Family Correlations of Metacarpal Bones – Heritable (h²) and Environmental (c²) Components of Total Phenotypic Variation

T. Škarić-Jurić and P. Rudan

ABSTRACT

The analysis of family data of 18 metacarpal morphometric dimensions (bone length - L, total diaphysis width - T and medullary canal width - M of the second, third and fourth metacarpals of both hands) has been performed on 956 randomly sampled adult examinees (age 18 to 85), inhabitants of the islands of Brač and Hvar and the Pelješac peninsula, Croatia. Interclass (for parent-offspring family pairs) and intraclass (for siblings) correlation coefficients have been calculated as well as heritability coefficient (h^2) and coefficient quantifying effects of common sibling environment (c^2) have been estimated. Heritability estimates (h^2) for the medullary canal width dimensions (54%–71%) showed to be at least as high, and c^2 (2%-14%) values showed to be at least as low as those obtained for bone length dimensions ($h^2 = 51\%-65\%$; $c^2 = 5\%-16\%$) suggesting a strong influence of genetic factors in medullary canal width formation. For both traits the highest heritability and the lowest environmental component is found for dimensions of 4th metacarpal bone, which could be explained by lower biomechanical pressures acting on that bone owing to it's anatomical position. Analysis of family resemblance for medullary canal width showed the tendency of female family pair (Mother-daughter) to be less correlated than other family pairs, which is especially pronounced in fourth metacarpals. We assume that lower correlation values of Motherdaughter pair can be the result of non-linearity of age dependent changes in medullary canal width dimensions associated with the osteoporotic process which is more active in females. Clearly lower heritability values obtained for total diaphysis width dimensions (25%-48%) and higher values obtained for c^2 (14%-23%), in addition to findings of higher correlation values in same sex family pairs (Father-son, Mother-daughter) speaks in favor of substantial importance of common family environmental factors particularly sexually specific physical activity – which through the short-term adaptation processes modify the total diaphysis width dimension phenotype.

Received for publication October 19, 1997.

The research was supported by the Ministry of Science and Technology of the Republic of Croatia (Project 019601), and by the U.S.-Croatian Joint Commission for Scientific Cooperation through the Smithsonian Institution (Project JF 259).

Introduction

The previous population structure analyses performed on the island populations of Middle Dalmatia, based, among others, on the analysis of diaphysis length (L), total diaphysis width (T) and medullary canal width (M) dimensions of metacarpal bones¹⁻⁵, showed that metacarpal bones morphometric dimensions are good an indicator of population structure. Additionally, the results of factor analysis performed on the same set of data⁶ indicated that not only genetics has an important role in the determination of investigated metacarpal traits, moreover, that it is even likely that few different loci with major effect (e.g. different sets of polygenes) are involved on the genetic determination of each of the three types of investigated metacarpal bone traits (L, T and M).

Since morphometric dimensions of metacarpal bones, just like other continuous traits of the human body, may be considered as multifactorially determined variables subject to the influence of a number of intrinsic (genetic) and extrinsic (environmental) factors (the abundant literature describing those factors is well presented in the work of Šimić⁶ et al.) the analysis of family data, as a complementary method, gives us a specific opportunity to quantify the relative impacts of genetic and environmental factors on their phenotypic expression. Therefore, estimation of two components of total phenotypic variation $(Vp = Va + Vd + Ve)^{7,8}$ represented by coefficients h² (additive genetic heritability) and c2 (»cultural heritability«, defined as the proportion of phenotypic variance due to a common sibship environment) as well as the presentation and interpretation of sex and generational structure of family resemblance for 18 metacarpal morphometric dimensions (bone length, total diaphysis width and medullary canal width of the second,

third and fourth metacarpals of both hands) is the objective of the present study. Special interest is focused on heritability of the medullary canal width dimensions because of its connection with the osteoporotic process⁹. Namely, because of the increased prevalence of osteoporosis in relatives it has been suspected that bone loss is familial ¹⁰⁻¹³, but the relative importance of genetic and environmental factors ^{14,15} still remains unclear.

Materials and methods

This research is a part of a holistic anthropological investigation of population groups of the Middle Dalmatia performed by the research team of the Institute for Anthropological Research, Zagreb, Croatia. The morphometric data of 18 metacarpal bone radiogrammetric dimensions as well as the evidence regarding the family relations used in this study are the subset of an extensive material (collected since 1978) on the populations of the islands of Brač and Hvar, and the Pelješac peninsula^{1-6,16-20}. The sample of the present study is the sub-sample of the randomly sampled individuals in the region for the purpose of population structure analyses. Therefore, the final number of subjects (956 examinees, age 18 to 85) was determined by the coincidence that two (or more) participants of the original random sample are the members of the same family.

The morphometry of metacarpal bones was performed on hand-wrist radiographs of both hands. Bone length (L), total diaphysis width (T) and medullary canal width (M) of the second (2), third (3) and fourth (4) metacarpal bones were measured on the left (L) and right (R) hands, according to Barnett and Nordin²¹. All the measurements (Figure 1) were performed by one investigator within a short time, using a millimeter ruler and a magnifying glass (× 10) with a scale permitting

0.05 mm accuracy. Measurements were rounded to 0.1 mm.

