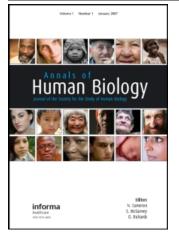
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Sex-specific differences of craniofacial traits in Croatia:

The impact of environment in a small geographic area Alena Buretić-Tomljanović ^a; Jasminka Giacometti ^b; Saša Ostojić ^a; Miljenko Kapović ^a

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ORIGINAL ARTICLE

Sex-specific differences of craniofacial traits in Croatia: The impact of environment in a small geographic area

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Abstract

Background: Craniometric variation in humans reflects different genetic and environmental influences. Long-term climatic adaptation is less likely to show an impact on size and shape variation in a small local area than at the global level.

Aim: The aim of this work was to assess the contribution of the particular environmental factors to body height and craniofacial variability in a small geographic area of Croatia.

Subjects and methods: A total of 632 subjects, aged 18–21, participated in the survey. Body height, head length, head breadth, head height, head circumference, cephalic index, morphological face height, face breadth, and facial index were analysed regarding geographic, climatic and dietary conditions in different regions of the country, and correlated with the specific climatic variables (cumulative multiyear sunshine duration, cumulative multiyear average precipitation, multiyear average air temperatures) and calcium concentrations in drinking water. Significant differences between groups classified according to geographic, climatic or dietary affiliation, and the impact of the environmental predictors on the variation in the investigated traits were assessed using multiple forward stepwise regression analyses.

Results: Higher body height measures in both sexes were significantly correlated with Mediterranean diet type. Mediterranean diet type also contributed to higher head length and head circumference measures in females. Cephalic index values correlated to geographic regions in both sexes, showing an increase from southern to eastern Croatia. In the same direction, head length significantly decreased in males and head breadth increased in females. Mediterranean climate was associated with higher and narrower faces in females. The analysis of the particular climatic variables did not reveal a significant influence on body height in either sex. Concurrently, climatic features influenced all craniofacial traits in females and only head length and facial index in males. Mediterranean climate, characterized by higher average sunshine duration, higher average precipitation and higher average air temperatures, was associated with longer, higher and narrower skulls, higher head circumference, lower cephalic index, and higher and narrower faces (lower facial index). Calcium concentrations in drinking water did not correlate significantly with any dependent variable.

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Conclusion: A significant effect of environmental factors on body height and craniofacial variability was found in Croatian young adult population. This effect was more pronounced in females, revealing sexspecific craniofacial differentiation. However, the impact of environment was low and may explain only 1.0–7.32% variation of the investigated traits.

Keywords: Body height, craniofacial traits, environmental influence

Introduction

Possible for craniofacial alteration over time are climatic reasons adaptation (Guglielmino-Matessi et al. 1979; Froment and Hiernaux 1984; Hoppa and Garlie 1998; Bharati et al. 2001; Adak 2004; Roseman 2004), migrations (Relethford 2004) and changed socio-economic environment (Gyenis and Joubert 2004; Wescott and Jantz 2005), but it is also believed that craniofacial alterations are associated with improved health and nutrition as well as biomechanical responses to a more processed diet (Angel 1982; Jantz and Meadows Jantz 2000; Larsen 2003). Numerous articles refer to dolichocephalic cranial morphology as an adaptation response to dry and warm climate, thus following the ecological rules of Allen and Bergman (Weninger 1979; Crognier 1981; Bharati et al. 2001; Adak 2004). Adaptation to different climatic conditions resulted in differences of lengths and perimeters of the dental arches in children from southern and northern Finland (Huggare et al. 1993) or breadth and height of the skeletal nasal aperture (Wolpoff 1968). Recent investigations take into account the important role of genetic factors (Wade et al. 2001; Livshits et al. 2002; Sparks and Jantz 2002; Hanihara et al. 2003; Skarić-Jurić et al. 2003; Liu et al. 2004; Peter et al. 2004). Cephalic and nasal indices are found to discriminate populations of diverse ethnic origin but also climatic conditions in different regions in India (Bharati et al. 2005). Numerous studies show that data on anthropometric and craniometric variation in humans may be used for the investigation of recent or historical population structure and also to investigate biological diversity in modern humans (Hanihara et al. 2003; Slaus et al. 2004). Although skeletal morphology is determined by both genetic and environmental factors, it is shown that skeletal data are comparable to genetic data (Relethford 1994; Konigsberg and Ousley 1995). Multivariate analysis of global craniometric variation shows a distribution similar to those obtained for neutral genetic markers and DNA polymorphisms, suggesting that the majority of human diversity exists among individuals within local populations (Relethford 2002). Relethford (2004) has elaborated the main effects of migration to craniometric distances in terms of developmental plasticity of cranial traits in response to climatic stress, natural selection and gene flow. It has been shown that climatic adaptation optimizes cranial size and shape and its effect is more pronounced on the global than local level owing to more global climatic heterogeneity.

Secular changes of body height and several cranial measures were established in Croatian student population and children (Prebeg et al. 1995; Prebeg 2002; Buretić-Tomljanović et al. 2004) during the second half of the last century. Moreover, a specific regional distribution of mean cephalic index value was found. Croatia covers a small geographic area (42°23'N to 46°33'N latitude and 13°30'E to 19°27'E longitude) but may be divided into several regions due to different geographic and climatic features. This makes Croatia an interesting region to investigate possible environmental influences on craniofacial morphology. Croatia is also interesting regarding the aforementioned effects of migrations on cranial variation, since it has experienced multiple migrations and invasions throughout

its history prior to, during and since medieval times. Morphometrical distinction between southern coastal (Dalmatian) and eastern continental (Pannonian) regions, separated by the Dinaric mountain ranges, was evidenced during the medieval period (Šlaus 1998; Šlaus 2000a, 2000b). The two regions were subject to intrusions from different areas, which provide possible evidence for differentiation of morphometrically distinct populations.

