 2). The climate Euclidean distance matrix was computed using all six standardized population climatic variables. mtDNA distances were calculated as described above (Table 3). These distance matrices were then submitted to two and three way Mantel tests that assessed associations among morphological and climate distance matrices without (two-way) and with (three-way) genetic distances taken into account (Table 4).

Associations among morphological (33 standardized craniometric variables as well as subsets) and standardized climatic data were further investigated using partial least squares analysis (PLS) (Rohlf and Corti, 2000; Klingenberg, 2011; Meloro et al., 2011; Noback et al., 2011). This approach has known benefits relative to Mantel tests with regard to statistical power (Bookstein, 2007) and interpretability of the resulting ordinations in terms of variable loadings, allowing associations among morphological and climate blocks of data to be related to specific morphological and climatic variables (Fig. 3). Loadings were summarized in bar charts to facilitate interpretability (Fig. 4; Supporting Information Table S6).

Note that, while in the analyses of the whole set of craniometric measurements there are 33 variables, for the graphical representation by anatomical region of singular vector (SV) loadings from PLS (in Fig. 4) we used 37 variables, where 4 (cavity-2 and -3 and choanae-3 and -4) are

TABLE 3. *Matrix of pairwise mtDNA distances*

	Evenks	Buryats	Yakuts	Inuit	Ulch	Khanty	Mongols	East Asia
Evenks	0.0000							
Buryats	0.2426	0.0000						
Yakuts	0.1009	0.0761	0.0000					
Inuit	0.3742	0.5495	0.4850	0.0000				
Ulchi	0.4577	0.2982	0.3791	0.7118	0.0000			
Khanty	0.5788	0.2704	0.4211	0.6575	0.5781	0.0000		
Mongols	0.3501	0.1511	0.1872	0.5496	0.2712	0.5316	0.0000	
East Asia	0.5551	0.3253	0.3337	0.5500	0.3983	0.6607	0.1273	0.0000

TABLE 4. *Associations between morphology, climate and genetic distances*

Cranial measurements	Eight groups, Mantel test[a]	Eight Groups, RV-coefficients[b]	Seven groups, Mantel test[a]	Seven groups, RV-coefficients[b]	Eight groups, three-way Mantel test[c]	Seven groups, three-way Mantel test[c]
33 Variables	**0.74/0.002**	**0.73/0.002**	**0.59/0.01**	**0.77/0.02**	**0.59/0.008**	0.36/0.083
Nasal bones (six variables)	−0.10/0.45	0.40/0.27	0.38/0.08	**0.72/0.017**	−0.14/0.64	0.23/0.22
"Premaxilla" (nine variables)	0.20/0.17	0.48/0.25	0.20/0.23	0.57/0.14	0.22/0.23	0.13/0.32
Maxilla (nine variables)	**0.91/0.0006**	**0.77/0.013**	**0.65/0.005**	**0.78/0.0043**	**0.69/0.014**	0.46/0.07
Nasal cavity (nine variables)	**0.78/0.007**	**0.77/0.0025**	0.43/0.06	0.61/0.17	**0.58/0.016**	0.15/0.23
Choanae (four variables)	0.28/0.28	0.39/0.40	0.29/0.88	0.32/0.81	0.20/0.25	−0.09/0.62