Assuming that age and sex exert a considerable effect on morphometric variables of the metacarpal bones^{4,22–25}, the adjustment for age and sex variation (age, sex, age \times sex, age²) by means of multivariate linear regression was performed and residual scores were used in further analyses. The adjustment was made for each family pair separately. Intraclass (ANOVA) correlations are calculated for Sibling-sibling family pair, and interclass (Pearson's product-moment) correlation coefficients (r) are calculated for Fathermother pair as well as for all inter-generational, parent-offspring pairs^{26,27}, Pearson's correlation coefficients are computed using the Pairwise method which means that correlations are computed between all possible family member pairs as all pairs of values are independent. Differences in correlation values between various parent-offspring and offspring-offspring pairs are tested using Fisher's ztransformation of the correlation coefficients. Estimation of components of total phenotypic variation (Vp = Va + Vd +Ve)^{7,8} is represented by coefficients h²,

defined as the proportion of phenotypic variance due to additive genetic effects and c2, »cultural heritability«, defined as the proportion of phenotypic variance due to a common sibship environment. Heritability of all 18 variables is estimated according to the Fisher method^{7,8} using duplicated Parent-offspring correlation values corrected for phenotypic assortative mating: $h^2 = 2 r$ Parent-offspring / (1) + r Father-mother). Environmental component (c²) is estimated using difference of inter-generational versus intra-generational family correlation values: $c^2 = 2 r$ Sibling-sibling $-h^2/2(1 + r \text{ Father-mother})$ $\times h^2)^{28}$

Results

Table 1 presents sample sizes (n), as well as means (\bar{X}) and standard deviations (sd) of 18 morphometric dimensions of metacarpal bones and age for the Mothers, Fathers, Daughters, Sons (constituting all parent-offspring pairs) and separately for the Sisters and Brothers family member groups (constituting Sibling-sibling pair). Since the participants of the present study are randomly selected, the groups of Sisters and Brothers partially

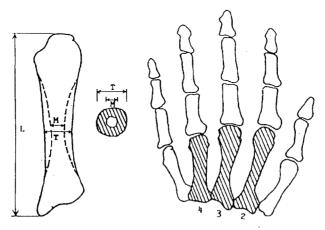


Fig. 1. Schematic presentation of metacarpal bones (2 - second, 3 - third, 4 - fourth) and measured dimensions $(L - bone \ length, T - total \ diaphysis \ width, M - medullary \ canal \ width)$.

consist of subjects which are not members of the parent-offspring pairs and who contribute only in Sibling-sibling pair. At the other hand, some of the participants of groups of Daughters and Sons are only included in parent-offspring pairs and not in Sibling-sibling pair which is happening in case when family has only one child. Therefore, the mean age of the Mothers and Fathers (with age range 39–81 and 41–79 respectively) is only about 10 years older than the mean age of the Sisters and Brothers (age ranges 20–80 and 22–85), while age of the Daughters and Sons ranged 18–58 and 20–55 respectively.

Table 2 presents parent-offspring correlation values for 18 examined metacarpal bone dimensions. Differences in correlation values among parent-offspring

pairs tested by Fisher's z-transformation of correlation coefficient proved to be significant only in correlations for total diaphysis width dimensions (T): for R2T Mother-daughter (r = 0.538) pair have significantly higher values than Mother son (r = 0.263) and Father-son (r = 0.176)pairs, and for R3T Father-son (r = 0.524)correlation is significantly higher than in Father-daughter (r = 0.163) pair. Although the differences in correlation values revealed significance only in total diaphysis width dimensions (T), the pattern of parent-offspring correlations differed with respect to examined metacarpal bone trait (L. T and M).

For bone length (L) dimensions, all parent-offspring pairs have significant correlation values, ranged from the small-

TABLE 1
SAMPLE SIZES (N), AVERAGE VALUES (X) AND STANDARD DEVIATIONS (sd) OF AGE AND
EXAMINED MORPHOMETRIC DIMENSIONS OF METACARPAL BONES FOR MOTHERS, FATHERS,
DAUGHTERS, SONS, SISTERS AND BROTHERS

	$\begin{array}{c} \text{Mothers} \\ (\text{n} = 182) \\ \bar{\text{X}} \text{sd} \end{array}$		Fathers $(n = 113)$ \bar{X} sd			$\begin{array}{c} \text{Daughters} \\ \text{(n = 114)} \\ \bar{X} \text{sd} \end{array}$		$\begin{array}{c} Sons \\ (n = 142) \\ \bar{X} sd \end{array}$		Sisters (n = 280) X sd		$\begin{array}{c} \text{Brothers} \\ (\text{n} = 218) \\ \bar{\text{X}} \text{sd} \end{array}$	
Age	57.2	9.4	59.3	7.1	31.9	9.3	31.5	8.6	49.4	13.1	48.7	12.7	
L2L	693.2	39.1	743.8	80.5	692.7	37.4	752.8	41.2	690.6	57.0	754.3	42.3	
R2L	700.1	39.5	746.5	80.9	697.3	38.3	756.7	41.2	699.7	41.1	751.7	83.2	
L3L	644.4	36.8	681.4	99.1	645.1	34.8	697.4	39.3	645.1	38.6	695.1	60.9	
R3L	644.3	61.7	690.2	76.2°	645.9	36.3	698.2	39.4	647.5	39.4	696.4	60.9	
L4L	577.5	35.4	617.8	68.4	575.3	33.6	620.8	36.2	577.7	36.3	622.7	55.0	
R4L	580.1	56.4	622.7	69.4	575.7	64.3	623.8	36.8	579.0	61.1	627.3	56.3	
L2T	84.5	9.2	95.8	7.1	82.9	6.7	94.3	10.5	84.1	6.1	96.3	9.6	
R2T	86.5	9.4	97.8	7.8	84.5	7.1	97.0	7.4	85.7	6.3	97.5	10.2	
L3T	85.6	9.1	95.6	7.0	84.7	7.0	94.5	7.6	84.0	10.7	95.5	10.0	
R3T	87.3	6.5	97.5	6.7	85.1	6.7	96.2	7.3	85.8	6.3	97.8	7.5	
L4T	70.2	6.3	77.9	10.2	67.6	6.3	76.5	9.0	68.3	5.9	77.7	10.5	
R4T	70.9	8.2	80.2	10.0	69.8	6.4	78.1	11.5	70.1	7.3	79.7	11.8	
L2M	36.2	9.9	40.3	9.3	28.8	9.0	37.6	9.7	33.5	10.7	40.8	9.8	
R2M	36.3	10.1	40.4	9.0	29.2	8.6	37.2	9.8	33.8	10.1	40.1	10.2	
L3M	39.7	10.2	44.4	9.5	33.8	10.5	40.2	11.4	36.7	10.9	43.0	12.0	
R3M	39.9	10.2	44.8	10.3	33.3	10.8	40.0	11.0	37.4	10.9	43.4	12.2	
L4M	29.5	8.4	34.5	9.1	26.3	8.7	32.0	8.8	27.2	9.0	33.4	10.0	
R4M	29.9	9.1	35.1	8.7	26.3	9.2	32.6	9.7	28.5	9.5	34.7	9.9	

