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The occurrence of directional and fluctuating limb asymmetry in a recently identified collection of human bones

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Abstract. This study is based on the metric processing of, in particular, the long bones of the upper and lower limbs of a rare, identified collection of bones originating in the first half of the 20th century (143 males and 157 females). It concentrates on the study of fluctuating asymmetry (FA), antisymmetry, directional (DA) and cross asymmetry in the length parameters of the upper and lower limbs. The presence of antisymmetry has not been recorded in this assemblage. For the lower limbs, FA was found to occur more frequently than DA. The size of the FA reached negligible values given the size of the indicators (method after Palmer & Strobeck, 1986). Limb DA occurred more often, and with greater absolute differences, among women than among men; in all of the assessed bones it was more common in the upper limbs than the lower, in the majority of cases in favour of the right side. The most pronounced DA appeared in the humerus, with all dimensions showing significant differences between sides. The lengths of the forearm bones were also highly asymmetrical, while DA was apparent least often in the scapula. The clavicle is shorter and more robust on the right side. In the lower limbs significant differences were only noted in the femur, while DA was not found in the crural bones. Femur DA occurred in most cases favouring the left side, and only in some epiphyseal dimensions the right side was greater. More pronounced DA in the lower limbs was manifest in the diaphyseal and epiphyseal dimensions than in length parameters. The presence of cross asymmetry was not universally confirmed, this occurring only among men (with longer right or left humerus), in the lengths of the fibula and tibia.

■ fluctuating asymmetry, directional asymmetry, cross asymmetry, antisymmetry, identified modern collection of bones, sexual dimorphism

INTRODUCTION

Asymmetry, a fundamental characteristic of all living organisms, is defined as a deviation from the overall symmetry of the organism and its different parts in relation to the median plane of the body (Škvařilová 1999). It thus appears in skeletal human remains, and has been studied for many reasons; this study concentrates on asymmetry in the size and shape of long bones in the post-cranial human skeleton, and on the differentiation of their individual types. Asymmetry is one of the major markers of stress, developmental stability and unequal functional loads on the two sides of the body. Several studies have demonstrated that a certain degree of asymmetry is in fact the norm in the length of the humerus and femur (e.g. Helmkampf & Falk 1990), while the genetic basis of asymmetry, its ontogenesis and the influences of age, sex and external environment have also been studied.

At the present time three basic types of asymmetry are distinguished for the variability of bilateral markers: directional asymmetry, fluctuating asymmetry and antisymmetry, arising out of different causes (Van Valen 1962, Palmer & Strobeck 1986, Palmer 1994; see Fig. 1).

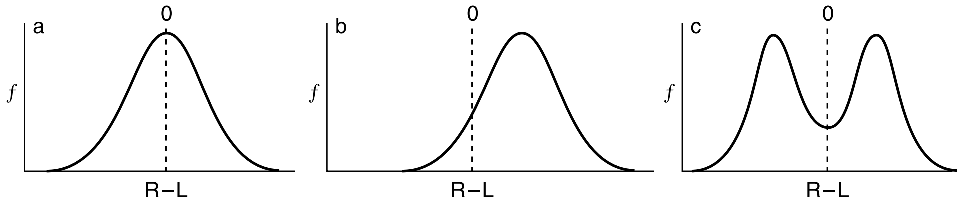

Fig. 1. Distribution of right-left difference in bilateral organisms: (a) FA, (b) DA, (c) antisymmetry (Palmer 1994).

Directional asymmetry (DA) displays itself in the preponderance of a given marker on the right or left side in the sample. This is a bilateral asymmetry, where the average deviation of the marker from the right and left sides in the studied collection is always greater or less than zero. A distribution of differences of the right and left sides is normal. The most conspicuous example in the human skeleton is to be found in the longer and more robust right upper and left lower limb, in connection with the functional laterality of the limbs (Schell et al. 1985, Škvařilová 1999, Čuk et al. 2001). Some authors hold that it is possible that DA is found very early in ontogenesis (Schultz 1937, Pande & Singh 1971) and that it develops further (in childhood – Van Dusen 1939; in adolescence – Schell et al. 1985, and in adulthood – Laubach & McConville 1967, Malina & Buschang 1984), for example in association with biomechanical factors acting differently on the two sides of the body. The most significant cause of asymmetrical development of the upper limbs in particular is regarded as being handedness (i.e. the preference for one – the right or left – upper limb; right- and left-handedness respectively). This is the influence of a high mechanical load placed during life asymmetrically on one side of the body (Ruff & Jones 1981, Schell et al. 1985, Roy et al. 1994, Steele & Mays 1995, Škvařilová 1999, Čuk et al. 2001). The causes of the occurrence of DA may also, however, have a genetic basis (Schultz 1937, Stirland 1993). Environmental stress is an important factor (Albert & Greene 1999), while ontogenetic factors linked to age and sex (Helmkampf & Falk 1990, Stirland 1993) evidently have an influence, too. Among children a dependency of DA upon age has been identified, but not upon sex (Škvařilová 1999). Many works have found no difference in the development of asymmetry between the sexes (Steele & Mays 1995, Plochocki 2002), while others indicate greater asymmetry rather among women (Schultz 1937), but sometimes among men (adolescents – Schell et al. 1985).

Fluctuating asymmetry (FA) is the type of bilateral asymmetry, which occurs when the deviations of the right and left sides in a sample are normally distributed around a mean of zero (Palmer 1994). It is probably caused by instability during ontogenesis (developmental noise), which developmental stability (the ability of the organism to create ideal/symmetrical forms under a particular set of environmental conditions; Zakharov & Graham 1992) and canalization (the ability of the organism to develop along an ideal developmental trajectory under diverse environmental conditions; Palmer 1994 attempt to counteract or buffer. FA has thus been taken as a measure of the developmental stability, health and fitness of the organisms and the environmental stresses acting upon them (Palmer & Strobeck 1986, Zakharov & Graham 1992, Albert & Greene 1999). Environmental stress (temperature extremes, a polluted environment, parasitism, nourishment, population density etc.) increases FA (Zakharov & Graham 1992, Palmer 1994). FA has no genetic basis, but several genetic factors may of course increase it (inbreeding, lower heterozygosity, mutation etc.; Livshits & Kobyliansky 1989, 1991).

Antisymmetry has a platykurtic or bimodal distribution of left-right difference around a mean of zero; in other words, one side always predominates (in terms of significant differences), but which it is – whether right or left – is variable (Van Valen 1962).

A further aim of this project was to establish the presence of cross asymmetry; this is a relationship between the asymmetry of the upper and lower limbs, where for example an individual with a longer and more robust right humerus also has longer and more robust bones in the lower left limb, or vice versa. Moreover, according to some authors right-handed individuals have a more developed right upper limb and left-handers a more developed left upper limb (Ingelmark 1946, Siniarska & Sarna 1980, Ruff & Jones 1981, Steele & Mays 1995). According to some studies the size dominance of the upper right limb is associated with handedness (Steele & Mays 1995), while the lower left limb is larger regardless of the hand preference (Macho 1991). The authors therefore divide the lower limbs into supportive leg and dominant leg, which demonstrated cross asymmetry of tibia with humerus. The supportive leg is in most cases the left, the left femur having a stronger diaphysis; in contrast, the right femur has a greater epicondylar width, showing that greater loads are placed on the non-supportive leg at the knee (Singh 1970, Plato et al. 1985, Macho 1991, Čuk et al. 2001).