Bold values indicate significant at $P < 0.05$.
[a] Matrix correlations between morphology and climate/significance (two-way Mantel test).
[b] RV-coefficients between morphology and climate/significance.
[c] Climate-morphology association controlled for mtDNA distances.
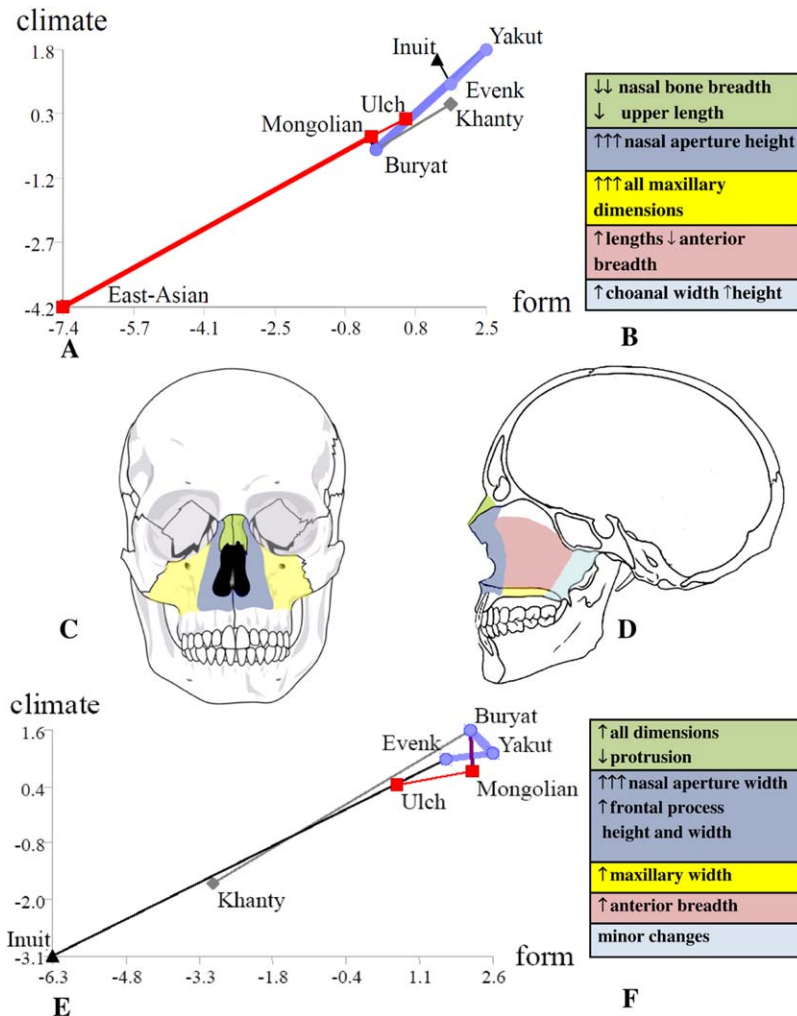
Fig. 3. Associations between mid-facial and climate variables. **A**, **E**. Plots of the first singular vectors from partial least squares analyses of eight (A) and seven (E) groups. Colors connecting population means indicate genetic groupings from Figure 1b. Boxes **B**, **F** summarize loadings of morphological variables on SV1 with arrows approximating their magnitudes and indicating the direction of change with more positive scores on SV1 of form. The colors in the boxes correspond to the colors used in C, D to indicate anatomical and functional regions. Green: nasal bones; violet: "premaxillary" region or anterior cavum; yellow: the maxilla; red: the internal nasal cavity; light blue: choanae region or posterior cavum. See Results section for details of morphological features associated with climate.

repeated. This is because these four can be considered as belonging to two anatomical regions. This duplication has negligible impact on the results when compared with analyses that use 33 rather than "37" morphological variables. Thus, variable loadings on SV1 generally differ only in the third decimal place and the RV-coefficient between 33 measurements and 6 climatic variables is 0.75 ($P = 0.0013$) while for 37 measurements it is 0.73 ($P = 0.002$).

The East Asians were very distinct in terms of mid-facial morphology and climate. Their distinctiveness may have inflated apparent associations between morphology and climate. To assess this potential impact of East Asians on apparent associations all the above mentioned analyses were repeated for the seven North Asian groups alone (minus the East Asians).

RV-coefficients were calculated in MorphoJ (Klingenberg, 2011). The PLS, PCA and Mantel-tests were performed using PAST (Hammer et al., 2001) and the three-way Mantel tests using NT-SYS (Rohlf, 2009).