L = left hand, R = right hand, 2 = second, 3 = third, 4 = fourth metacarpal bone, L = bone length, T = total diaphysis width, M = medullary canal width

 $\begin{array}{c} \textbf{TABLE 2} \\ \textbf{MOTHER-SON, MOTHER-DAUGHTER, FATHER-SON AND FATHER-DAUGHTER} \\ \textbf{INTERCLASS CORRELATION COEFFICIENTS (r) OF EXAMINED MORHOMETRIC DIMENSIONS} \\ \textbf{OF METACARPAL BONES} \end{array}$

	Mother-son $(n = 129)$		Mother-daughter $(n = 83)$		Father-son $(n = 73)$		Father-daughter $(n = 53)$	
	\mathbf{r}	p	\mathbf{r}	p	\mathbf{r}	p	r	p
L2L	0.339	***	0.449	***	0.235	*	0.472	***
R2L	0.354	***	0.388	***	0.354	**	0.480	***
L3L	0.425	***	0.398	***	0.332	**	0.365	**
R3L	0.399	***	0.312	非米	0.390	***	0.421	**
L4L	0.371	***	0.431	***	0.371	**	0.390	**
R4L	0.371	***	0.392	***	0.437	***	0.403	非非
L2T	0.279	**	0.383	***	0.137		0.436	**
R2T	0.263	**	0.538	***	0.176		0.275	*
L3T	0.368	**	0.397	***	0.445	***	0.249	*
R3T	0.321	***	0.456	***	0.524	***	0.163	
L4T	0.282	**	0.381	***	0.408	***	0.344	**
R4T	0.214	*	0.230	*	0.344	**	0.213	
L2M	0.230	**	0.202	*	0.474	***	(d) 0.327	**
R2M	0.267	**	0.296	**	0.278	**	0.285	*
L3M	0.277	**	0.210	*	0.313	**	0.374	**
R3M	0.257	**	0.235	*	0.373	**	0.470	***
L4M	0.242	**	0.279	妆妆	0.434	***	0.471	***
R4M	0.365	***	0.201	*	0.373	**	0.440	***

^{***} $p \le 0.001$; ** $p \le 0.01$; * $p \le 0.05$

est value of 0.235 for L2L in Father-son pair to the highest value of 0.480 for R2L in Father-daughter pair. Higher significance found in mother-offspring pairs is probably the reflection of sample size differences among the pairs, since the correlation values of metacarpal length dimensions (L) tended to be higher in pairs of parents and daughters than in pairs of parents and sons.

Parent-offspring correlations for total diaphysis width (T) showed a wider range of values than it was found in metacarpal length dimensions (L) owing to high discrepancy among correlation values in Father-son pair. Namely, Father-son pair have the two exceptionally low values (for L2T, R2T) as well as very high values for

the fourth and especially the third total diaphysis width (R3T, L3T, L4T). Therefore the correlation values in parent-offspring pairs have the following range: from 0.137 for L2T in Father-son pair to 0.538 for R2T in Mother-daughter pair. Mother-daughter pair show in T dimension the largest significance (five out of six of them on p < 0.001 level), whereas father-offspring pairs both have two nonsignificant correlation values. Despite the fact that two lowest correlation values (for L2T and R2T) among T dimensions are reached by Father-son pair, in general, the correlation values for T dimensions tended to be greater in samesex parentoffspring pairs (Mother-daughter and Father-son) than in opposite sex pairs.