Figure 1 shows the studied geographic regions of Croatia. The geographic distribution follows different climatic features in separate regions, as shown in Table I. The coastal region in southern and north-western Croatia has a temperate Mediterranean climate with



Figure 1. Geographic regions of Croatia.

Table I. Climatic elements and drinking water calcium concentration in Croatian geographic regions.

Geographic region	Cumulative multiyear sunshine duration (h)	Cumulative multiyear average precipitation (mm)	Multiyear average air temperatures (°C)	Multiyear average calcium concentration (mg1 ⁻¹)
Southern North-western Central	$\begin{array}{c} 2640.3 \pm 15.74 \\ 2008.2 \pm 15.38 \\ 1943.3 \pm 15.26 \end{array}$	$\begin{array}{c} 915.0 \pm 30.41 \\ 1535.4 \pm 30.00 \\ 862.4 \pm 29.74 \end{array}$	$\begin{array}{c} 16.7 \pm 1.52 \\ 14.6 \pm 1.89 \\ 12.0 \pm 1.49 \end{array}$	$\begin{array}{c} 68.7 \pm 13.84 \\ 80.7 \pm 28.25 \\ 86.1 \pm 20.30 \end{array}$
Eastern	1903.9 ± 15.74	629.9 ± 31.10	11.4 ± 1.49	60.9 ± 32.90

more sunny days and higher average annual temperatures (the average temperature in January of $5-10^{\circ}$ C and in August of $26-30^{\circ}$ C) while central and eastern Croatia are characterized by a temperate continental climate with an average temperature in January of -1 to -3° C and in August of $22-26^{\circ}$ C.

Based on geographic distribution, cultural and historical tradition, we divided diet into three types. The Mediterranean diet relates to the southern region, mixed Mediterraneancontinental diet to the north-western and continental diet to the central and eastern regions. The Mediterranean diet is based on pasta, vegetables, fruits, marine food and vegetable oils consumption as a lipid source. In the past, olive oil was the only vegetable oil used. Continental regions of Croatia have eating habits similar to those in Germany and Hungary: the diet is high in fat and carbohydrates, and deficient in fruits and vegetables. Hungarian and German basic dishes consist of fatty meat with predominant saturated fatty acids (stearic and palmitic acids) in meat and lard as a lipid source, while unsaturated fatty acids dominate in the Mediterranean diet (especially monounsaturated oleic acid). Even though the consumption of processed food has changed the nutritional habits in Croatia during the past 30 years (Colić-Barić et al. 2000), the differences between the Mediterranean and continental diets have not been completely eliminated.

In addition, because of mountainous terrain in the north-western and southern regions (Karst aspects) and considering different hydrological conditions in Croatia, we also studied a possible influence of the amount of calcium in drinking water on the variability of body height and craniofacial measures. Calcium intake from other sources was assumed not to differ significantly between regions (Colić-Barić et al. 2004).

The aim of this work was to assess the particular environmental influences on body height and craniofacial variability in a small geographic area of Croatia. Our hypothesis is that climate and nutrition, and calcium intake from drinking water, might have a substantial impact on variation in body height and craniofacial traits.

Historical background

The history of the region provides possible explanations for these differences. Based on scientific evidence, it is believed that medieval peoples inhabiting coastal and continental Croatia were mainly of Slavic descent (Guldescu 1967; Fine 1983; Magocsi 1993).

The Slavic peoples, however, were not the initial inhabitants of the region. It is believed that three indigenous populations (Illyrians, Thracians and Dacians) originally occupied the lands north of modern day Greece. The Illyrians inhabited the areas of Dalmatia, Istria, Epirus, north-western Macedonia, Bosnia, Herzegovina, and western Serbia.

Prior to Slavic invasions the Balkan region was an important part of the Roman Empire. The Roman influence in Dalmatia was so significant that the major port cities in the region retained its Roman character throughout the Middle Ages. During the first century AD, the Romans began moving inland from the Adriatic coast toward the Danube. With the formation of Constantinople as the capital of the Empire, the Balkans were split among three prefectures, and the regions of Pannonia, Istria and Dalmatia became part of the Italian Prefecture (Fine 1983; Magocsi 1993a). The regions of Dalmatia and Pannonia were established as separate Croatian states. According to historical data, the early medieval period (6th–9th century) was characterized by mass migrations, political instability and warfare (Šišić 1925; Klaić 1971). During this period, continental Croatia was inhabited by various ethnic groups, including Eastern Goths, Langobards, Gepids, Slavs and Avars. The latter were themselves a conglomerate of different ethnic groups, including Central

Asian populations, Bulgars, Kutrigurs, and the remains of conquered Germanic tribes. Along the Dalmatian coast, there were clear ethnic and cultural separation between the pre-Slavic Romanized populations of the walled cities and the newer Slavic populations in the hinterland (Fine 1983). According to Slaus et al. (2004), early medieval Croats were of Slavic ancestry and migrated to the east Adriatic coast from an, as yet, unidentified location to the north of modern Croatia during the late 6th and early 7th century. In the 10th century, Croatian king Tomislav unified Dalmatia and Pannonia. During the 11th to 13th centuries Croats crossed the Dinaric mountain and expanded north first into modern Bosnia and Herzegovina and then into modern continental Croatia. The influence of Hungary, especially in the Pannonian region, became substantial after joining unified Croatia and Hungary in the 12th century. Trade with Hungary and other states spurred the development of towns and the growth of the merchant class that brought new peoples to the area including Hungarians, Germans and Jews (Fine 1983). The Dalmatian towns continued close interaction with Italian cities and many of them were ruled by Venice through the 15th century (Magocsi 1993b). The encroachment of the Ottoman Empire into the southern lands of Hungary-Croatia during next centuries encouraged Habsburg resettlement of the Danubian basin, resulting in greater ethnic diversity in the area, especially in the Hungary-Croatian region of Slavonia (Magocsi 1993c). The early modern history (1900-1990) of each nation of the former Yugoslavia was also characterized by national, political, ethnical and economic migrations, especially after the Second World War. Various ethnic groups were relocated during the post-war period including Serbo-Croats, Hungarians, Germans (Danube Swabians), Italians and others, and colonization of Slavonia from southern rural Croatian areas was encouraged. The post-communist developments in the region of Central and Eastern Europe, as well as Croatia, generated new trends in international migrations. Ethnic, social and gender divisions are a result of these new kinds of mobility and changes of labour markets in both receiving and sending countries. The most recent migration flow was the one during the wars in Croatia and Bosnia (early 1990s) when more than 5 million citizens of the former Yugoslavia were displaced.