RESULTS

How climate variables covary among groups

Figure 1c presents a plot of the first two principal components of the covariance matrix among standardized climate variables (PC1, 59.3% and PC2, 28.6% of total variance). East Asians occupy the most distinctive climatic zone being distant from other groups on the first PC. Inuit and Khanty are also somewhat, but less distinctly, separated from the remaining North Asians at the positive pole of PC2. From variable loadings (Supporting Information Table S4), East Asians are distinguished at the positive extreme of PC1 in occupying a climate that is warmer and wetter all year; the loadings of five of six variables on this PC are positive. They are, in order of loading magnitude: mean precipitation of the wettest month, highest monthly vapor pressure, mean temperatures of the warmest and coldest months, with precipitation of the driest month having a small negative loading. East Asians occupy the
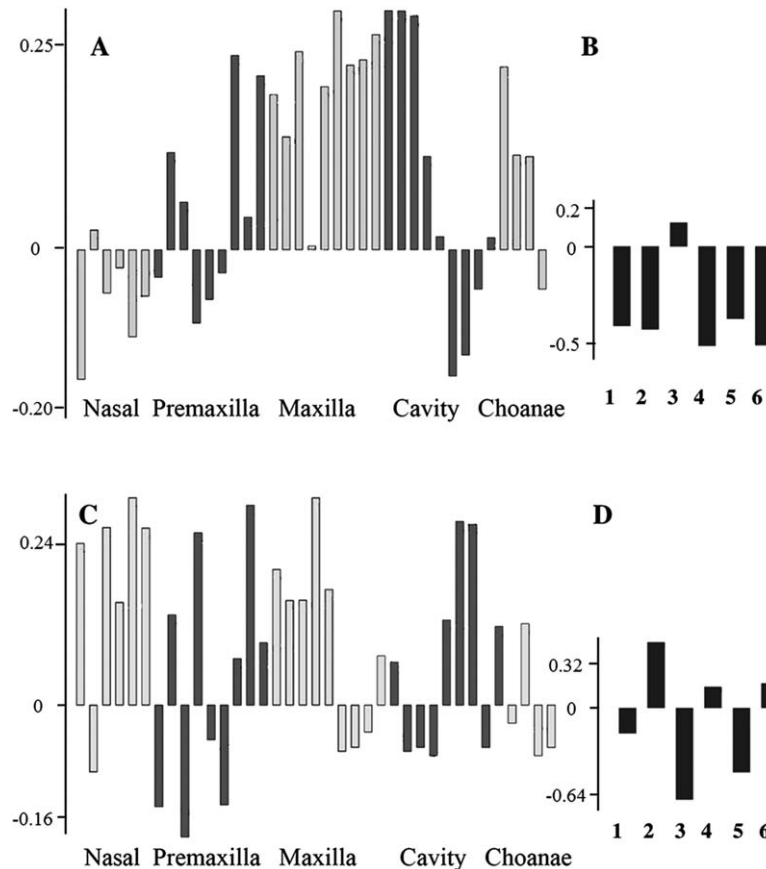
Fig. 4. Loadings of form and climatic variables on the first singular vector from PLS. Loadings of morphological (**A**) or climate (**B**) variables on the first singular vector arising from the eight-group PLS. Loadings of morphological (**C**) or climate (**D**) variables on the first singular vector arising from the seven-group PLS. Vertical axes are loading magnitudes and horizontal axes, variables: the first six columns of lighter color depict measurements of the nasal bones, the next nine, darker: of the premaxilla etc. (see Table 2 for details of morphological variables). Climate variables numbered as in Table 1.

positive extreme of PC1 while Inuit and Khanty and the other populations are towards the negative extreme. This separation reflects the climatic distinction between East Asians who inhabit a temperate climatic region and the rest who inhabit cold dry climatic regions.

Inuit and Khanty plot at the positive extreme of PC2. On this PC the mean precipitation of the driest month and lowest monthly vapor pressure are most strongly and positively loaded, mean temperature of the coldest month is also positively but less strongly loaded, while mean temperature of the warmest month is loaded negatively. Thus, to the extent that they are distinguished on PC2, their climate is relatively cold in summer while in winter it is particularly humid though not as cold as the climate of other North Asian populations. Ulchi are intermediate on PC2 between Inuit and Khanty on the one hand and, North Asians on other. This reflects the fact that the Ulchi also occupy a coastal region but are further south than Inuit and Khanty.

Associations between mid-facial and climate variables

The standardized mid-facial measurements are strongly associated with the climatic variables. Thus for eight populations, the RV coefficient between all 33 craniometric and 6 climatic variables is 0.73 and highly sig-

nificant ($P = 0.002$; Table 4). The association remains strong when either maxillary or nasal cavity measurements are considered alone (RV = 0.77 for both, $P = 0.013$ and 0.0025, respectively). This association is confirmed by Mantel tests (Table 4) using among population morphological and climatic Euclidean distance matrices from standardized morphological and climatic variables (see Methods).