Research into bone asymmetry first appeared in the professional literature as early as during the 19th century. The first study of bone asymmetry was probably that by the anatomist Philipp Friedrich Arnold in 1844 (Škvařilová 1999), which revealed the dominance of the right humerus and forearm bones and the left femur in length. In general, a greater absolute symmetry in the lengths of different segments of the upper and lower extremity was reported than asymmetry in the total length of the extremity (Jurowska 1972). Thus far all studies have demonstrated the fact that the most conspicuous bilateral bone asymmetry appears in the bones of the upper limb, while that of the lower limb is less obvious. The reason for this is probably the very asymmetric loads on the upper limbs associated with handedness, while the lower limbs are used more or less evenly e.g. in walking (Schell et al. 1985, Čuk et al. 2001). Some authors believe that the degree of asymmetry reflects the size of the load placed on the given limb, while localisation of the asymmetry indicates the type of effort exerted (Čuk et al. 2001).

DA is more frequent than FA in the upper limbs (Škvařilová 1999). In the upper limb DA is expressed, according to most studies, in the longer and more robust bones of the right side, and mainly in connection with asymmetric loads on the upper limbs (e.g. Stirland 1993, 1998, Steele & Mays 1995, Čuk et al. 2001). Only the clavicle is, particularly among adult individuals, shorter and more robust on the right side, probably thanks to massive development of the muscles at this location at the expense of its growth (Mays et al. 1999). The most asymmetric bone is the humerus (e.g. Čuk et al. 2001). Some studies indicate that the proximal epiphysis of the humerus is more asymmetric that the distal, while in the bones of the forearm the situation is reversed. It seems clear to the author that the wrist and shoulder are more asymmetrically stressed than the elbow (Čuk et al. 2001). It would seem that among right-handed individuals DA favours the right upper limb, while among left-handers it favours the left limb (Ingelmark 1946, Steele & Mays 1995, Čuk et al. 2001). In modern European society around 80–82 % of the population are right-handed, while 15 % are left-handed and 3–5 % exhibit no preference (Annett & Kilshaw 1983). The same figures come out of several studies of skeletal material where handedness is unknown (Schultz 1937, Steele & Mays 1995, Čuk et al. 2001), where the individuals concerned are divided according to the length of the humerus into probable right- and left-handed. Although it is only in the present that there have been relaxed cultural pressures against left-handedness and the percentage of left-handers in society is gradually increasing (Fleminger et al. 1977, Steele & Mays 1995), in the skeletal material the representation is relatively stable. It is likely that asymmetry in bone development is a reflection of the loads arising out of repetitive or power tasks, rather than fine manipulation such as writing; for this reason skeletal DA may be more resistant to cultural pressures for handedness switching (Steele & Mays 1995).

Studies of asymmetry in the lower limbs generally show a heavier and more robust left lower limb, regardless of the handedness (Latimer & Lowrance 1965, Singh 1970, Macho 1991). In studying the asymmetry of the femur, the authors in most instances come to the conclusion that the left femur has the usual stronger diaphysis (particularly among women) and is heavier than the right, but that DA is not apparent in the length of the bone (Ruff & Hayes 1983, Macho 1991, Ruff 1992). This may be connected with the fact that the length growth of the bone concludes between the 18^{th} and 25^{th} year, while width growth undergo biomechanical influences throughout life (Čuk et al. 2001). Furthermore, several studies speak of "more rounded" diaphyses of the right femur (Macho 1991). According to these results the femur should be regarded as an expression of the left lower limb as the supportive and load-bearing leg, again regardless of the handedness (Macho 1991, Čuk et al. 2001). The right lower limb is used for more specific tasks (e.g. kicking), and the load is applied in particular to the knee; DA thus appears in several epiphyseal dimensions to favour the right side (Čuk et al. 2001). In contrast, in the study by Čuk et al. (2001) the tibia exhibits cross asymmetry with humerus, i.e. a longer right humerus/longer left tibia and vice versa. The leg with a more supportive function (characterised by a more developed femur) is thus in most cases the left, while the dominant leg (expressed by a more developed tibia) is, depending on handedness, for right-handers generally the left and vice versa.

MATERIALS AND METHODS

Bones were studied in the modern osteological assemblage so-called Pachner collection dated to the 1930s. It originated under the direction of Professor Pachner for the purposes of studying sexual indicators in the human pelvis at the Institute of Anatomy of the First Medical Faculty of Charles University in Prague, Czechoslovakia. Originally the postcranial skeletons of 100 females and 115 males were studied post mortem; later the collection was expanded to 305, now regrettably incomplete, skeletons of adult individuals. The advantage of working with this collection is the excellent degree of preservation of the majority of the bones, and the identifications of the skeletons (sex, height, age, name, year of autopsy, in some cases cause of death etc.). The only skeletons not included in the analysis were those with pathological deformations and those for which sex was not recorded. This meant that for this study of asymmetry the skeletal remains of a total of 157 women and 143 men were measured. The assemblage cannot be considered to be a sample for a normal, modern population, as these are all adult individuals of the lower social orders (Pachner 1937). At the present time the greater part of the collection is stored in the osteological depository of the Department of Anthropology and Human Genetics of the Faculty of Natural Sciences at Charles University in Prague, Czech Republic, with the rest in the collections of the Institute of Anatomy of the First Medical Faculty at Charles University in Prague.

The metric characteristics of the bones were selected such that they most precisely described their sizes and shapes with regard to robusticity and degree of preservation. The precisely defined dimensions were taken following Martin & Saller (1957–1962) and Velemínský (2000). All of the surviving limb bones in the collection were metrically processed. From the upper limb, the clavicle, scapula, humerus, radius and ulna were studied; from the lower limb the femur, tibia and fibula. A total of 27 linear and circumferential metric characteristics were measured for the lower limb and 21 for the upper (for the dimensions see Tabs 1, 3). The assemblage of adult skeletal remains was not divided into exact age categories. Given the size of the assemblage and the conspicuous sexual dimorphism, all data were processed separately for men and women.

Basic statistical indicators were calculated for all of the data obtained. The reliability of the measurements was verified by the repeated measurement of 16 individuals (Steele & Mays 1995, Mays et al. 1999), with consideration given to inter-individual error (reliability coefficient) and to systematic error (paired t-test). Testing using ANOVA revealed that the FA was not conditioned by measurement error (Little et al. 2002, Roy et al. 1994). A t-test for independent samples was employed to compare size differences between men and women. The normal distribution of right-left differences and the consequent ruling out of the presence of antisymmetry (bimodal or platykurtic curve) were verified graphically. Given the size of the data set it is not possible to publish all of these calculations here, but along with others they are included in the theses by Fialová (2004) and Žaloudková (2004).

A paired t-test was used for the actual establishing of directional asymmetry. The null hypothesis of the coincidence of the population right and left side average was tested to a 5 % significance level, and significant differences were regarded as being directional asymmetry. Other deviations from symmetry were adjudged to be fluctuating asymmetry, after the approach of Škvařilová (1999).