Subjects and methods

Data for this study were collected between 2000 and 2006, and included 632 subjects (404 females and 228 males). All subjects were students at the University of Rijeka, School of Medicine, and were born between 1982 and 1987. The mean age was 19.82 ± 1.01 for males, and 19.66 ± 0.82 for females. We selected the student population since in this age group the effects of particular environmental factors, such as quality of healthcare and ageing factors, were excluded (Vercauteren 1990; Schousboe et al. 2004). Therefore, the phenotype of our subjects was the closest to that genetically assigned.

The samples were classified by sex and geographic origin in Croatia. The main criterion for geographic distribution was the place of prior primary and secondary education. National differentiation was excluded. Table II shows the number and percentage of subjects from four Croatian geographic regions. The male and female subjects from different geographic regions were further grouped according to type of climate into Mediterranean (southern and north-western regions) and continental climate groups (central and eastern regions), and according to diet type into three groups: Mediterranean diet (southern region), mixed Mediterranean–continental diet (north-western region) and continental diet (central and eastern regions).

	N	lales	Fe	males
Geographic region	n	%	n	%
Southern	42	18.42	51	12.62
North-western	86	37.72	194	48.02
Central	74	32.46	120	29.7
Eastern	26	11.40	39	9.65
Total	228		404	

Table II. Samples used in the study.

Since our students come from all parts of Croatia, they represented a large student population of the same age. All students participated voluntarily in the research.

The variables investigated in this research were body height, craniofacial measures (head length, head breadth, head height, head circumference, morphological face height and face breadth) and two indices (cephalic index and facial index). Standing height measurements were taken on a barefooted subject from the ground to the highest point of the subject's head (while the head was in Frankfort horizontal) using a stadiometer. All craniofacial measurements were taken with the subject sitting in chair in a relaxed condition and the head in anatomical position. The head length (glabella–opisthocranion), head breadth (euryon–euryon), head height (vertex–porion while head was in Frankfort horizontal) and face breadth (zygion–zygion) were measured using a spreading caliper. A sliding caliper was used to measure the morphological face height (nasion–gnathion). We assessed head circumference by circling the tape around the head covering glabella and opisthocranion. Cephalic index (CI) was determined using the formula: $CI = (maximal head breadth \times 100)/maximal head length, while facial index (FI) was determined using the formula: <math>FI = (facial width \times 100)/morphological face height.$

The values of calcium concentration in drinking water in each geographic region were based on a 10-year data collection period (data from the Croatian National Institute of Public Health). The assessed climatic variables in this study (means given in Table I) were obtained during a 10-year period (1995–2004, data from the Meteorological and Hydrological Services).

Body height and craniometric analyses were performed using Statistical Software Package for Windows 2001 (by Statsoft Inc.). Each statistical analysis was completed for males and females separately. Descriptive statistics (means and standard deviations) were obtained for all studied variables.

To determine whether significant differences exist between different geographic, climatic or dietary groups of subjects, or according to distribution of calcium concentration in drinking water in our sample, we performed separate multiple forward stepwise regression analyses for the body height and each craniofacial variable. Multiple stepwise regression analysis enabled the identification of the independent variable (s) (predictors or correlates) that are most highly correlated to the dependent variable, i.e. the models that best explained the variation in the dependent variable. In the separate multiple forward stepwise regression analyses, we assessed the potential effects of several climatic predictors, defined as cumulative multiyear sunshine duration, cumulative multiyear average precipitation and multiyear average air temperatures, on all dependent variables. For all analyses, the significance level was set at p < 0.05. Multiple forward stepwise regression analyses started with no predictor variables in the regression equation. Variables were added in the subsequent steps according to defined criteria (F=4.0 to enter, F=1 to remove). In the first step the predictor variable with the largest correlation with the dependent variable entered the regression equation. In the second step, if possible, the predictor variable was selected based on the highest partial correlation with the dependent variable. The multiple forward regression analyses performed in this research revealed two models of significant predictor variables, the first included one predictor and the second included two predictors significantly related to dependent variable.

Socio-economic conditions were not investigated in this work.

Results

Descriptive statistics (means and standard deviations) for body height and all evaluated head and face measures with regard to geographic regions, climate, diet type and sex are shown in Tables III and IV.

The multiple forward stepwise regression analysis revealed significant and sex-specific differences in craniofacial measures between subjects according to geographic, climatic or dietary distribution (Table V). The stepwise approach was used to select the distribution type that best describes the variation in the dependent variable. The slopes of the independent variables (regression coefficients β) in the multiple linear regression models measure the changes in the dependent variable that correspond to an increase of one unit in independent variable, if all other independent variables are held constant.

Geographic regions significantly differentiated head length measures in males ($\beta = -0.24$, p < 0.001), head breadth measures in females ($\beta = 0.162$, p < 0.01) and cephalic indices in both sexes ($\beta_{males} = 0.146$, p < 0.05 and $\beta_{females} = 0.265$, p < 0.00001). The positive values of the regression coefficient showed, in both sexes, an increase in cephalic index from the southern and north-western regions to the central and eastern parts of Croatia. Cephalic index means were the lowest in southern Croatian females and north-western males. The highest means were found in eastern Croatia in both sexes (Table III). Since cephalic index is a head shape measure, these results suggested that dolichocephalic head shape prevailed in the eastern continental region in Croatia.