The PLS analysis of all eight populations indicated two principal patterns of association between climate and morphology. The first is evident on the first pair of singular vectors (Fig. 3). These differentiate East Asians from groups to the west and north. The first pair of singular vectors explains 24% of the total variance of standardized mid-facial variables among group means (this was calculated as: variance of scores on SV1 of the midfacial block/total variance of this block among means). These first singular vectors explain 59% of the total variance among group means of standardized climatic variables. These singular vectors also account for 62% of the total covariance between blocks (morphological and climatic variables). Loadings of morphological and climate variables on SV1 (Supporting Information Table S6) are presented graphically in Figure 4a,b. Based on these variable loadings, the contrast between East Asians and the other population means (Fig. 3a) is due to the colder and drier climate of North Asians being associated with

narrower and shorter nasal bones, a longer but anteriorly narrower nasal cavity, increased height of the nasal aperture (without decrease in breadth in absolute terms), a larger maxilla, and small choanae relative to very big maxillae (Fig. 3b–d; Supporting Information Table S6). These morphological associations with climate are schematically represented in Figure 3b where colors of boxes correspond to craniofacial units indicated in the same colors in Figure 3c,d. The number of arrows in each box approximately indicate the magnitudes of loadings, hence the regions of greatest morphological difference represented by SV1.

The second principal pattern of association between climate and morphology is seen on the second pair of singular vectors (not shown). These distinguish Inuit and Khanty from the rest to a moderate degree and represent: 26.6% of the total variance among group means of standardized mid-facial variables, 29% of the total variance among group means of standardized climatic variables and 33% of total covariance between blocks. These second singular vectors from the eight group analysis are very similar to the first singular vectors from an analysis of seven populations, where East Asians are excluded. This is discussed further, below.

The East Asians act as an influential case, whose distinctiveness dominates the analyses of covariation among morphological and climatic data. To focus on the North Asian populations we excluded East Asians and repeated the analyses. After this, a significant association remains between overall mid-facial morphology and climate (RV = 0.77, $P = 0.02$). For subsets of measurements the association with climate remains strong in the nasal bones (RV = 0.72, $P = 0.017$) and maxilla (RV = 0.78, $P = 0.0043$). Mantel tests (Table 4) likewise find a strong association between distance matrices computed using all 33 standardized mid-facial and 6 climate variables ($r = 0.59$, $P = 0.01$) and for the maxilla ($r = 0.65$, $P = 0.005$), but the result for nasal bones is not significant ($r = 0.38$, $P = 0.08$). The first singular vectors of this analysis of seven groups account for 78.8% of total covariance, 35% of total mid-facial variance among means, and 56% of the total variance among means of standardized climatic variables.

The plot of the first pair of singular vectors from the seven group analysis excluding East Asians is shown in Figure 3e. As mentioned earlier, this is very similar to that of SV2 from the analysis of eight groups. Loadings of variables on the resulting first singular vectors are shown graphically in the bar charts of Figure 4c,d (also listed in Supporting Information Table S6). The plot of first singular vectors distinguishes coastal Khanty and Inuit from the remaining North Asians. From the loadings of Figure 4d (standardized climate variables) and c (standardized measurements), inland groups experience colder winters with less precipitation and less vapor pressure as well as warmer summers than coastal. Coastal groups experience more precipitation and greater vapor pressure during winter, which is a bit warmer than in inland regions, while summer is colder. This is associated with less protrusive but larger nasal bones, a larger frontal process, greatly increased nasal aperture width, and moderately increased maxillary and anterior nasal cavity widths in inland groups. As with the eight-group analysis, these morphological associations with climate are schematically represented in Figure 3e,f using colors to indicate craniofacial units (Fig. 3c,d) and the number of arrows in each box to indicate

the degree of morphological change (magnitude of loadings; Fig 4; Supporting Information Table S5).