Only for those dimensions where the presence of DA and antisymmetry had been ruled out was the size of the FA established with the aid of models from Palmer & Strobeck (1986); the presence of DA or antisymmetry could have impaired the calculation of FA (Palmer & Strobeck 1986). The FA1 and FA2 models, which yield information on absolute asymmetry, were employed, as were FA4 and FA6, which are suitable for establishing the signed asymmetry. At the same time, FA2 and FA6 are not biased by size-dependence of the right-left difference.

FA1: mean $|R–L|$

FA2: mean $\{|R–L| / [(R+L) /2]\}$

FA4: var $(R–L)$

FA6: var $\{(R–L) / [(R+L) /2]\}$

The presence of cross asymmetry (where a given individual would have both longer right upper and left lower limb, or vice versa) was tested on the basis of the maximum lengths of the humerus, femur, tibia and fibula. The individuals were divided on the basis of humerus length into those with a longer right/left humerus (hypothetically right-and left-handers respectively; Steele & Mays 1995, Čuk et al. 2001). Within these "groups" the proportion of individuals with longer right/left lower limb bones was then assessed.

The data obtained were processed using Statistica Base 6 and Microsoft Excel 2003 software.

RESULTS

Measurement reliability was tested through the use of the reliability coefficient, ANOVA and systematic error testing, and showed the high degree of reliability of the repeated measurements. Reliability koeficient has never decreased below the value 0.8, thus all measurements were meaningful. The ANOVA revealed no differences between the first and second measurements of the right and left sides; the variability between the indicators is therefore not caused by measurement error. Asymmetry was established separately for both sexes, as in all of the indicators studied men were highly significantly larger than women (Fialová 2004, Žaloudková 2004).

Study of asymmetry

The graphic depiction (Fig. 2) of the right-left differences in individual dimensions confirms the normal distribution of said differences. The presence of asymmetry was thus ruled out in all cases, as no distribution was platykurtic or bimodal.

DA appears far more often in the upper limb than in the lower. In the upper limb DA generally trends towards the right (with the exception of clavicle length), and in the lower to the left (with the exception of some epiphyseal dimensions).

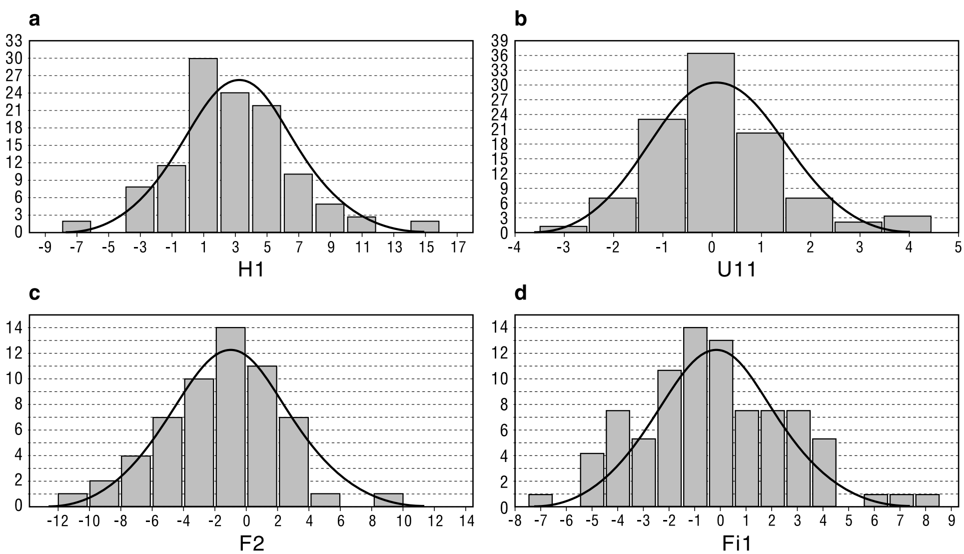

Fig. 2. Examples of the graphic depiction of the distribution of right-left differences.
a – H1 (maximum lenght of the humerus) – DA trends towards the right; males (N = 117)
b – U11 (sagittal diameter of the diaphysis of the ulna) – FA; males (N = 103)
c – F2 (physiological length of the femur) – DA trends towards the left; females (N = 58)
d – Fi1 (maximum length of the fibula) – FA; females (N = 81)

Table 1. DA: Results of paired t-tests of the dimensions of the upper limbs of males (diameters given in mm; SD – standard deviation, N – number of dimensions, t – value of the t-test (df = N-1), p – test level attained; significance levels: * = 0.05, ** = 0.01, * = 0.001).**

				Mean	SD	N	t	p		
SCAPULA	anatomical width	Sc1	sin	161.9	9.10					
			dx	161.3	8.55	80	1.334	0.186		
	anatomical length	Sc2	sin	104.6	6.29					
			dx	104.0	5.83	112	3.104	0.002	**	sin
	length of the margo lateralis	Sc3	sin	138.3	8.06					
			dx	138.0	8.53	112	1.000	0.319		
CLAVICULA	maximum clavicle length	Cl1	sin	150.8	7.97					
			dx	149.2	7.82	97	3.334	0.001	**	sin
	vertical diameter	Cl4	sin	11.1	1.29					
			dx	11.3	1.47	112	-1.815	0.072		
	sagittal diameter	Cl5	sin	12.6	1.44					
			dx	13.0	1.36	112	-3.040	0.003	**	dx
HUMERUS	maximum length of the humerus	H1	sin	322.4	17.30					
			dx	325.7	16.71	117	-9.933	0.000	***	dx
	width of the upper epiphysis	H3	sin	50.5	2.33					
			dx	51.4	2.34	118	-8.274	0.000	***	dx
	width of the lower epiphysis	H4	sin	61.7	3.77					
			dx	62.2	3.86	118	-3.544	0.001	***	dx
	maximum diameter of the middle of the diaphysis	H5	sin	23.2	1.93					
			dx	23.8	2.05	120	-5.344	0.000	***	dx
	minimum diameter of the middle of the diaphysis	H6	sin	18.6	1.67					
			dx	18.9	1.69	120	-4.698	0.000	***	dx
	maximum transverse diameter of the head	H9	sin	44.3	2.05					
			dx	44.7	2.26	112	-3.145	0.002	**	dx
	maximum vertical diameter of the head	H10	sin	48.0	2.37					
			dx	48.5	2.22	118	-4.148	0.000	***	dx
ULNA	maximum length of the ulna	U1	sin	255.4	13.18					
			dx	257.5	13.08	100	-6.387	0.000	***	dx
	sagittal diameter of the diaphysis	U11	sin	14.3	1.27					
			dx	14.4	1.39	103	-0.904	0.368		
	width of the diaphysis	U12	sin	17.5	1.39					
			dx	17.7	1.49	103	-1.618	0.109		
RADIUS	maximum length of the radius	R1	sin	237.0	11.92					
			dx	239.7	12.04	96	-8.445	0.000	***	dx
	maximum width of the diaphysis	R4	sin	17.8	1.57					
			dx	18.2	1.74	97	-3.523	0.001	***	dx
	sagittal diameter of the diaphysis	R5	sin	12.4	1.12					
			dx	12.5	1.11	97	-1.026	0.308		
	width of the middle of the diaphysis	R4a	sin	16.7	1.57					
			dx	17.3	1.63	98	-4.570	0.000	***	dx
	sagittal diameter of the middle of the diaphysis	R5a	sin	12.7	1.07					
			dx	12.8	1.00	98	-1.440	0.153		

In the upper limb (Tabs. 1, 2) DA is present in all of the studied bones, among a total of 74 % of the metric indicators studied. DA appeared most conspicuously, and in all dimensions, on the humerus, and is also obvious in the maximum lengths of the forearm bones; it was found least often in the scapula. Men mostly have a greater length of the left scapula, and in women a longer length of the margo lateralis of the right scapula is present. The majority of the individuals have a shorter and more robust right clavicle, the sagittal diameter of the clavicle is on average greater on the right side. The humerus is

Table 2. DA: Results of paired t-tests of the dimensions of the upper limbs of females (for legend see Tab. 1).