Dietary distribution revealed significant differentiation of body height measures in both sexes. Significant differences in other craniofacial measures were found among females according to dietary or climatic distribution. Except body height, dietary distribution influenced head length and head circumference means, while climatic distribution revealed significant differences between females in all the three facial measures (Table V). Therefore, in females, significant correlate(s) were determined for each dependent variable, except head height. The negative β values of diet type as a predictor variable (Table V) explained that changes of the Mediterranean type of diet to mixed Mediterranean-continental or continental diet are associated with decreasing body height in males and females $(\beta = -0.16 \text{ and } \beta = -0.10, \text{ respectively, } p < 0.05), \text{ and decreasing head length } (\beta = -0.26, \beta = -0.26)$ p < 0.00001) and head circumference values ($\beta = -0.14$, p < 0.01) in females, as shown also in Table IV. It may be argued that the Mediterranean type of diet contributed to higher body height means in both sexes, and higher head length and head circumference means in females. Concerning face breadth values in females, a confounding effect of climate and diet type was indicated, although it seemed that climate alone might better explain face breadth variation in females ($\beta_{\text{climate}} = 0.466, p < 0.0001; \beta_{\text{climate and diet}} = -0.27, p < 0.05$). From the results presented in Table V, it follows that climate and diet type influenced head breadth in

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Table III. Descriptive statistics of mean body height and craniofacial measures in the studied geographic regions of Croatia.

	Sout	Southern	North-western	vestern	Central	tral	Eastern	ern
	Females	Males	Females	Males	Females	Males	Females	Males
BH^{1}	170.30 ± 5.69	184.57 ± 5.57	169.07 ± 6.13	183.55 ± 5.82	168.21 ± 5.44	181.62 ± 6.92	168.96 ± 5.91	182.31 ± 5.84
HL^2	18.71 ± 0.80	19.65 ± 0.57	18.51 ± 0.71	19.53 ± 0.66	18.16 ± 0.73	19.34 ± 0.82	18.21 ± 0.76	19.06 ± 0.68
HB^3	14.01 ± 0.68	14.73 ± 0.64	14.11 ± 0.68	14.74 ± 0.77	14.24 ± 0.74	14.70 ± 0.76	14.45 ± 0.70	14.88 ± 0.75
HH^4	14.19 ± 0.60	15.00 ± 0.73	13.97 ± 0.69	14.81 ± 0.66	13.95 ± 0.56	14.77 ± 0.64	14.11 ± 0.64	14.79 ± 0.69
HC^{5}	56.42 ± 1.95	57.74 ± 1.60	55.89 ± 1.50	58.16 ± 1.68	55.63 ± 1.64	57.80 ± 1.85	55.76 ± 1.32	57.74 ± 1.69
CI^6	75.32 ± 3.79	75.66 ± 4.20	76.39 ± 4.72	75.50 ± 4.49	78.56 ± 5.15	76.22 ± 4.99	79.49 ± 5.07	78.31 ± 4.92
MFH^7	10.97 ± 0.72	11.90 ± 0.71	10.92 ± 0.67	11.80 ± 0.74	10.70 ± 0.52	11.78 ± 0.68	10.69 ± 0.60	11.66 ± 0.73
FB^8	10.53 ± 0.52	10.93 ± 0.70	10.29 ± 0.60	11.08 ± 0.70	10.64 ± 0.62	11.10 ± 0.65	10.59 ± 0.58	11.15 ± 0.69
FI^9	96.39 ± 8.19	92.20 ± 8.18	94.10 ± 9.90	94.51 ± 7.40	99.54 ± 6.62	94.48 ± 6.88	99.28 ± 6.57	96.75 ± 8.93
¹ Bodv hei	ght: ² head length: ³ l	head hreadth: ⁴ head	Bodv height: ² head length: ³ head breadth: ⁴ head beight: ⁵ head circumference: ⁶ cenhalic index: ⁷ momhological face height: ⁸ face breadth: ⁹ facial index.	ference: ⁶ cenhalic in	ldex: ⁷ morphological	l face height: ⁸ face h	readth: ⁹ facial index.	

racial index. morphological face height; 'face breadth; index; cepnanc nead circumierence; neignu; preadin; nead nead body neight; nead length;