TABLE 3 SIBLING-SIBLING INTRACLASS, PARENT-OFFSPRING AND FATHER-MOTHER INTERCLASS CORRELATION COEFFICIENTS (r) AND ESTIMATES OF GENETIC (h^2) AND CULTURAL (e^2) COMPONENT OF THE TOTAL PHENOTYPIC VARIATION OF EXAMINED MORHOMETRIC DIMENSIONS OF METACARPAL BONES

Variables	s	ibling-s $(n = 2)$		Parent-o		Father-i		${\tt h}^2$	c 2
	\mathbf{r}	F	df	r	p	r	p		
L2L	0.376	2.34	(496, 223)	0.227	***	-0.110		51~%	13~%
R2L	0.404	2.51	(494, 222)	0.250	***	-0.078		54~%	14 %
L3L	0.413	2.57	(496, 223)	0.231	***	-0.148		54~%	16 %
R3L	0.403	2.50	(496, 223)	0.243	***	-0.157		58 %	12~%
L4L	0.411	2.55	(496, 223)	0.241	***	-0.189	*	59%	13%
R4L	0.366	2.28	(493, 222)	0.259	***	-0.198	*	65 %	5 %
L2T	0.271	1.83	(496, 223)	0.144	**	0.088		26 %	14 %
R2T	0.319	2.04	(496, 223)	0.137	**	0.080		25~%	19 %
L3T	0.402	2.50	(492, 221)	0.215	***	-0.095		48 %	17%
R3T	0.398	2.47	(498, 224)	0.201	***	0.006		40 %	20 %
L4T	0.396	2.46	(494, 222)	0.212	***	-0.018		43 %	18 %
R4T	0.368	2.28	(493, 223)	0.122	*	- 0.188	*	30 %	23 %
L2M	0.411	2.55	(496, 223)	0.286	***	0.064		54 %	14 %
R2M	0.350	2.20	(496, 223)	0.245	***	-0.132		56 %	8 %
L3M	0.404	2.51	(496, 223)	0.270	***	-0.014		55 %	13 %
R3M	0.409	2.54	(494, 222)	0.293	***	0.036		57 %	12~%
L4M	0.402	2.49	(494, 223)	0.307	***	-0.112		69 %	6 %
R4M	0.373	2.32	(497, 224)	0.319	***	-0.103		71%	2%

^{***} $p \le 0.001$; ** $p \le 0.01$; * $p \le 0.05$

For medullary canal width (M) dimensions the correlations ranged from 0.201 for R4M in Mother-daughter pair to 0.474 for L2M in Father-son pair. The pattern of family correlations for medullary canal width dimensions is characterized by lower correlation values in pairs of mothers and offspring.

Table 3 presents Sibling-sibling, Parent-offspring and Father-mother correlation coefficients (r) for 18 examined metacarpal bone dimensions as well as the h² and c² coefficients values which (as it is presented in Methods) are closely related to those correlations. Sibling-sibling intraclass correlation coefficients showed

consistently high and very narrow range of correlation values across the examined traits ranging from 0.271 (L2T) to 0.413 (for L3L). The correlation values for L (bone length) and M (medullary canal width) dimensions showed to be slightly higher than those obtained for T (total diaphysis width) dimensions, but virtually, all correlation values were very much at the same level. F-test showed that between-family variance is significantly (p < 0.005) higher than withinfamily variance for all examined metacarpal traits.

All Parent-offspring interclass correlation values for L, T and M dimensions

F: F among groups (between families, within families)

df: degrees of freedom (total number of participants, number of families)

revealed high significance (p < 0.001 and p < 0.01) with the exception of the one (for R4T) value which was significant at p < 0.05 level. Correlation values in Parent-offspring pair for M and L dimensions were both substantially higher than for T dimensions. Since heritability estimates are calculated from Parent-offspring correlation values, the relationship among 18 metacarpal dimensions is the same as for h^2 values, and that relations are visualized in Figure 2. Father-mother pair showed only three significant (at p < 0.05 level) correlation values (for L4L, R4L and R4T) and all of them were negative.

The magnitude of the difference between inter-generational and intra-generational correlation values is presented by coefficient c2 which ranged from 2% to 23% for metacarpal bones dimensions showing generally lower values than it is obtained for the genetic component (h2). The lowest c2 values were obtained for M and L dimensions ranging from 2% to 14% in M dimensions and from 5% to 16% in L dimensions, and values obtained in T dimensions (ranging from 14% to 23%) were at a higher level of values. Since from the total of 6 metacarpal bones in M dimensions 3 bones showed c2 values lower than 10% in comparison with only one bone (R4L) at the same level for L dimensions, one can conclude that medullary canal width (M) dimensions have the lowest environmental component among three types of metacarpal traits. Also M and L dimensions showed the lowest environmental component for R4 bone which is the bone that showed the highest c^2 value for T dimension. In contrast to M and L dimensions which did not show any recognizable pattern of difference between particular bones, T dimensions showed an astonishing regularity of differences in c^2 value (R4T > R3T > R2T > L4T > L3T > L2T) where all the metacarpal bones of the right hand (R) showed higher value than all bones of the left hand (L) and on

both hands the 4th metacarpal bones showed higher values than 3rd while the 2nd bones showed the lowest c² values.

Figure 2 presents a decreasing order of heritability coefficients (h²) for 18 examined metacarpal bone dimensions estimated from doubled values of Parent-offspring correlation coefficients. With the purpose of presenting the effects of age and sex adjustment, Figure 2 comparatively shows the results obtained from the original, age adjusted and age and sex adjusted data. According to all three estimates the total diaphysis width (T) dimensions of all six metacarpal bones showed a lower heritability level than all bone length (L) and medullary canal width (M) dimensions. Age adjustment of data affects primarily the medullary canal width (M) dimensions and increases heritability values of M dimensions (in comparison to the L dimensions), whereas age and sex adjustment slightly increased the values for bone length (L) and total diaphysis width (T) dimensions.