				Mean	SD	N	t	p		
SCAPULA	anatomical width	Sc1	sin	144.3	9.00					
			dx	144.4	8.92	78	-0.076	0.939		
	anatomical length	Sc2	sin	96.6	5.50					
			dx	96.7	5.56	112	-0.343	0.733		
	length of the margo lateralis	Sc3	sin	125.2	8.86					
			dx	126.3	8.81	106	-4.003	0.000	***	dx
CLAVICULA	maximum clavicle length	Cl1	sin	136.1	7.11					
			dx	134.4	7.14	75	4.548	0.000	***	sin
	vertical diameter	Cl4	sin	9.1	1.29					
			dx	9.2	1.22	108	-0.465	0.643		
	sagittal diameter	Cl5	sin	10.9	1.16					
			dx	11.4	1.28	108	-4.696	0.000	***	dx
HUMERUS	maximum length of the humerus	H1	sin	297.7	15.19					
			dx	301.2	15.24	125	-10.003	0.000	***	dx
	width of the upper epiphysis	H3	sin	44.8	2.47					
			dx	45.5	2.59	125	-7.016	0.000	***	dx
	width of the lower epiphysis	H4	sin	54.0	3.19					
			dx	54.8	3.33	126	-5.608	0.000	***	dx
	maximum diameter of the middle of the diaph.	H5	sin	20.6	1.65					
			dx	21.2	1.64	127	-6.655	0.000	***	dx
	minimum diameter of the middle of the diaph.	H6	sin	16.2	1.36					
			dx	16.4	1.50	127	-3.675	0.000	***	dx
	maximum transverse diameter of the head	H9	sin	39.0	1.97					
			dx	39.5	2.19	112	-4.578	0.000	***	dx
	maximum vertical diameter of the head	H10	sin	42.1	2.24					
			dx	42.5	2.54	119	-3.214	0.002	**	dx
ULNA	maximum length of the ulna	U1	sin	230.8	11.56					
			dx	234.0	12.18	118	-10.806	0.000	***	dx
	sagittal diameter of the diaphysis	U11	sin	11.9	1.09					
			dx	12.2	1.07	126	-4.024	0.000	***	dx
	width of the diaphysis	U12	sin	15.0	1.24					
			dx	15.3	1.25	126	-4.887	0.000	***	dx
RADIUS	maximum length of the radius	R1	sin	212.8	11.67					
			dx	216.3	12.17	123	-9.617	0.000	***	dx
	maximum width of the diaphysis	R4	sin	15.6	1.61					
			dx	15.9	1.53	128	-4.078	0.000	***	dx
	sagittal diameter of the diaphysis	R5	sin	10.6	0.81					
			dx	10.6	0.80	128	-0.961	0.338		
	width of the middle of the diaphysis	R4a	sin	14.7	1.44					
			dx	15.1	1.43	128	-6.121	0.000	***	dx
	sagittal diameter of the middle of the diaphysis	R5a	sin	10.6	0.77					
			dx	10.7	0.79	128	-2.350	0.020	*	dx

markedly asymmetrical in all dimensions in both men and women, in every case in favour of the right side. The greatest differences occur in the average values of maximum length in the humerus; men have a right humerus longer by an average of 3.3 mm, and women 3.5 mm. In the male forearm bones DA appears primarily in the lengths as well as in the width of the diaphysis of the radius. Among women DA appears in almost all dimensions of the forearm bones (the average differences in bone length being 3.5 mm). In all cases the right side is dominant in the bones of the forearm. While the differences between the sexes are not overly pronounced, greater differences were nevertheless observed in the average dimension values among women.

Table 3. DA: Results of paired t-test of the dimensions of the lower limbs of males (for legend see Tab. 1).

				Mean	SD	N	t	p		
FEMUR	maximum length of the femur	F1	sin	451.8	23.47					
			dx	450.9	22.83	66	1.457	0.150		
	physiological length	F2	sin	449.7	23.20					
			dx	448.0	22.62	66	2.761	0.007	**	sin
	sagittal diameter of the middle of the diaphysis	F6a	sin	28.5	2.43					
			dx	28.7	2.49	67	-1.130	0.262		
	transverse diameter of the middle of the diaphysis	F7a	sin	28.6	2.42					
			dx	28.5	2.33	67	0.639	0.525		
	upper transverse diameter of the diaphysis	F7b	sin	30.8	2.67					
			dx	30.6	2.69	67	1.390	0.169		
	upper sagittal diameter of the diaphysis	F7c	sin	28.7	2.21					
			dx	28.0	2.26	67	5.457	0.000	***	sin
	lower transverse diameter of the diaphysis	F7d	sin	35.9	3.96					
			dx	35.7	4.10	67	0.878	0.383		
	lower sagittal diameter of the diaphysis	F7e	sin	31.7	3.06					
			dx	31.1	2.94	67	4.243	0.000	***	sin
	subtrochanteric transverse diameter of the diaph.	F9	sin	33.7	2.62					
			dx	33.7	2.60	67	-0.168	0.867		
	subtrochanteric sagittal diameter of the diaphysis	F10	sin	28.9	2.19					
			dx	28.5	2.24	67	2.690	0.009	**	sin
	circumference of the middle of the diaphysis	F8	sin	87.3	5.68					
			dx	87.2	5.67	67	0.521	0.604		
	upper widht of the epiphysis	F13	sin	101.8	6.25					
			dx	102.0	5.92	66	-0.327	0.745		
	epicondylar width	F21	sin	82.1	4.52					
			dx	82.8	4.54	67	-3.339	0.001	**	dx
	vertical diameter of the head	F18	sin	48.6	2.59					
			dx	48.8	2.68	66	-0.976	0.333		
	transverse diameter of the head	F19	sin	48.3	2.45					
			dx	48.4	2.67	66	-0.757	0.452		
FIBULA	maximum length of the fibula	Fi1	sin	359.2	24.55					
			dx	359.3	23.77	93	-0.170	0.865		
TIBIA	overal length tibie	T1	sin	367.2	21.43					
			dx	367.7	20.76	47	-0.622	0.537		
	medial length	T1b	sin	356.8	20.32					
			dx	357.5	20.48	46	-0.811	0.422		
	maximum width of the upper epiphysis	T3	sin	74.6	2.92					
			dx	74.2	2.99	46	2.008	0.051		
	width of the lower epiphysis	T6	sin	48.5	3.02					
			dx	48.1	2.88	47	1.449	0.154		
	minimum diameter of the middle of the diaphysis	T8	sin	29.4	2.73					
			dx	29.5	2.32	53	-0.855	0.396		
	width of the middle of the diaphysis	T9	sin	22.7	1.95					
			dx	22.6	2.09	53	0.484	0.630		
	sagittal diameter in the upper foramen nutricium	T8a	sin	33.8	3.28					
			dx	33.7	2.98	51	0.409	0.684		
	width of the diaphysis in the upper for. nutric.	T9a	sin	25.0	2.12					
			dx	25.1	2.40	51	-0.461	0.647		
	circumference of the middle of the diaphysis	T10	sin	80.4	5.87					
			dx	79.8	5.61	53	1.965	0.055		
	circumference of the diaphysis on the for. nutric.	T10a	sin	91.2	7.34					
			dx	91.0	6.81	51	0.446	0.657		
	minimum circumference of the diaphysis	T10b	sin	71.8	5.10					
			dx	71.7	4.91	53	0.778	0.440		

Table 4. DA: Results of paired t-tests of the dimensions of the lower limbs of females (for legend see Tab. 1).