	Fen	Females	Με	Males		Females			Males	
	M^{10}	C ¹¹	M^{10}	C ¹¹	m^{12}	mc ¹³	c ¹⁴	m ¹²	mc ¹³	c^{14}
BH^{1}	169.33 ± 6.05	169.33 ± 6.05 168.40 ± 5.55	183.82 ± 5.73	181.80 ± 6.63	170.31 ± 5.63	$83.82 \pm 5.73 181.80 \pm 6.63 170.31 \pm 5.63 169.06 \pm 6.14 168.40 \pm 5.55 184.37 \pm 5.57 183.55 \pm 5.82 181.80 \pm 6.63 182.81 + 5.63$	168.40 ± 5.55	184.37 ± 5.57	183.55 ± 5.82	181.80 ± 6.63
HL^2	18.55 ± 0.73	18.17 ± 0.73	19.57 ± 0.63	19.27 ± 0.79	18.71 ± 0.79	18.50 ± 0.71	18.17 ± 0.73	19.65 ± 0.57	19.53 ± 0.66	19.27 ± 0.79
HB^{3}	14.09 ± 0.68	14.29 ± 0.73	14.74 ± 0.73	14.74 ± 0.76	13.99 ± 0.69	14.12 ± 0.68	14.29 ± 0.73	14.73 ± 0.64	14.74 ± 0.77	14.74 ± 0.76
HH^4	14.02 ± 0.67	13.98 ± 0.58	14.86 ± 0.69	14.77 ± 0.65	14.18 ± 0.60	13.97 ± 0.69	13.98 ± 0.58	15.00 ± 0.73	14.81 ± 0.66	14.78 ± 0.65
HC^{5}	56.00 ± 1.62	55.66 ± 1.56	58.03 ± 1.66	57.79 ± 1.80	56.41 ± 1.93	55.89 ± 1.50	55.66 ± 1.56	57.74 ± 1.60	58.16 ± 1.68	57.79 ± 1.80
CI ⁶	76.17 ± 4.56	78.78 ± 5.13	75.55 ± 4.38	76.75 ± 5.03	75.18 ± 3.87	76.44 ± 4.70	78.78 ± 5.13	75.66 ± 4.20	75.50 ± 4.49	76.75 ± 5.03
MFH^7	10.93 ± 0.68	10.70 ± 0.54	11.83 ± 0.73	11.74 ± 0.69	10.96 ± 0.71	10.92 ± 0.67	10.70 ± 0.54	11.90 ± 0.71	11.80 ± 0.74	11.74 ± 0.69
FB^8	10.34 ± 0.59	10.63 ± 0.61	11.03 ± 0.70	11.11 ± 0.65	10.54 ± 0.52	10.29 ± 0.60	10.63 ± 0.61	10.93 ± 0.70	11.08 ± 0.70	11.11 ± 0.65
FI^9	94.59 ± 9.59	99.48 ± 6.59	93.85 ± 7.67	95.09 ± 7.51	96.57 ± 8.19	94.03 ± 9.89	99.48 ± 6.59	92.20 ± 8.18	94.51 ± 7.40	95.09 ± 7.51
¹ Body	Body height; ² head length; ³ head breadth; ⁴ head height; ⁵ head circumference; ⁶ cephalic index; ⁷ morphological face height; ⁸ face breadth; ⁹ facial index; ¹⁰ Mediterranean	gth; ³ head bread	lth; ⁴ head height;	⁵ head circumfe	rence; ⁶ cephalic	index; ⁷ morphol	ogical face heigh	it; ⁸ face breadth;	⁹ facial index; ¹⁰	Mediterranean

Table IV. Descriptive statistics of mean body height and craniofacial measures according to the climatic and diet type.

⁰ Mediterranean	
⁹ facial index; ¹⁰	
⁸ face breadth;	
nological face height	liet.
alic index; ⁷ morph	diet; ¹⁴ continental c
d circumference; ⁶ ceph	erranean-continental d
lth; ⁴ head height; ⁵ hea	rranean diet; ¹³ Medit
length; ³ head brea	al climate; ¹² Medite
¹ Body height; ² head	climate; ¹¹ continent
	ody height; ² head length; ³ head breadth; ⁴ head height; ⁵ head circumference; ⁶ cephalic index; ⁷ morphological face height; ⁸ face breadth; ⁹ facial in

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Danandant		Males $(n = 228)$	= 228)				Females $(n = 404)$	=404)		
variable	Predictor variable (model) ^a	β	Multiple R^2	F^{b}	đ	Predictor variable (model) ^a	β	Multiple R^2	F^{b}	d
BH^{1}	Diet (1)	-0.16	0.027	6.165	0.0138	Diet (1)	-0.10	0.010	4.030	0.0454
HL^2	Geographic regions (1)	-0.24	0.057	13.650	0.0003	Diet (1)	-0.26	0.066	28.361	0.00000
HB^3	No significant predictors					Geographic regions (1)	0.162	0.026	10.775	0.0011
HH^4	No significant predictors					No significant predictors				
HC^{5}	No significant predictors					Diet (1)	-0.14	0.020	7.557	0.00627
CI^6	Geographic regions (1)	0.146	0.021	4.864	0.0284	Geographic regions (1)	0.265	0.070	30.385	0.00000
MFH^7	No significant predictors					Climate (1)	-0.17	0.030	11.482	0.00078
FB^8	No significant predictors					Climate (1)	0.466	0.051	19.715	0.00001
						Diet (2)	-0.27	0.068	6.571	0.0108
FI^9	No significant predictors					Climate (1)	0.271	0.0733	28.946	0.00000
¹ Body height ^a Models of p ^b Criteria usec	Body height; ² head length; ³ head breadth; ⁴ head height; ⁵ head circumference; ⁶ cephalic index; ⁷ morphological face height; ⁸ face breadth; ⁹ facial index Models of predictor variables: (1) – includes one predictor variable; (2) – includes two predictor variables.	⁴ head heig es one pred	h; ⁴ head height; ⁵ head circumference; ⁶ cephalic in a des one predictor variable; (2) – includes two prentry or removal: F to enter = 4, F to remove = 1	aference; $^{(1)}$ 2) - inclue = 4, F to r	cephalic ir des two pro-	idex; ⁷ morphological face heig edictor variables.	ht; ⁸ face br	eadth; ⁹ facial inc	dex.	

opposite directions. The probable reasons for such result were the finding of the lowest mean face breadth value in north-western females (Table III) and the fact that north-western region was defined as a separate unit of dietary distribution. As we shall show later, the lowest mean in north-western face breadth measures in females may be associated with the specific climatic feature of this region (cumulative multiyear average precipitation).

Changes of Mediterranean to continental climate were associated with a decrease in morphological face height ($\beta = -0.17$, p < 0.001), and an increase in face breadth and facial index values ($\beta = 0.466$, p < 0.0001 and $\beta = 0.271$, p < 0.00001, respectively) in females. Mediterranean climate, therefore, contributed to higher and narrower faces in females from southern and north-western regions, while continental climate was associated with lower and broader faces in females from central and eastern Croatia (shown also in Table IV).