According to original data the highest heritability (h2) is found for R4L dimension (69%) whereas age and age and sex adjustment of data revealed the highest heritability estimates for medullary canal width dimensions of the fourth metacarpal bones: for R4M and L4M (79%) (age adjusted data) and for R4M (71%) and L4M (69%) (age and sex adjusted data). According to all three estimates, the lowest heritability is found for R2T dimension (25%). One could also see that irrespective of age and sex adjustment of data for the T dimensions, the heritability order among different bones remained the same. In the bone length (L) and medullary canal width (M) dimensions the highest heritability is estimated for the fourth metacarpals of both hands, whereas the highest heritability in diaphysis width dimensions (T) showed to be for the third metacarpal bones. For all three types of metacarpal traits the low-

h ² (%)	Oı	iginal d	ata	Age	e adjuste	d data	Age and sex adjusted data			
	L	Т	М	L	Т	M	L	Т	M	
78, 79						R4M,L4M				
76, 77										
74, 75										
72, 73									200	
70, 71				R4L					R4M	
68, 69	R4L								L4M	
66, 67										
64, 65	L4L		R4M	L4L			R4L			
62, 63	R3L			R3L		R2M				
60, 61	L3L		L4M	L3L						
58, 59						L3M,R3M	L4L,R3L		D011 D011	
56, 57	\			R2L		L2M			R3M,R2M	
54, 55			R3M	L2L			L3L,R2L		L3M,L2M	
52, 53	L2L		R2M							
50, 51							L2L			
48, 49								L3T		
46, 47	1		L2M				1			
44, 45		L3T	L3M		L3T			W 489		
42, 43		L4T			L4T			L4T		
40, 41								R3T		
38, 39		R3T			R3T					
36, 37	l									
34, 35										
32, 33					_			D. (D.		
30, 31					R4T			R4T		
28, 29		R4T						T 0.000		
26, 27		L2T			L2T		1	L2T		
24, 25		R2T			R2T			R2T		

Fig. 2. Decreasing order of heritability estimates of examined morhometric dimensions of metacarpal bones. Comparation of estimations using original, age adjusted and age and sex adjusted data. h2 = 2 r Parent-offspring / (1 + r Father-mother); n = 338.

est heritability is estimated for the second metacarpal bones.

Discussion

Presented results show that the examined metacarpal bone dimensions – the bone length (L), total diaphysis width (T) and medullary canal width (M) – have different patterns of family correlations. According to the Parent-offspring correlation coefficients values, estimated heritability (age and sex adjusted data) of all examined metacarpal bone length (51% to 65%) and medullary canal width dimen-

sions (54% to 71%) proved to be higher than the heritability of total diaphysis width dimensions (25% to 48%).

Since estimated heritability is the proportion of total variance attributable to genetic effects $^{7.8}$, high heritability estimates for M dimensions (54% to 71%) obtained in present study make us assume that the influences of genetic factors in medullary canal width formation are at least as high as they are for metacarpal bone length dimensions ($h^2 = 51\% - 65\%$). Where high heritability estimates are expected since they are found in many

other longitudinal body dimensious^{29,30}. Since in traits influenced by environment, the familial resemblance is not necessarily entirely due to the genetic transmission of a trait, there is a possibility that heritability of M dimensions is not as high as the estimates obtained in the given population showed to be (as indicated by low heritability for cortex thickness in the work of Kimura³¹). High heritability estimates for M dimensions as well as high correlation values found in all family pairs (with exception of Mother-daughter pair) than should be the result of the influence of common family environment. According to the results of the present study, it seems that it is not the case. Since during growth and development period, in contrast to the environment of parents and their offspring, siblings share the similar family environment, it is assumed that the differences between inter-generational (Parent-offspring) and intra-generational (Siblingsibling) similarity level can be attributed to common environmental factors. The results of the present study showed that estimated c2 values, which show the proportion of influence of the common sibship family environment, is higher for L dimensions than for M dimensions.

It is interesting that L and M metacarpal dimensions beside the similar level of estimated heritability also showed some similarities with respect to the heritability pattern of the particular metacarpal bones. The highest heritability was estimated for the fourth and the lowest for the second metacarpal bones and higher estimates are obtained for the right than for the left respective bones. The highest heritability values of the fourth metacarpal bones in both the metacarpal length and medullary canal width dimensions could be explained by lower biomechanical pressures acting on the fourth metacarpal bone owing to it's anatomical position. The lower heritability values obtained for

left respective bones in both L and M dimensions are quite an unexpected result of the present study.

We also found quite intriguing the fact that Mother-daughter pair weakly correlated in highly heritable M dimensions. Interpretation difficulties arise from the assumption that female phenotypic values are good representatives of the genetic structure as it proved to be in many other biometric features 17-20,32-42. Since the medullary canal width is greatly affected by osteoporotic changes which are more pronounced in females than they are in males^{6,9,23,43–46}, one could assume that the contrast between resemblance of pure female and other parent-offspring family pairs can be the result of nonlinearity of age dependent changes in medullary canal width dimensions associated with the osteoporotic process (timing of bone mineral turnover). Namely family correlations will artificially show lower values in case when relation is not linear (and when variability of the trait in the investigated sample is low). If the sample age structure is not causing significant bias and if the obtained relations are realistic, one should assume that low correlations of female pair in those highly heritable traits is the product of the highly age-dependent osteoporotic process which diminishes the resemblance of female family pair.