				Mean	SD	N	t	p		
FEMUR	maximum length of the femur	F1	sin	415.0	19.17					
			dx	414.6	19.59	58	0.681	0.499		
	physiological length	F2	sin	411.6	19.33					
			dx	410.5	19.81	58	2.106	0.040	*	sin
	sagittal diameter of the middle of the diaphysis	F6a	sin	25.9	2.00					
			dx	25.9	2.19	64	-0.244	0.808		
	transverse diameter of the middle of the diaphysis	F7a	sin	26.8	2.50					
			dx	26.5	2.23	64	2.116	0.038	*	sin
	upper transverse diameter of the diaphysis	F7b	sin	29.3	2.55					
			dx	28.6	2.76	64	3.550	0.001	***	sin
	upper sagittal diameter of the diaphysis	F7c	sin	25.7	2.29					
			dx	25.2	2.06	64	2.657	0.010	**	sin
	lower transverse diameter of the diaphysis	F7d	sin	33.0	3.71					
			dx	33.0	3.76	64	0.000	1.000		
	lower sagittal diameter of the diaphysis	F7e	sin	28.7	2.23					
			dx	28.0	2.42	64	3.832	0.000	***	sin
	subtrochanteric transverse diameter of the diaph.	F9	sin	31.5	2.30					
			dx	31.2	2.52	63	1.474	0.146		
	subtrochanteric sagittal diameter of the diaphysis	F10	sin	25.9	1.90					
			dx	25.9	2.16	63	0.000	1.000		
	circumference of the middle of the diaphysis	F8	sin	80.2	5.91					
			dx	79.6	5.60	65	2.100	0.040	*	sin
	upper width of the epiphysis	F13	sin	88.1	5.62					
			dx	88.6	5.85	59	-2.151	0.036	*	dx
	epicondylar width	F21	sin	73.8	3.93					
			dx	73.9	3.75	59	-0.769	0.445		
	vertical diameter of the head	F18	sin	43.1	2.80					
			dx	43.1	2.87	58	-0.136	0.892		
	transverse diameter of the head	F19	sin	42.5	2.18					
			dx	42.7	2.27	58	-1.763	0.083		
FIBULA	maximum length of the fibula	Fi1	sin	328.6	16.43					
			dx	328.3	16.60	81	0.762	0.449		
TIBIA	overal length tibie	T1	sin	338.5	17.50					
			dx	337.9	17.24	63	1.257	0.214		
	medial length	T1b	sin	329.4	17.65					
			dx	328.9	17.42	59	1.137	0.260		
	maximum width of the upper epiphysis	T3	sin	66.7	3.40					
			dx	66.6	3.70	55	0.457	0.649		
	width of the lower epiphysis	T6	sin	44.0	2.64					
			dx	44.1	2.71	54	-0.339	0.736		
	minimum diameter of the middle of the diaphysis	T8	sin	26.6	2.40					
			dx	26.7	2.54	69	-0.173	0.863		
	width of the middle of the diaphysis	T9	sin	20.6	1.88					
			dx	20.8	2.33	69	-1.396	0.167		
	sagittal diameter in the upper foramen nutricium	T8a	sin	29.9	2.56					
			dx	29.9	2.52	69	0.346	0.730		
	width of the diaphysis in the upper for. nutric.	T9a	sin	22.2	1.98					
			dx	22.3	2.30	69	-0.956	0.343		
	circumference of the middle of the diaphysis	T10	sin	72.1	4.91					
			dx	72.1	6.01	70	-0.082	0.935		
	circumference of the diaphysis on the for. nutric.	T10a	sin	80.8	5.42					
			dx	80.9	6.06	70	-0.271	0.788		
	minimum circumference of the diaphysis	T10b	sin	65.5	4.45					
			dx	65.6	4.85	71	-0.518	0.606		

Table 5. Results of evaluation of the FA of the dimensions of the upper limbs (FA1, FA2, FA4, FA6: indices of the calculation of FA values, see section on 'Materials and methods'; DA – dimension for which DA presence was found).

			male				female			
			FA1	FA2	FA4	FA6	FA1	FA2	FA4	FA6
SCAPULA	anatomical width	Sc1	2.925	0.018	13.423	0.001	2.981	0.015	19.230	0.001
	anatomical length	Sc2	DA	DA	DA	DA	1.723	0.018	6.110	0.001
	length of the margo lateralis	Sc3	2.304	0.017	8.917	0.000	DA	DA	DA	DA
CLAVICULA	maximum clavicle length	Cl1	DA	DA	DA	DA	DA	DA	DA	DA
	vertical diameter	Cl4	0.821	0.073	1.301	0.010	0.713	0.078	1.063	0.013
	sagittal diameter	Cl5	DA	DA	DA	DA	DA	DA	DA	DA
HUMERUS	maximum length of the humerus	H1	DA	DA	DA	DA	DA	DA	DA	DA
	width of the upper epiphysis	H3	DA	DA	DA	DA	DA	DA	DA	DA
	width of the lower epiphysis	H4	DA	DA	DA	DA	DA	DA	DA	DA
	maximum diameter of the middle of the diaphysis	H5	DA	DA	DA	DA	DA	DA	DA	DA
	minimum diameter of the middle of the diaphysis	H6	DA	DA	DA	DA	DA	DA	DA	DA
	maximum transverse diameter of the head	H9	DA	DA	DA	DA	DA	DA	DA	DA
	maximum vertical diameter of the head	H10	DA	DA	DA	DA	DA	DA	DA	DA
ULNA	maximum length of the ulna	U1	DA	DA	DA	DA	DA	DA	DA	DA
	sagittal diameter of the diaphysis	U11	0.913	0.063	1.695	0.008	DA	DA	DA	DA
	width of the diaphysis	U12	0.602	0.034	0.719	0.002	DA	DA	DA	DA
RADIUS	maximum length of the radius	R1	DA	DA	DA	DA	DA	DA	DA	DA
	maximum width of the diaphysis	R4	DA	DA	DA	DA	DA	DA	DA	DA
	sagittal diameter of the diaphysis	R5	0.608	0.049	0.785	0.005	0.383	0.035	0.411	0.004
	width of the middle of the diaphysis	R4a	DA	DA	DA	DA	DA	DA	DA	DA
	sagittal diameter of the middle of the diaphysis	R5a	0.541	0.042	0.589	0.004	DA	DA	DA	DA

In the lower limb (Tabs. 3, 4) DA was recorded only in the size characteristics of the femur, specifically in 47 % of the studied dimensions among women and 33 % among men. The women in this assemblage from a modern population are thus more asymmetrical than the men. DA could not be demonstrated in the fibula or tibia. In both sexes femur DA was observed in the dimensions of length and of the diaphysis in favour of the left side, and in the dimensions of the epiphysis in favour of the right side. Significant differences in sides (trending to the left) were recorded in men only in the physiological length and in all sagittal diameters of the femur shape; among women they were also found in the transveral diameters of the shape and circumference of the diaphysis. DA towards the right was recorded in men in the epicondylar width, and in women in the upper width of the epiphysis.