 R^2 shows the proportion of the variation of the dependent variable that can be explained by the regression model. From Table V it is evident that geographic, dietary or climatic distribution of our subjects may explain only 1–2.7% of the variation in body height $(R^2_{\text{females}} = 0.010, R^2_{\text{males}} = 0.027), 2–7.3\%$ of craniofacial variability in females $(R^2_{\text{head}}_{\text{circumference}} = 0.020, R^2_{\text{facial index}} = 0.073)$, and 2.1–5.7% of craniofacial variability in males $(R^2_{\text{cephalic index}} = 0.021, R^2_{\text{head length}} = 0.057)$. Climatic and dietary distribution showed a confounding effect on face breadth measures in females, although climate may explain 5.1% of the variation, and diet type contributed only an additional 1.7% of the variance (Table V).

The contribution of multiyear average calcium concentration in drinking water was also examined under the same statistical procedure but this independent variable failed to enter the regression equation. We expected a higher multivear average calcium concentration in drinking waters in the Karst area. The Karst area includes the islands and the Dinaric Alps region (coastland and hinterland) (Figure 1). The multiyear average calcium concentration did not follow the geographic and hydrological distribution covered in this research (Table I) and the regression model used in this study did not show a significant correlation to any dependent variable in either sex. That is, the multiyear average calcium concentration in drinking water was not a significant predictor of craniofacial morphology or body height. However, multiple stepwise regression analysis of different climatic conditions showed a significant correlation of cumulative multiyear sunshine duration and cumulative multiyear average precipitation values with the dependent variables' variability (cranial and facial measures in females, and head length and facial index in males) and revealed again a specific pattern of differentiation between males and females (Table VI). Multiyear average air temperatures showed little influence on the studied variables except in the case of head length among females ($\beta = 0.18, p < 0.001$).

Investigated climatic characteristics did not correlate significantly with body height in either sex. Multiyear average sunshine duration significantly correlated with head height $(\beta = 0.109, p < 0.05)$ and head circumference $(\beta = 0.142, p < 0.01)$ measures in females, and facial index values $(\beta = -0.144, p < 0.05)$ in males. This predictor variable may explain 1.2–2.1% of above-mentioned cranial measures' variation $(R^2_{head height} = 0.012, R^2_{head circumference} = 0.020, R^2_{facial index} = 0.021)$. The effect of cumulative multiyear average precipitation was highly significant to face breadth and facial index values $(\beta = -0.253 \text{ and } \beta = -0.268, \text{ respectively}, p < 0.00001)$ in females. However, this predictor variable can explain 6.4–7.2% of these traits' variation $(R^2_{face breadth} = 0.064, R^2_{facial index} = 0.072)$. A confounding effect of sunshine exposure and precipitation was significantly correlated with head length in males $(\beta = 0.154, p < 0.05)$, and head breadth $(\beta = -0.111, p < 0.05)$, cephalic index $(\beta = -0.196, p < 0.0001)$ and morphological face height $(\beta = 0.116, p < 0.05)$ in females. These two independent variables may explain the range from 2.3 to 6.9% of the dependent variables' variation $(R^2_{head breadth} = 0.023, R^2_{morphological face height} = 0.029$,

variable Pred	4	(n - 220)	(077				Females $(n = 404)$	n = 404)		
	Predictor variable (model) ^a	β	Multiple R ²	F^{b}	þ	Predictor variable (model) ^a	β	Multiple R^2	F^{b}	þ
BH ¹ Nc HI ²	No significant predictors Sunshine (1)	0 182	0.026	5 960	0.0154	No significant predictors Temperatures (1)	0.180	0 0325	13315	0.0003
	Precipitation (2)	0.154	0.049	5.414	0.0209					
HB ³ Nc	No significant predictors					Sunshine (1)	-0.121	0.0113	4.524	0.034
						Precipitation (2)	-0.111	0.0234	4.888	0.028
	No significant predictors					Sunshine (1)	0.109	0.012	4.286	0.039
10	No significant predictors					Sunshine (1)	0.142	0.020	7.462	0.0066
CI ⁶ Nc	No significant predictors					Sunshine (1)	-0.201	0.031	12.630	0.00043
						Precipitation (2)	-0.196	0.069	16.062	0.00007
MFH ⁷ Nc	No significant predictors					Precipitation (1)	0.142	0.0159	5.862	0.0160
						Sunshine (2)	0.116	0.0292	4.940	0.0270
FB ⁸ Nc	No significant predictors					Precipitation (1)	-0.253	0.064	24.727	0.000001
FI^9	Sunshine (1)	-0.144	0.021	4.162	4.162 0.043	Precipitation (1)	-0.268	0.072	28.018	0.00000

Table VI. Summary of multiple forward stepwise regression models for body height and craniofacial traits predicted by climatic features.

^b products of predictor variable's entry or removal: F to enter = 4, F to remove = 1. ^b Criteria used for independent variable's entry or removal: F to enter = 4, F to remove = 1. Sunshine, cumulative multiyear sunshine duration; Precipitation, cumulative multiyear average precipitation; Temperatures, multiyear average air temperatures.

 $R^2_{head length} = 0.049$, $R^2_{cephalic index} = 0.069$). The positive values of the regression coefficients β (Table VI) showed that higher head length measures in both sexes were associated with an increase in average sunshine duration, temperatures and precipitation values that are the features of Mediterranean climate. In females, higher sunshine exposure was also associated with higher head height, head circumference measures and higher morphological face height (positive β values, Table VI). Face breadth, head breadth, and both indices in females, as well as facial index in males, were significantly lower (negative β values) under the characteristics of the Mediterranean climate (high average sunshine duration and high average precipitation).