Low heritability of T dimensions obtained in the present study was in accordance with the findings of Kimura³¹ for R2T dimension, where higher correlation values of dizigotic than of monozigotic twin boys produced an even negative heritability value. Those results provide further evidence of the high ecolability of T dimensions indicated by other authors^{5,6,9,23,47,48}. Observations on left-right asymmetry of metacarpal bone dimensions previously reported by other authors^{5,9,48} suggest that physical activity (physical stress) is the most important

environmental modifying force which through the process of short-term adaptation influence the metacarpal bones phenotype. On the other hand, Song⁴⁹ did not find the participation in sports activities to be a significant determinant of metacarpal bone dimensions in adolescent girls, which does not prove that it is not the case during the adulthood. If physical activity is the major determinant of diaphysis width dimensions of metacarpal bones, a tendency of higher family resemblance of diaphysis width dimensions in Mother-daughter and Father-son pairs (with exception for the second metacarpal bones) than in other family pairs suggests that occupational stress is common among samesex family members. We have to point out that a higher resemblance of the samesex than of the opposite sex family pairs can partially be due to the sexual dimorphism which proved to be greater in width than in length dimensions of hand bones⁵⁰. Results based on the factor analytic approach indicated different loadings of the first »cumulative environmental / genetic« factor in males (with T, M and age) and in females (only with M and age) suggesting a higher ecolability of the metacarpal diaphysis width in males than in females⁶. Since the examined population is exposed through daily activity to hard physical work5, we assume that the common environmental influence could be addressed primarily to the similar – sex specific – work exposure. According to the presented results, the total diaphysis width dimensions (T with h² below 50%) are more influenced by environmental factors than the bone length (L) and the medullary canal width (M) dimensions (with h² estimated between 50%-75%). Although in many ways the bone length (L), and the medullary canal width (M) dimensions show a similar patern of family resemblance, it is highly improbable that these two types of bone traits are determined by the same sets

of polygenes, as stated earlier. Namely, the bone length formation takes place during the growth and development period, in contrast to the medullary canal width dimensions which are directly influenced by the dynamic process of bone formation and resorption which occurs during the entire course of life and which in advanced age can lead to functional impairment of skeletal system. Since the balance of the bone remodeling process depends on the interactions of numerous extrinsic (environmental) and intrinsic factors (including neuro-hormonal status, i.e. »inner-environment«) which are also determined by the environment-gene interactions and the genetically determined »capacity of an organism to adapt«51, one could expect lower heritability estimates for the medullary canal width dimensions, but, according to our presumptions the results of the present study are in favor of the efforts directed at the discovery of one or several genetic determinants which have a major effect on the homeostatic mechanisms important for bone remodeling.

Conclusion

Since the heritability of medullary canal width dimensions (M) as a measure of the osteoporotic process provokes a special interest, it was important to examine which range of estimates reflects the heredity of M, that is, whether the determinants are predominantly genetic or whether a substantial proportion is related to the environment. The obtained heritability estimates for M dimensions which showed to be almost the same as the heritability estimates (50% to 70%) reported for bone density of various skeletal sites^{13,52,53}, allow us to conclude that genetic determination of medullary canal width of metacarpal bones is not still in question and that the task of providing evidence indicating the existence of a major locus governing trait variation is worth-while.

Acknowledgements

The authors wishes to thank the participants in the study from Brač, Hvar and Pelješac whose willing cooperation made the study possible; the anthropological field staff for data gathering; to Dr.sc. Veljko Jovanović and Dr.sc. Lajos

Szirovicza for their help concerning the statistical procedures for this study. Special thanks go to Dr.sc. Nina Smolej-Narančić for her valuable comments. The authors would like to thank Ms. Francine C. Berkowitz, Director of the International Relations of Smithsonian Institutions, and Prof. Linda A. Bennett, the Project Co-Principal Investigator, for their continuous friendship and support.

REFERENCES

1. RUDAN, P., J. L. ANGEL, L. A. BENNETT, B. FINKA, B. JANIĆIJEVIĆ, V. JOVANOVIĆ, M. F. LETHBRIDGE, J. MILIČIĆ, M. MIŠIGÓJ, N. SMOLEJ-NARANČIĆ, A. SUJOLDŽIĆ, L. SZIRO-VICZA, D. ŠIMIĆ, P. ŠIMUNOVIĆ: Anthropological research of the Eastern Adriatic, I. Biological and cultural microdifferentiation of rural populations of the island of Korčula and Pelješac peninsula. (In Croat.) (HAD, Zagreb, 1987). — 2. RUDAN, P., B. FINKA, B. JANIĆIJEVIĆ, V. JOVANOVIĆ, V. KUŠEC, J. MILIČIĆ, M. MIŠIGOJ-DURAKOVIĆ, D. F. RO-BERTS, LJ. SCHMUTZER, N. SMOLEJ-NARAN-ČIĆ, A. SUJOLDŽIĆ, L. SZIROVICZA, D. ŠIMIĆ, P. ŠIMUNOVIĆ, S. M. ŠPOLJAR-VRŽINA: Anthropological research of the Eastern Adriatic, II. Biological and cultural microdifferentiation of rural populations of the island of Hvar. (In Croat.) (HAD, Zagreb, 1990). - 3. RUDAN, P., L. A. BENNETT, B. FINKA, B. JANIĆIJEVIĆ, V. JOVANOVIĆ, V. KUŠEC, M. LETHBRIDGÉ-ČEJKU, J. MILIČIĆ, LJ. SCHMUT-ZER, N. SMOLEJ-NARANČIĆ, A. SUJOLDŽIĆ, D. ŠIMIĆ, P. ŠIMUNOVIĆ, S. M. ŠPOLJAR-VRŽINA: Anthropological research of the Eastern Adriatic, III. Biological and cultural microdifferentiation of rural populations of the island of Brač. (In Croat.) (HAD, Zagreb, 1990). — 4. KUŠEC, V., D. ŠIMIĆ, A. CHA-VENTRÉ, J. D. TOBIN, C. C. PLATO, P. RUDAN, Coll. Antropol., 13 (1989) 163. — 5. KUŠEC, V., D. ŠIMIĆ, A. CHAVENTRÉ, J. D. TOBIN, C. C. PLATO, S. TUREK, P. RUDAN, 1990, Coll. Antropol., 14 (1990) 273. — 6. ŠIMIĆ, D., A. CHAVENTRÉ, C. C. PLATO, J. D. TOBIN, P. RUDAN, Ann. Physiol. Anthrop., 11 (1992) 3. — 7. FISHER, R. A., Trans. Roy. Soc. Edinb., 52 (1918) 399. — 8. FALCONER, D. S.: Introduction to quantitative genetics. (Oliver and Boyd, Edinburgh, 1960). — 9. PLATO, C. C., A. H. NORIS, Hum. Biol., 52 (1980) 131. — 10. EVANS, R. A., G. M. MAREL, E. K. LANCASTER, S. KOS, M. EVANS, S. Y. P. WONG, Ann. Intern. Med., 109 (1988) 870. — 11. SEEMAN, E., J. L. HOPPER, L. A. BACH, M. E. COOPER, E. PARKINSON, J. McKAY, G. JERUMS, New Engl. J. Med., 320 (1989) 554. — 12. KELLY, P. J., T. NGUYEN, J. HOPPER, N. POCOCK,