The size of FA (Tabs. 5, 6) was evaluated only for those dimensions where the presence of DA had already been ruled out. FA occurred more often in the lower limb than in the upper. The variance or absolute deviation of the FA, which is sensitive to size-dependence of the right-left difference (FA1, FA4), reached its greatest values in the dimensions

Table 6. Results of evaluation of the FA of the dimensions of the lower limbs (FA1, FA2, FA4, FA6: indices of the calculation of FA values, see section on 'Materials and methods'; DA – dimension for which DA presence was found).

			male				female			
			FA1	FA2	FA4	FA6	FA1	FA2	FA4	FA6
FEMUR	maximum length of the femur	F1	3.500	0.008	22.845	0.000	3.517	0.008	21.070	0.000
	physiological length	F2	DA	DA	DA	DA	DA	DA	DA	DA
	sagittal diameter of the middle of the diaphysis	F6a	0.985	0.034	2.255	0.003	0.813	0.031	1.030	0.002
	transverse diameter of the middle of the diaphysis	F7a	0.970	0.034	1.765	0.002	DA	DA	DA	DA
	upper transverse diameter of the diaphysis	F7b	1.147	0.038	14.008	0.003	DA	DA	DA	DA
	upper sagittal diameter of the diaphysis	F7c	DA	DA	DA	DA	DA	DA	DA	DA
	lower transverse diameter of the diaphysis	F7d	1.164	0.033	2.744	0.002	1.877	0.075	17.110	0.065
	lower sagittal diameter of the diaphysis	F7e	DA	DA	DA	DA	DA	DA	DA	DA
	subtrochanteric transverse diameter of the diaph.	F9	1.045	0.031	2.104	0.002	1.250	0.041	2.331	0.002
	subtrochanteric sagittal diameter of the diaphysis	F10	DA	DA	DA	DA	0.889	0.034	1.333	0.002
	circumference of the middle of the diaphysis	F8	1.567	0.018	4.385	0.001	DA	DA	DA	DA
	upper widht of the epiphysis	F13	2.364	0.023	8.955	0.001	DA	DA	DA	DA
	epicondylar width	F21	DA	DA	DA	DA	0.912	0.012	2.893	0.000
	vertical diameter of the head	F18	0.864	0.018	1.269	0.001	0.614	0.014	0.930	0.000
	transverse diameter of the head	F19	0.864	0.018	1.277	0.001	0.397	0.009	0.441	0.000
FIBULA	maximum length of the fibula	Fi1	2.559	0.007	13.243	0.000	2.296	0.007	8.408	0.000
TIBIA	overal length tibie	T1	3.574	0.010	30.973	0.000	2.794	0.008	12.816	0.000
	medial length	T1b	3.957	0.011	37.410	0.000	2.966	0.009	13.420	0.000
	maximum width of the upper epiphysis	T3	1.217	0.016	2.554	0.000	1.364	0.020	4.184	0.001
	width of the lower epiphysis	T6	1.167	0.024	2.608	0.001	0.796	0.018	1.423	0.001
	minimum diameter of the middle of the diaphysis	T8	1.132	0.040	2.530	0.003	0.928	0.035	1.912	0.003
	width of the middle of the diaphysis	T9	1.000	0.044	1.972	0.004	0.765	0.035	1.458	0.003
	sagittal diameter in the upper foramen nutricium	T8a	1.235	0.037	2.873	0.003	0.957	0.032	1.910	0.002
	width of the diaphysis in the upper for. nutric.	T9a	0.863	0.034	1.445	0.002	0.629	0.028	1.001	0.002
	circumference of the middle of the diaphysis	T10	1.358	0.017	3.759	0.001	1.543	0.020	8.342	0.001
	circumference of the diaphysis on the for.nutric.	T10a	2.157	0.024	9.648	0.001	1.300	0.016	4.809	0.001
	minimum circumference of the diaphysis	T10b	1.170	0.016	3.059	0.001	1.099	0.016	3.311	0.001

of length. FA based on the size of the indicators (FA2, FA6) attains generally negligible or null values.

In order to establish whether cross asymmetry was present the individuals were divid-

Table 7. Absolute and relative frequencies of potentially right-handed (R) and left-handed (L) men and women, and of individuals showing no preference in the upper limbs (A).

	N	%			N	%
male R	95	81.2		female R	102	81.6
male L	14	12.0		female L	17	13.6
male A	8	6.8		female A	6	4.8
Total	117	100.0		Total	125	100.0

Table 8. Cross asymmetry evaluation. Absolute and relative frequencies of potentially right-handed (male R, female R) and left-handed (male L, female L) individual with longer bones of the right (R) or left (L) lower limbs, or with both bones the same length (A). N – number of individuals; F1 – maximum length of the femur; F2 – physiological length of the femur; T1 – overall length of the tibia; T1b – medial length of the tibia; Fi1 – maximum length of the fibula.

	male R		male L		female R		female L	
	N	%	N	%	N	%	N	%
F1 R	22	47.8	4	66.7	16	38.1	1	14.3
F1 L	18	39.1	1	16.7	19	45.2	3	42.9
F1 A	6	13.0	1	16.7	7	16.7	3	42.9
Total	46	100.0	6	100.0	42	100.0	7	100.0
F2 R	29	60.4	5	83.3	20	48.8	4	57.1
F2 L	15	31.3	0	0.0	15	36.6	2	28.6
F2 A	4	8.3	1	16.7	6	14.6	1	14.3
Total	48	100.0	6	100.0	41	100.0	7	100.0
T1 R	12	36.4	3	75.0	20	47.6	1	12.5
T1 L	19	57.6	1	25.0	16	38.1	5	62.5
T1 A	2	3.0	0	0.0	6	14.3	2	25.0
Total	33	100.0	4	100.0	42	100.0	8	100.0
T1b R	12	37.5	3	75.0	19	46.3	1	16.7
T1b L	19	59.4	1	25.0	18	43.9	3	50.0
T1b A	1	3.1	0	0.0	4	9.8	2	33.3
Total	32	100.0	4	100.0	41	100.0	6	100.0
Fi1 R	24	36.4	7	77.8	30	49.2	4	40.0
Fi1 L	30	45.5	2	22.2	21	34.4	6	60.0
Fi1 A	12	18.2	0	0.0	10	16.4	0	0.0
Total	66	100.0	9	100.0	61	100.0	10	100.0

ed by humerus length into those with a longer right humerus, those with a longer left humerus, and those in which both bones were the same length (Steele & Mays 1995, Čuk et al. 2001; Tab. 7). Testing was done in these groups to ascertain the asymmetry appearing in the bone lengths of the lower limbs (Tab. 8). The studied groups had, as expected, a similar percentage representation in the assemblage to the distribution of right- and left-handers and those showing no preference in modern European population. There were an insufficient number of individuals to demonstrate cross asymmetry, which requires paired bones from both limbs. In general, cross asymmetry was not recorded; it was found only among men with a longer right or left humerus, in the lengths of the tibia (57–59 %) and fibula (45.5 %).