Genetic relationships, climate, and mid-facial morphology

Distances computed using mitochondrial DNA (Table 3) were used as a proxy for population relatedness (Fig. 1b). It is worth noting that these distances were not correlated with climate (correlation between climate and mtDNA distances is 0.19, NS). The mtDNA relationships are not concordant with the pattern of covariation between mid-facial morphology and climate suggested by the plots of singular vectors from PLS (Fig. 3a,e). In particular East Asians are not dramatically distinct from the main core of populations in terms of mtDNA distances (Fig. 1b), while they are far from all other populations in terms of morphological correlates of climatic factors (Fig. 3a). In contrast, Khanty and Inuit are relatively distant in terms of mtDNA (Fig. 1b), but fairly similar in terms of morphological association with climate (Fig. 3e).

This apparent lack of congruence between genetic distances and patterns of association of mid-facial morphology and climate was further assessed by three-way Mantel tests (Smouse et al., 1986; Table 4). For the eight populations, a three-way test between distance matrices from all 33 standardized morphological variables, 6 standardized climate variables, and mtDNA distances indicated that a significant association between morphology and climate remains when genetic distances are taken into account ($r = 0.59$, $P = 0.008$); the same applies when a subset of nine measurements from the maxilla ($r = 0.69$ and $P = 0.014$) or a subset of nine measurements from the nasal cavity ($r = 0.58$ and $P = 0.016$) are considered. As anticipated, these associations are somewhat weaker than found in the earlier two-way Mantel tests based on morphological and climate distances without taking the genetic distance into account.

When the East Asian sample is excluded, the three-way Mantel test finds no strong support for the association between morphology and climate ($P > 0.05$), although r was relatively large in two tests and marginally ($P < 0.1$) significant despite the low power in an analysis where only seven data points are left (Table 4): 33 standardized measurements ($r = 0.36$, $P = 0.083$); maxillary subset ($r = 0.46$, $P = 0.07$). This finding suggests that the contrast between Khanty and Inuit on the one hand and the remaining North Asian populations on the other, which is evident on the plot of first singular vectors from the seven-group analysis (and SV2 from the eight-group analysis), is partly accounted for by genetic relatedness (Fig. 3e).

In summary, there is evidence to suggest that mid-facial morphology covaries with and is adapted to climate when all of our eight central North Asiatic populations are considered. East Asian distinctiveness in both climate and mid-facial morphology largely drives this conclusion. There is weaker evidence that climatic adaptation may also explain shared distinctive features of Inuit and Khanty mid-facial morphology.

DISCUSSION

This study aims to describe how mid-facial and nasal morphologies vary among peoples from very cold continental and Arctic regions and to assess the extent to which any associations between extreme climate and

morphology parallel what has been previously described for more temperate versus tropical climates.

Different parts of the mid-facial skeleton show different patterns of association with climate. Thus, all but one (M-4) loadings of maxillary variables are large and positive on singular vector (SV) one from the eight-group analysis, suggesting relative maxillary size is important. While the first four of the nasal cavity measurements have large and positive loadings, the remaining ones have small and mostly negative loadings, indicating shape differences are also important. Loadings of premaxillary and other morphological variables vary in magnitude and sign. This association cannot be described as uniform increase or decrease in overall size, but the methodological differences between this study and GMM-based studies should be taken into account when comparing results (Mitteroecker et al., 2013).

The association between climate and mid-facial morphology is marked in comparison to many previous studies describing either a part of the naso-facial complex (e.g., nasal aperture shape (Thomson and Buxton, 1923; Davies, 1932; Leon, 1975; Froment and Hiernaux, 1984); the maxillary sinus and nasal cavity (Shea, 1977; Butaric et al., 2010; Holton et al., 2012, 2013); nasal bridge protrusion (Carey and Steegmann, 1981); or more complex structures (Harvati and Weaver, 2006a; von Cramon-Taubadel, 2009a,b; Hubbe et al., 2009; Noback et al., 2011). The morphological associations with climate found in the analysis of all eight groups are in very good agreement with physiological predictions and prior studies of mid-facial cold-adaptation in more temperate regions. Thus, the aperture becomes narrow *relative* to its height increasing air mixing and decreasing the airstream velocity (Thomson and Buxton, 1923; Charles, 1930; Wolpoff, 1968; Leon, 1975; Churchill et al., 2004; Doorly et al., 2008); the inner nasal cavity becomes longer and the surface/volume ratio increases, improving the efficiency of conditioning (Lushchik, 1992; Franciscus, 1995; Keck et al., 2000; Churchill et al., 2004; Yokley, 2006, 2009; Doorly et al., 2008; Noback et al., 2011; Holton et al., 2012); additionally choanal size decreases *relative* to maxillary size. This relative reduction in choanal size has been suggested to reduce airstream velocity and so, heat and water loss from exhaled air (Lushchik, 1992; Franciscus, 1995).