P. SAMBROOK, J. EISMAN, J. Bone Miner. Res., 8 (1993) 11. — 13. KRALL, E. A., B. DAWSON-HUGHES, J. Bone Miner. Res., 8 (1993) 1. - 14. MATKOVIĆ, V., K. KOSTIAL, I. ŠIMONOVIĆ, R. BUZINA, A. BRODAREC, B. E. C. NORDIN, Am. J. Clin. Nutr., 32 (1979) 540. — 15. BEHLULI, I., M. LETHBRIDGE-ČEJKU, C. C. PLATO, P. RUDAN, W. A. STINI, J. D. TOBIN, Med. Jad., 21 (1991) 55. 16. RUDAN, P., Coll. Antropol., 4 (1980) 35. — 17. SMOLEJ, N., Ann. Hum. Biol., 11 (1984) 469. -RUDAN, P., D. ŠIMIĆ, N. SMOLEJ-NARANČIĆ, L. A. BENNETT, B. JANIĆIJEVIĆ, V. JOVANOVIĆ, M. LETHBRIDGE, J. MILIČIĆ, D. F. ROBERTS, A. SU-JOLDŽIĆ, L. SZIROVICZA, Am. J. Phys. Anthropol., 74 (1987) 417. — 19. SMOLEJ-NARANČIĆ, N., Coll. Antropol., 12 (1988) 377. — 20. SMOLEJ-NARAN-ČIĆ, N., P. RUDAN, L. A. BENNETT, Anthropometry and the biological structure of the population (example from the island of Brač). In: CHAVENTRÉ, A., D. F. ROBERTS (Eds.): Pluridisciplinary approach of human isolates. (In French) (INED, Paris, 1990). — 21. BARNETT, L., B. E. C. NORDIN, Clin. Radiol., 11 (1960) 166. — 22. BEHRENTS, R. G., E. F. HARRIS, Ann. Hum. Biol., 14 (1987) 277. — 23. PLATO, C. C., Coll. Antropol., 11 (1987) 59. — 24. KIMURA, K., Ann. Hum. Biol., 17 (1990) 399. — 25. PLATO, C. C., J. D. TOBIN, Coll. Antropol., 14 (1990) 57. - 26. SOKAL, R. R., F. J. ROHLF: Biometry. (W. H. Freeman & Co., San Francisco, 1981). — 27. DONNER, A., M. ELI-ASZIW, J. Clin. Epidemiol., 44 (1991) 449. — 28. RAO. D. C., R. WETTE, W. J. EWENS, Am. J. Hum. Genet., 42 (1988) 506. — 29. SUSANE, C., Ann. Hum. Biol., 2 (1975) 279. — 30. COMUZZIE, A. G., M. H. CRAW-FORD, Hum. Biol., 62 (1990) 101. — 31. KIMURA, K., Am. J. Phys. Anthropol., 60 (1983) 491. — 32. LIVSON, N., D. McNEILL, K. THOMAS, Science, 98 (1962) 818. — 33. TANNER, J. M., W. J. ISRAEL. SOHN, Ann. Hum. Genet., 26 (1963) 245. — 34. WELON, Z., T. BIELICKI, Hum. Biol., 43 (1971) 517. - 35. MALINA, R. M., W. H. MUELLER, J. D. HOL-MAN, Hum. Biol., 48 (1976) 475. — 36. ROBERTS, D. F., Methods and problems in physiological genetics. In: WEINER, J. S. (Ed.): Physiological variation and