Discussion

It is well established that craniofacial features are characterized by both environmental and genetic factors. Their impact is well documented at the global and regional levels. Global craniometric variation has been shaped by gene flow (mainly via geographic distance) showing correlations with aspects of population structure or population history, natural selection (via climatic adaptation) showing significant correlations with various measures of climate and developmental plasticity. The influences of all these factors have a confounding effect (Relethford 2004). For instance, the data of Boas (1912) argue for developmental plasticity of cranial shape in the descendants of American immigrants from Europe. Later revisions of his data revealed that the pattern of relationship between ethnic groups had not been affected to large extent (Sparks and Jantz 2002; Gravlee et al. 2003). Furthermore, Bharati et al. (2005) have found that the cephalic index discriminates well among populations of different ethnic origin but also climatic conditions in different regions in the Indian subcontinent. All these findings suggest a strong genetic component of cranial traits that is assumed to have a polygenic mode of inheritance.

In our study, we determined a significant influence of the environmental (geographic, climatic or dietary) conditions on body height and craniofacial variability observed in Croatia. Environmental factors affected craniofacial traits more in females than males, showing sex-specific differentiation (Tables V and VI). A closer look at the geographic position, specific shape (Croatia has a shape that resembles a crescent or a horseshoe) and the landscape of Croatia may explain the first finding. The Dinaric Mountain range extends along the coast making a narrow coastal zone, clearly dividing the coast from the hinterland of the southern and north-western regions, as well as from continental Croatia, thus substantially affecting climatic conditions in different regions (as shown in Table I). Because of geographic isolation, the coastal and continental parts of Croatia have been, throughout its history, exposed to different cultural influences including different dietary habits. Thus, despite covering a small geographic area, Croatia is characterized by distinct geographic, climatic and dietary conditions.

Climatic division into only two groups (Mediterranean and continental climate) was insufficient to reveal a significant effect on cranial measures in either sex, as presented in Table V. Only a high climatic influence on facial measures in females was evident. Table VI resolves better the influences of different climatic conditions showing a high effect of sunshine exposure and wetness to cranial and facial measures, including both indices. The effect was more pronounced in the female sex. We did not find the influence of average air temperatures to craniofacial variability, except for head length in females. That was a surprising result since craniometric traits have shown considerable correlations with temperature (Relethford 2004). A possible reason for that finding was the use of average annual temperatures in our analysis while annual means for the coldest and the warmest months were not investigated.

It is widely accepted that natural selection optimizes cranial size and shape in terms of heat loss and our results fit well with this assumption, at least in females. More sunny days, higher average temperatures and more wetness (Mediterranean climate) correlated significantly with longer and narrower heads (i.e. dolichocephaly, lower cephalic index), higher head height and head circumference and higher and narrower faces (leptoprosopic morphology, lower facial index) (Table VI). The impact of wetness may be specifically connected with face breadth measures in females. Face breadth had the lowest mean in the north-western females (Table III), not southern as expected from the southern–northwestern–northeastern distribution of many craniofacial traits. It may be explained by a low correlation of head breadth and face breadth measures and their relative independence (Lieberman et al. 2000). The north-western region had the highest cumulative multiyear average precipitation (Table I) and we pointed to the effect of wetness on face breadth measures and, consequently, facial index values (Table VI).

Distribution according to diet type revealed significant differences in body height in our population showing the same pattern in both sexes. The Croatian population is among the tallest in Europe, i.e. regional male means range from 181 to 184 cm and female means range from 168 to 170 cm (Table III). Significant variability in body height has also been observed among other European populations (Silventoinen et al. 2003), including regional variability of body height for example in the Netherlands and Italy, where the people are on average taller in the north (Fredriks et al. 2000; Cacciari et al. 2002; Danubio et al. 2003). The Croatian sample showed the opposite distribution, with the tallest individuals in the south and the lowest in the central (northern) region. Stature has a strong genetic component, showing less global variation and not following latitudinal gradient (Ruff 2002) but may be modulated by environmental factors. We expected that sunshine exposure significantly influenced the growth not only of craniofacial but also of other skeletal bones since the subjects from southern Croatia were the tallest in our sample. The influence of sunshine exposure on bone metabolic changes has been recognized in children and in adults (Feliciano et al. 1994; Dawodu et al. 1998; Yonei et al. 1999; Das et al. 2006). However, except for sunshine duration, bone development is probably influenced by other environmental factors such as food type and quality, healthcare, hygienic conditions or family size. The obtained results showed that the multiyear average sunshine duration was not significantly correlated with body height in either sex (Table VI), but suggested that diet type may modulate body height to small extent in both sexes (1-2.7%) body height variability may be explained by diet type, Table V).

The effects of diet on physical growth and ontogenetic plasticity are documented in the literature (DeRousseau and Reichs 1987; de Meer et al. 1993; Cole 2000; Castilho and Lahr 2001). Such effects of diet may be attributed to different lipid consumption since the Mediterranean and continental diet differ significantly regarding lipid composition. Lipids have been shown to play an important role in skeletal biology and bone health (Watkins et al. 2000, 2001). The n - 3/n - 6 ratio of polyunsaturated fatty acids in the Mediterranean diet (mainly from fish and olive oil sources) has changed due to the industrial introduction of the vegetable oil technology and popularized use of cooking oils from sunflower, soybean and corn. These oils are all good sources of n - 6 polyunsaturated fatty acids. Their wide usage changes have upset the balance between dietary n - 6 and n - 3 fatty acids, causing an enhanced dietary n - 6/n - 3 ratio and also an increasing incidence of chronic degenerative diseases (Cordain et al. 2005). Results presented in Table V suggest that the type of diet may, to some extent, influence craniofacial measures (head length and head circumference in females).