From our findings it is plausible that adaptation to extremely cold climates differs from adaptation to temperate regions, which have also been considered "cold" by some authors (Crognier, 1981; Franciscus, 1995; Yokley, 2009; Butaric et al., 2010). Thus, nasal aperture breadth is greater in groups that inhabit *inland* regions with very cold and dry climates (Evenk, Buryat, Yakut, Ulch, Mongolian) than in East Asians from a more temperate climate (Figs. 3 and 4). The nasal aperture is quite wide in absolute terms, as in Neanderthals (Franciscus, 1995; Holton and Franciscus, 2008; Maddux, 2011), albeit relatively narrow with respect to the increased nasal height (Fig. 4). However, compared with inland populations, Inuit and Khanty who live in coastal regions with more humid winters, have absolutely narrower nasal apertures but similar heights (Figs. 3f and 4). This is similar to morphologies reported for Northern European groups from areas with high levels of precipitation (Davies, 1932; Hubbe et al., 2009).

All populations in this study manifest among the lowest levels of nasal protrusion observed among modern humans (Woo and Morant, 1934; Alexeev and Gohman,

1984; Howells, 1989; Hanihara, 2000; Maddux, 2011). Nasal protrusion is not increased in the cold-adapted groups relative to the East Asians. Indeed, for the inland populations nasal protrusion is even more reduced (Fig. 4; Supporting Information Table S6). This contrasts with the increased nasal protrusion previously demonstrated in Europeans, who are also considered cold adapted, when compared with sub-Saharan Africans (Carey and Steegmann, 1981; Franciscus, 1995; Hubbe et al., 2009). It also contrasts with the situation in Neanderthals. In the latter, unlike modern humans, the whole anterior nasal cavity is more prominent, forming a characteristic parasagittal infraorbital morphology (Maddux, 2011). In Neanderthals this is associated with a marked overall increase in mid-facial prognathism. These inconsistencies may arise because nasal bone and piriform aperture morphology play relatively minor roles in adaptation to extremely cold-dry climates compared with the maxilla and the nasal cavity, which show stronger associations with climate in this (Table 4) and some previous analyses (Harvati and Weaver, 2006a; Yokley, 2006, 2009; von Cramon-Taubadel, 2009a).

Anteroposterior elongation of the nasal cavity in the Northern Asian populations relative to the East Asians comes about through an increase in the overall size of the maxilla. The maxilla is extraordinarily large in the North Asian groups relative to other living *Homo sapiens* (Howells, 1989; Hanihara, 2000), particularly among those living inland (continental climate) (Supporting Information Table S3). In contrast, relative lengthening of the cavity in Europeans compared with sub-Saharan groups seems to be related to greater nasal protrusion rather than increased maxillary size (Charles, 1930; Carey and Steegmann, 1981; Lushchik, 1992; Franciscus, 1995; Yokley, 2006, 2009; Hubbe et al., 2009; Holton et al., 2013). Among North Asians the considerable increase in maxillary dimensions is not accompanied by increased internal nasal cavity breadth, resulting in a long and relatively narrow cavity compared with East Asians who possess quite a small maxilla but about the same breadth of the nasal cavity (Fig. 4; Supporting Information Tables S3 and S6). That adaptation might act separately on cavity width is plausible given that the internal walls of the nasal cavity show relatively independent growth (Enlow, 1975; Yokley, 2006, 2009; Holton et al., 2013).

The morphological features associated with extreme cold in the Northern Asian groups are expensive both physiologically and developmentally (Webster, 1952). Thus, they tend to make inhalation more costly and increase exposure of the nasal mucosa to desiccation (Franciscus, 1995; Churchill et al., 2004; Hall, 2005; Doorly et al., 2008). These considerations raise intriguing questions concerning the physiological costs and benefits of adaptation to extreme cold through such morphological changes.