DISCUSSION

In the bones of the upper limb bilateral asymmetry is in most cases directional (DA), while by contrast in the lower limb bilateral asymmetry is usually insignificant, ascribed to FA.

It is very important, particularly when studying FA, to remove or qualify the measurement error. In this study repeated measurements were applied only to 16 individuals (Steele & Mays 1995, Mays et al. 1999), and no measurement error was found. It is therefore adjudged that the established asymmetry is indeed a product of biological variability in the skeletal material studied. Nevertheless, for the study of FA measurements must be repeated several times for a large sample, and the measurement error, even if slight, must be estimated, in order that it not negatively influences the values of the size of FA. As Palmer (1994) has, for example, recommended, for a quantitative establishment it is appropriate to use, e.g. the FA10 index for a precise correction of the measurement error. For this reason, this study cannot be used to draw general conclusions regarding FA size, and thereby to directly evaluate the developmental stability and fitness of this sample of the population.

In the lower limbs FA was more common that DA, which confirms that there was no great asymmetric stressing, and that loads in general acted equally on both sides. As is true of earlier studies (e.g. Škvařilová 1999), the results of this study too confirm that in the bones of the upper limb it is possible to identify primarily DA (there are strong asymmetric loads). No differences between the sexes were recorded in FA size.

FA reached its greatest values in the length dimensions of bones and in the dimensions of the scapula, dependent on the indicator size (FA1, FA4). After removing the influence of the size of the given indicator (FA2 and FA6), FA size was shown to be negligible (in the order of thousandths values, often null). For comparison, Škvařilová (1999), for example, found FA in the forearm length and the breadth of the lower epiphysis of the humerus in clinical material; such results were not however obtained in this study. Further comparisons with the literature were not possible, as no other FA studies using the same statistical approach could be found.

The DA study results (Fig. 3) accord with the results presented in several publications, as the DA of the upper limbs trends in a vast majority of cases to the right, while in the lower limbs it favours the left side (Škvařilová 1999, Čuk et al. 2001). Schell et al. (1985) also recorded right side asymmetry among the upper limbs of adolescents, but do not confirm DA in the lower limbs (although according to many studies asymmetry generally increases with age: Steele & Mays 1995). Similarly, the present study confirms that DA does not appear in the lower limbs as often as it does in the upper (Steele & Mays 1995, Škvařilová 1999, Čuk et al. 2001).

In this assemblage DA is very frequent in the dimensions of the upper limbs, appearing on all bones. The most asymmetrically loaded bone is the humerus (the right humerus is longer and more robust), with all its dimensions being directionally asymmetrical. Moreover, the division of individuals by humerus length really does reflect distribution of handedness in modern European population (Annett & Kilshaw 1983). This leads the authors to conclude that in the humerus in particular, but also in the bones of the forearm (where the right is longer and more robust), asymmetric load during power tasks is the main cause of DA. This is supported by the conclusions of several other studies: foetuses generally have an even longer left humerus (but generally suck the right thumb), juveniles generally have a longer right humerus and ulna, while adolescents almost always have longer right upper limb. Evidently, then, DA develops post-natally, and in children in particular increased with age and with long-term loads (Hepper et al. 1991, Steele & Mays 1995, Škvařilová 1999). It is therefore possible that the individuals in the "Pachner Collection" were heavily loaded on one (dominant) upper limb. The presumption stemming from the study of, for example, Čuk et al. (2001), that the proximal epiphysis of the humerus is more asymmetrical than the distal epiphysis, could not be confirmed. It is not, therefore, possible to state that the shoulder section is more asymmetrically mechanically loaded than the elbow.

It should not be forgotten that asymmetry can also be conditioned by such non-specific loads as unsuitable living conditions and lack of nourishment (Livshits & Kobyliansky 1987, Graham et al. 1993). It is necessary to bear such environmental stress in mind in this series, too, given the poor social standing of the individuals concerned (Pachner 1937).

It follows from earlier studies (e.g. Huggare & Houghton 1995, Mays et al. 1999), that the right clavicle is shorter and more robust in a majority of individuals; this study accords with such conclusions. This phenomenon is explained by the assumption that the growth of the clavicle of the dominant limb is suppressed thanks to greater muscular development (connected with hand preference) in this area (Mays et al. 1999).

In the lower limbs DA appears less often than FA, in almost all cases trends to the left, so that the dimension of the left side is significantly greater than that of the right side. In this collection, DA was recorded in the lower limbs in a small number of femur diaphyses, but not in the tibia or fibula. In this collection asymmetry appeared more obviously in the dimensional measurements of the bone diaphysis than in the lengths. The authors agree with Čuk et al. (2001) that this arises from the fact that the length growth of the bone finishes in adulthood, while the width increases under biomechanical influences throughout life.

In this assemblage the femur is longer on the left side. In comparing this result with those published elsewhere, conclusions as to the occurrence of asymmetry in femur length are diverse. Velemínský (2000) has recorded DA in the femur length of males favouring the right side, while Latimer & Lowrance (1965) and Singh (1970) confirm a heavier lower left limb, but found no asymmetry in the bone length; similarly, Ruff (1992) could not confirm differences in femur length. The results of the present study accord with those of Čuk et al. (2001), where DA was found to favour a longer left femur. The more massive diaphyses found in the femurs of both sexes by this study are confirmed by other studies, such as those by Ruff & Hayes (1983), Macho (1991), Čuk et al. (2001) and Velemínský (2000). The authors suppose that the reason for this is the main, supportive function of the lower left limb regardless of handedness. In terms of shape, men have the left femur with less anteroposterior flattening than the right. Similarly a more rounded diaphysis of the right femur was found by Macho (1991). The women in this modern assemblage are more asymmetrical in the lower limb than the men; it is therefore impossible to confirm the assumption that a lower degree of asymmetry will occur among women because of their certain genetic resistance to environmental stress (Schell et al. 1985, Lazenby 2002). A similar conclusion was reached by Ruff & Hayes (1983) and by Stránská et al. (2002), who found greater asymmetry in the femur shank among women. In contrast, Velemínský (2000) found asymmetry in the lower limbs to favour men more often.

The dimensions of the epiphysis are greater on the right side. This has been explained in a number of publications by the greater load placed on the knee (and hip) of the "non-supportive leg", used for special functions. Macho (1991) has also reported DA in the dimensions of the upper epiphysis in women.

In the present modern assemblage neither the tibia nor the fibula display DA. Insignificant differences are confirmed in men by a longer and more robust left tibia, similarly as in the studies of Čuk et al. (2001) and Velemínský (2000). The authors suppose that a more developed left tibia is an expression of the dominance of the left lower limb (given handedness, the reverse of the upper limbs). Women have in the insignificant differences more robust and longer the right tibia, in contrast to the men.

In terms of sexual dimorphism in the occurrence of asymmetry, studies to date have come to contradictory conclusions. Some authors have not found differences between the sexes (Steele & Mays 1995, Škvařilová 1999, Plochocki 2002), while others believe that this is a factor contributing to asymmetry (e.g. Schultz 1937). The results of this study do show a difference in asymmetry between the sexes; women appeared to be more asymmetrical (in 81 % of the upper limb dimensions and 47 % of the lower limb dimensions). Greater asymmetry among women has also been described in a study by Ruff & Hayes (1983). The authors, like Ruff (1992), found no differences between the sexes in the asymmetry of the dimensions of length.