However, the sex-specific differentiation of craniofacial traits in the Croatian population was intriguing. The results showed greater influences of climatic and dietary conditions on craniofacial morphology in females than in males (Tables V and VI). One possible reason could be a smaller number of male than female subjects in our sample, although that was not expected to affect group means substantially. A possible explanation are differences in the craniofacial growth processes between males and females. Sexes display dimorphism in their craniofacial complexes. Regarding processes of facial growth, differences between sexes are displayed during the phase of active growth (related to the timing, amount and localization of growth) and also during the non-active phase thereafter, during adulthood, when girls change from a horizontal to a vertical growth pattern while boys maintain their vertical growth pattern from puberty (Carels 1998). It is worth mentioning that the head and face display the major growth velocity before and after birth, during the first year of life (Rosales-Lopez et al. 1992) although following different growth trajectories (the cranium follows neural trajectories and the face follows the general pattern of growth seen for body dimensions). This is exactly the period of growth in which secular changes operate on skull dimensions. For above-mentioned reasons, we assume that the different response of sexes to environmental influences in our population may be connected with the observed processes of secular changes of the particular craniofacial traits, shown in our recent studies (Buretić-Tomljanović et al. 2004, 2006). The changes of the craniofacial dimensions in our young adult population are consistent with dolichocephalization. Dolichocephaly rises on account of the large brains on the narrow cranial base. The beginning of secular changes of body height and cranial dimensions was reported in mid 20th century in our population (Kovač 1984) and in a great number of European and other populations (Gyenis 1994; Hauspie et al. 1996; Casado de Frias 1999; Zellner et al. 1999; Cole 2000; Fredriks et al. 2000; Sanna and Soro 2000; Castilho and Lahr 2001). It has been shown that head breadth dimension is constrained by cranial base breadth dimension. Cranial base is the part of the skull that showed the highest secular trend during the last century in Americans (Wescott and Jantz 2005). Cranial base reaches adult size early in life constraining head breadth and, to some extent, face breadth dimension. That imposes the substantial environmental impact of, as yet unidentified mechanisms, to head and face dimensions during infancy and childhood (Jantz and Meadows Jantz 2000). It is generally believed that environmental forces such as better socio-economic conditions, or improved nutrition and healthcare cause secular changes of head and body dimensions, although other causes are also possible. It has been reported that males respond faster than females to changes in the environment (Cole 2000) and, possibly, to the forces that drive secular changes. Therefore, we suggest that sexes responded differently to secularization forces, i.e. a faster response to environmental changes diminished regional differentiation of particular craniofacial traits in the men in the present study. This may also explain the highest frequency of dolichocephalics among our men in all geographic regions (42.3–64.0%, data not shown). A different pattern of the craniofacial growth and slower mode of reaction to environmental forces in women allowed a stronger influence of climatic and dietary conditions and so, better differentiation between female groups in our population. Examples of sex-specific response to environment may be found in other species as well. For instance, as a response to a warmer climate, red deer males grow more rapidly during early development, while females respond better to earlier plant

phenology (Post et al. 1999). The increased rate of shape changes is observed during cranial sexual dimorphism ontogeny in Bornean orangutan males (*Pongo pygmaeus pygmaeus*) (Leutenegger and Masterson 1989). These phenomena, as well as sexual dimorphism, are probably related to different strategies of growth in relation to reproduction since females invest more in early sexual maturity.

Several studies have shown that the variation of the total craniofacial shape is more clearly patterned by structural-historical aspects of the population than by some important nongenetic differences (Ross 2004; González-José et al. 2005). In an attempt to assess the contribution of nongenetic factors to induction of developmental plasticity, González-José et al. (2005) based their analysis on the functional components of the skull, and demonstrated the plasticity of the masticatory complex, reflecting the environmental influence of the diet and mechanical loading of the face. However, the total craniofacial shape is patterned according to structural-historical aspects of population. Ross (2004), for instance, also does not attribute the craniofacial differentiation between Croatians and Bosnians (who originated from the same Slav ancestry) to either environmental plasticity or geographic isolation. She points out the genetic (reproductive) isolation due to culturally imposed religious segregation. From numerous data concerning this point it follows as an oversimplification to attribute the vast range of variability observed among local and geographic populations to environmental adaptation. Since the present study was not designed to assess the effects of migrations and gene flow that had influenced the genetic structure of our population (evidenced through many migration events during past and recent history), we may only speculate about the existence of the population substructure in Croatia. Population substructure is evidenced for isolates of many middle and southern Dalmatian islands due to endogamy, inbreeding and genetic drift (Smolej-Narančić et al. 1994; Vitart et al. 2006). The analyses of uniparentally inherited mtDNA (Tolk et al. 2000) and Y chromosome markers (Barać et al. 2003) in eastern Adriatic islands and the Croatian mainland suggest that the founding groups of people might have been of multiple, diverse origin. The genetic structure of the population may be also balanced by environment (climate and/or diet composition), as shown for APOH allele frequencies and latitude (probably connected to diet composition) (Vitale et al. 2002).

Our results showed significant regional differences in body height and craniofacial features in Croatia that may be associated with geographic, climatic or dietary distribution, or with the variability of different climatic characteristics, suggesting their confounding effect. The results were consistent with a significant but low impact of the environment on body height and craniofacial measures in young adults in Croatia. The features of the Mediterranean climate and diet type were associated with higher longitudinal (head length) and vertical (head height, morphological face height) craniofacial measures, lower horizontal (head and face breadth) craniofacial measures and with increasing body height. The pattern of the observed environmental impact on craniofacial traits was different in males and females. However, the models revealed in this study may explain a very low percentage of variability of the investigated traits (1-7.32%). This may be due to a strong association between body height and craniofacial measures, and genetic factors. Our results are in accordance with the postulate that the long-term effect of climatic adaptation on cranial size and shape is less pronounced at the local than global level owing to more global climatic heterogeneity. Therefore, the body height and craniofacial measures in Croatian young adults have been modulated to a small extent by different geographic, climatic or dietary conditions. That means that historical and cultural differences, and admixture must be also taken into account.

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