When compared with East Asians, Inuit and Khanty are morphologically similar to other North Asian groups (very large maxilla, very long and narrow nasal cavity). However, they uniquely share a further narrowing of the anterior nasal cavity and a somewhat more protruding nasal bridge. These differences are concentrated in the nasal region and, from loadings of the climate variables on SV1 in the seven-population PLS analysis, they seem mostly associated with wetter winters and colder summers (Fig. 4; Supporting Information Table S6).

Physiological studies suggest that the main function of the nasal mucosa is humidification of inspired air (Webb, 1951; Proctor and Andersen, 1982; Keck et al., 2000) and so adaptations to cold dry versus cold wet climates can be expected to impact differently on mid-facial morphology. Thus, Thompson and Buxton (1923) suggested that air humidity is most constant in coastal areas. Further, Davies (1932) found the nasal index in Inuit to be closer to that of European groups from areas with high levels of precipitation, while most Siberian groups possess relatively broad noses. As such, our finding, that both temperature and precipitation are important covariates of mid-facial morphology, is consistent with previous studies and the work of Noback et al. (2011), who found that the first singular vector from a two-block PLS reflected morphological associations with temperature and the second, a combination of low temperatures with high humidity, albeit much more weakly. This apparently interesting association with both temperature and precipitation has, however, to be tempered by the statistical finding that differences between coastal and inland North Asian groups may equally be explained by their population relatedness as discussed below.

Many prior studies have indicated that the mid-face seems to be among the regions of the skull least strongly correlated with neutral genetic markers while being among the most correlated with climate (Hernández et al., 1997; Roseman, 2004; Harvati and Weaver, 2006a; von Cramon-Taubadel, 2009a,b; Smith, 2009). In our study we used mtDNA to assess congruence between relatedness and patterns of covariation (Tables 3 and 4; Fig. 1b). The genetic differences are consistent with our current understanding of history and differences in language (Alexeev and Gohman, 1984). The main finding is that the genetic relationships among populations do not explain the striking associations between morphology and climate that are observed when East Asians are compared with North Asians. Thus, in the PLS analysis of all eight populations (Fig. 3a), the seven from extremely cold habitats cluster despite their relative genetic differences. The three-way Mantel tests, taking into account genetic distances, largely support this result (Table 4). Excluding East Asians, Inuit, and Khanty show similarities in their morphology, possibly linked to climate, despite their large geographical and genetic distances (Fig. 3e, Table 4). In this case, however, the three-way Mantel test indicates that when genetic relatedness is taken into account, the association between climatic and morphological distances is at best marginal. More populations need to be included in the analysis to increase power and robustly explore potential correlations.

A very important question is if the observed climate-morphology associations noted from RV coefficients, Mantel tests and PLS are due to directional natural selection or ontogenetically-mediated plasticity. While our analyses provide almost no basis for testing these alternative hypotheses, there are some reasons to choose the former explanation. First, while there is considerable evidence supporting a direct effect of masticatory loadings on the growing facial skeleton (Moss and Young, 1960; Chierici at al., 1973; Kopher and Mao, 2003; Herring, 2008), there are to our knowledge no data suggesting faster or more intense growth of the facial skeleton in response to cold, such as might explain the relatively large maxillae of North Asians. Furthermore, studies of

rats grown in cold environments (Steegmann and Platner, 1968; Rae at al., 2006) have demonstrated that facial structures seem to decrease a little in size. Finally, there is abundant data showing that descendants of Siberian or Central Asian groups who have migrated to milder climates, e.g., Kalmyks from Lower Volga, retain their facial morphology (Alexeev and Gohman, 1984).

All this taken together makes it more likely that the specific morphology of North Asian groups presented in this study reflects long-term genetic adaptation to extreme cold rather than ontogenetically mediated plasticity.

CONCLUSIONS

We find separate strong associations between mid-facial morphology and extremes of temperature as well as humidity in winter. The morphological findings with respect to specific anatomical features are consistent with the predictions of upper airway physiological models, but there are several novel aspects of mid-facial morphology, such as a wide aperture, reminiscent of Neanderthals, that are associated with environmental harshness. Morphology is more strongly associated with climate than with genetic relatedness. Thus, extreme climate rather than population history likely explains the peculiarities of mid-facial morphology of Northern Asians.

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