From the results of the paired t-test it is apparent that the DA of the upper limbs always trends towards the right, while the DA of the lower limbs generally trends to the left. Such results may indicate the presence of cross asymmetry. To establish cross asymmetry the lengths of the long bones of the upper and lower limbs were compared. Generally, it has been found that right-handers have a better developed right upper limb and, with this, left lower limb (Ingelmark 1946, Siniarska & Sarna 1980, Ruff & Jones 1981), the greatest length of the humerus was therefore used to divide the sample into hypothetical right-handers (with a longer right humerus) and left-handers (with a longer left humerus), after, e.g., Steele & Mays (1995) and Čuk et al. (2001).

The studied assemblage was observed to have a similar percentage representation of individuals with a longer right (81 %) or left (12–13 %) humerus, or both the same length (5–7 %) as in the modern population according to previous studies (e.g. Annett & Kilshaw1983: 82 % right-handers, 15 % left-handers, 3 % with no preference; Steele & Mays 1995: 81 % right-handers, 16 % left-handers, 3 % with no preference).

Cross asymmetry was tested for in the tibia, as was the presumption that the femur would be longer on the left side regardless of handedness (the supportive leg; Čuk et al. 2001). In the assemblage used for the present study cross asymmetry was found only among men (both the hypothetically right-handed and left-handed), in the lengths of the tibia and fibula. A possible explanation of this might be the fact that men were more likely to come under hard physical loads than women; further interpretations within other "groups" are not possible, given the insufficiently large numbers of individuals concerned. The supportive function of the left lower limb regardless of handedness is expressed in the significant left-right differences in the femur; in the individual groups, however, this assumption could not directly be affirmed.

CONCLUSIONS

This study has considered fluctuating, directional and cross asymmetry as well as antisymmetry in the human skeleton. The investigated material comprised an identified, osteological collection dating to the 1930s. A total of 157 adult female and 143 adult male postcranial skeletons were measured, with 21 metric characteristics of the bones of the upper limbs (the humerus, radius, ulna, clavicle and scapula) and 27 metric characteristics of the bones of the lower limbs (the femur, tibia and fibula) being recorded. The results obtained may be summarised into the following points:

Antisymmetry was not found in any of the studied indicators.

The presence of DA was noted in particular in the upper limb, while in the lower limb

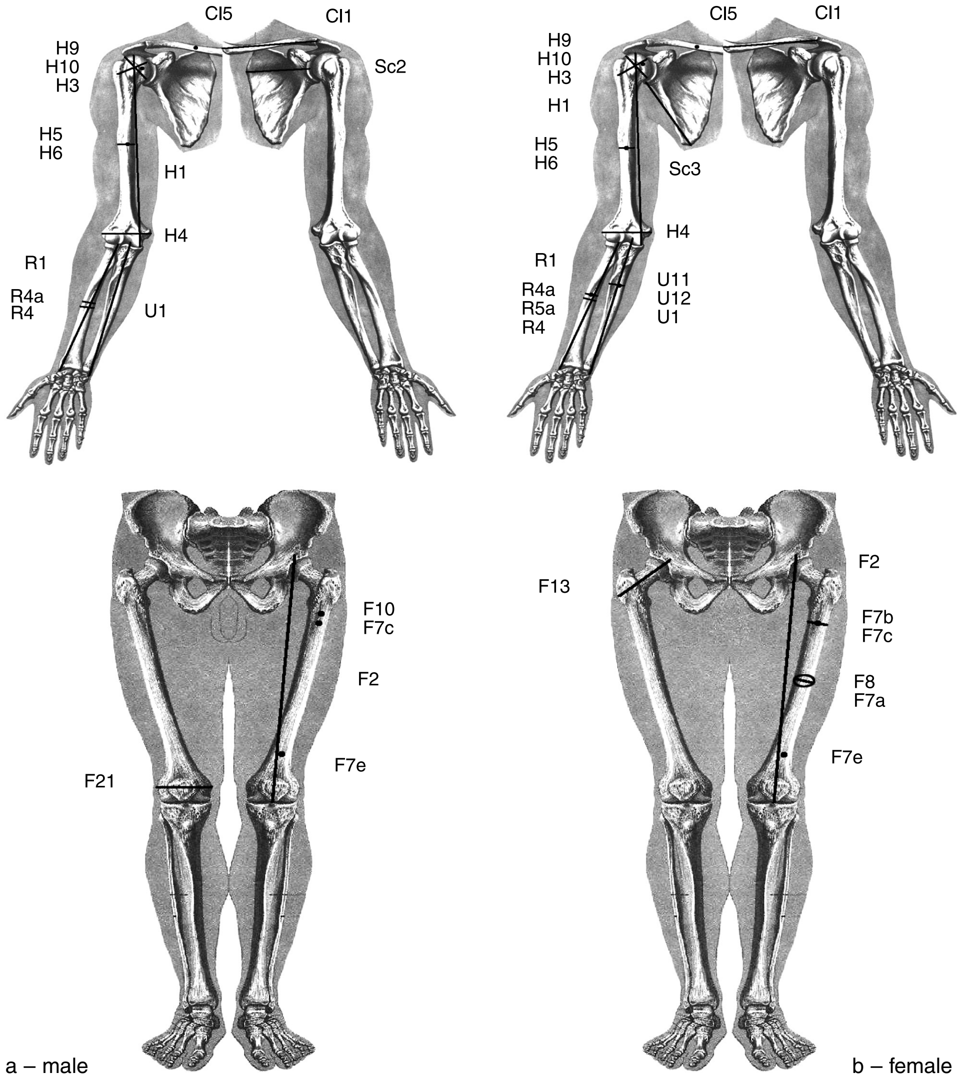

Fig. 3. Depiction of the dimensions in which directional asymmetry was observed.

FA was apparent in most of the dimensions, albeit at very low values. This may be explained by the more asymmetric use of the upper limbs as opposed to the lower, the load on which comes in particular from "symmetrical" walking.

The most asymmetric bone is the humerus, probably reflecting a hand preference. DA was recorded in all of the dimensions of the humerus, always favouring the right side. The proportion of individuals divided according to humerus length matches the division of right-handers, left-handers and those displaying no preference in the modern population. Similarly, the forearm bones also display (especially in their dimensions of length) a tendency to favour the right side expressed in DA. It is therefore likely that DA in the long bones of the upper limbs reflects the handedness of the individuals concerned. Skeletal asymmetry thus seems resistant to cultural pressures to "correct" handedness.

The clavicle is more robust on the right side, but shorter. At this point it is possible to seek out a correlation with suppressed growth of the clavicle to its length on the side on the dominant limb due to the greater development of the muscles in this area.

DA is more frequent in the upper limbs than in the lower. In the lower limbs it was found only in the femur, in most cases favouring the left side. DA appeared more often among women than among men.

Cross asymmetry in the tibia was found only among men, and probably expresses the dominance of the opposite lower limb to that of the preferred upper limb. The supportive function of the lower left limb is expressed in the strong DA of the femur, regardless of handedness.

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