its genetic basis. (Taylor & Francis, London, 1977). -37. ROBERTS, D. F., W. Z. BILLEWICZ, I. Z. McGRE-GOR, Ann. Hum. Genet., 42 (1978) 15. — 38. NANCE, W. E., A note on assoratative mating and maternal effects. In: SING, C. F., M. SKOLNIC (Eds.): Genetic analysis of common diseases: Applications to predictive factors in coronary disease. (Alan R. Liss, New York, 1979). - 39. RUDAN, P., J. L. ANGEL, L. A. BENNETT, B. JANIĆIJEVIĆ, M. F. LETHBRIDGE, J. MILIČIĆ, N. SMOLEJ-NARANČIĆ, A. SU-JOLDŽIĆ, D. ŠIMIĆ, Acta Morphol. Neerl. Scand., 25 (1986) 69. - 40. SMOLEJ, N., J. L. ANGEL, L. A. BENNETT, D. F. ROBERTS, P. RUDAN, Hum. Biol., 59 (1987) 667. — 41. BOLDSEN, J. L., C. G. N. MAS-CIE-TAYLOR, Hum. Biol., 62 (1990) 767. — 42. TIRET, L., P. DUCIMETIERE, J. L. ANDRE, R. GUEGUEN, B. HERBETH, Y. SPYCKERELLE, R. RAKOTOVAO, F. CAMBIEN, Ann. Hum. Biol., 18 (1991) 259. — 43. GARN, S. M., C. G. ROHMANN, P. NOLAN, The developmental nature of bone changes during ages. In: BIRREN, J. E. (Ed.): Relations of development and aging. (Thomas, Springfield, 1964). — 44. GARN, S. M., Bone loss and aging. In: GOLD-MAN, R., M. ROCKSTEIN (Eds.): The physiology and pathology of aging. (Academic Press Inc., New York, 1975). - 45. NORDIN, B. E. C., J. ARON, R. SPEED, R. G. CRILLY, Lancet, 2 (1981) 277. — 46. CANTO, M., C. PRADO, Int. J. Anthropol., 8 (1993) 205. — 47. PLATO, C. C., W. W. GREULICH, R. M. GARRUTO, R. YANAGIHARA, Am. J. Phys. Anthropol., 63 (1984) 57. — 48. ROY, T. A., C. B. RUFF, C. C. PLATO, Am. J. Phys. Anthropol., 94 (1994) 203. — 49. SONG, J. K., A. L. CLAESSENS, G. P. BEUNEN, J. LEFEVRE, Am. J. Hum. Biol., 6 (1994) 585. - 50. SMITH, S. L., Int. J. Anthropol., 8 (1993) 259. — 51. PROSSER. C. L., Perspectives of adaption: Theroetical aspects. In: DILL et al. (Ed.): Handbook of Physiology, Sect. 4, »Adaption to the Environment«. (Amer. Phys. Soc., Washington, DC, 1964). — 52. LUTZ, J., R. TESAR, Am. J. Clin. Nutr., 52 (1990) 872. - 53. SOWERS, M.R., M. BOEHNKE, M. L. JANNAUSCH, M. CRUTCHFIELD, G. CORTON, T. L. BRUNS, Calcif. Tissue Int., 50 (1992) 110.

T. Škarić-Jurić

Institute for Anthropological Research, Ulica grada Vukovara 72/IV, 10000 Zagreb, Croatia

OBITELJSKE KORELACIJE KOD METAKARPALNIH KOSTIJU – NASLJEDNA I OKOLIŠNA KOMPONENTA UKUPNE VARIJABILNOSTI FENOTIPA

SAŽETAK

Analiza obiteljskih podataka provedena je za 18 morfometrijskih dimenzija metakarpalnih kostiju (duljina kosti – L, ukupna širina dijafize – T i širina medularnog kanala – M druge, treće i četvrte metakarpalne kosti u obje ruke) na slučajno odabranom uzorku od 956 ispitanika odrasle dobi (dob 18–85 g.), stanovnika otaka Brača i Hvara te poluotoka Pelješca, Hrvatska. Izračunati su interklas (za parove roditelja i djece) te intraklas (za braću i sestre) koeficijenti korelacije, te izvršena procjena genetske komponente (h²) te komponente utjecaja zajedničkog obiteljskog okoliša (c²). Procijenjena nasljednost (h²) za širinu medularnog kanala (M) pokazala je barem jednako visoke (h² = 54% do 71%), odnosno c² komponenta je pokazala barem jednako niske vrijednosti (c² = 2% do 14%) kao što su one dobivene za duljinu metakarpalne kosti (h² = 51% do 65%; c² = 5% do 16%), što sugerira snažan utjecaj genetskih čimbenika na formiranje širine međularnog kanala. I za duljinu kosti i za širinu međularnog kanala najviša procijenjena nasljedna komponenta te najniža vrijednost komponente učinka zajedničkog obiteljskog okoliša nađena je za dimenzije četvrte metakarpalne kosti, što se može protumačiti anatomskom pozicijom četvrte kosti koja je manje izložena bio-

mehaničkim silama. Analiza obiteljske sličnosti za širinu medularnog kanala također je pokazala tendenciju najmanje sličnosti (osobito izraženu kod četvrte metakarpalne kosti) kod čistog ženskog obiteljskog para (Majka-kći). Pretpostavljamo da su niže vrijednosti nasljednosti para Majka-kći rezultat nelinearnosti o dobi ovisnih promjena širine medularnog kanala koje su vezane uz, kod žena izraženiji, proces osteoporoze. Za ukupnu širinu dijafize dobivene su jasno niže vrijednosti procijenjene nasljednosti (h 2 = 25% do 48%), te više vrijednosti komponente utjecaja obiteljskog okoliša (c 2 = 14% do 23%). One, a uz nalaz viših korelacija dobivenih za obiteljske parove istog spola (Otac-sin, Majka-kći) govore u prilog velike važnosti čimbenika zajedničkog obiteljskog okoliša, posebice onih vezanih uz tjelesnu aktivnost koja je karakteristična za pojedini spol, a koja putem procesa kratkoročne adaptacije modelira fenotip ukupne širine dijafize.