

Limb bone bilateral asymmetry: variability and commonality among modern humans

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Abstract

Humans demonstrate species-wide bilateral asymmetry in long bone dimensions. Previous studies have documented greater right-biases in upper limb bone dimensions—especially in length and diaphyseal breadth—as well as more asymmetry in the upper limb when compared with the lower limb. Some studies have reported left-bias in lower limb bone dimensions, which, combined with the contralateral asymmetry in upper limbs, has been termed “crossed symmetry.” The examination of sexual dimorphism and population variation in asymmetry has been limited.

This study re-examines these topics in a large, geographically and temporally diverse sample of 780 Holocene adult humans. Fourteen bilateral measures were taken, including maximum lengths, articular and peri-articular breadths, and diaphyseal breadths of the femur, tibia, humerus, and radius. Dimensions were converted into percentage directional (%DA) and absolute (%AA) asymmetries. Results reveal that average diaphyseal breadths in both the upper and lower limbs have the greatest absolute and directional asymmetry among all populations, with lower asymmetry evident in maximum lengths or articular dimensions. Upper limb bones demonstrate a systematic right-bias in all dimensions, while lower limb elements have biases closer to zero %DA, but with slight left-bias in diaphyseal breadths and femoral length. Crossed symmetry exists within individuals between similar dimensions of the upper and lower limbs. Females have more asymmetric and right-biased upper limb maximum lengths, while males have greater humeral diaphyseal and head breadth %DAs. The lower limb demonstrates little sexual dimorphism in asymmetry. Industrial groups exhibit relatively less asymmetry than pre-industrial humans and less dimorphism in asymmetry. A mixture of influences from both genetic and behavioral factors is implicated as the source of these patterns.

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Introduction

Humans are unique among primates in the magnitude of directional bilateral asymmetry exhibited in both use and size of the upper limb, favoring the right side (Schultz, 1937; McGrew and Marchant, 1997). Some evidence for much smaller but systematic directional asymmetry favoring the left side has been reported in the human lower limb, especially in the femur (Schultz, 1937; Latimer and Lowrance, 1965; Ruff and Jones, 1981; Plochocki, 2004; see below). This trend has been termed a “crossed symmetry” pattern between contralateral limbs (Schaeffer, 1928; Plochocki, 2004).

Many studies assume a direct association between behavioral and morphological asymmetry through mechanically driven bone growth and remodeling (e.g., Steele, 2000; Lazenby, 2002). This hypothesis is strongly supported by observations of greatly increased asymmetry between the playing and non-playing arms of racquetball and tennis athletes (Jones et al., 1977; Krahl et al., 1994; Ruff et al., 1994; Kontulainen et al., 2001; Kontulainen et al., 2002; Bass et al., 2002), as well as between normal and mechanically compromised (i.e., paralyzed or otherwise mechanically restricted) limbs (Biewener and Bertram, 1993; Trinkaus et al., 1994). Left-handed individuals in the “normal” population have also been shown to have equivalent but reversed asymmetry in metacarpal dimensions compared to right-handed individuals (Roy et al., 1994). Such observations form the basis for using patterns of skeletal

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bilateral asymmetry in archaeological samples to infer asymmetry in mechanical loading due to behavior or pathology (e.g., Stirland, 1993; Churchill and Formicola, 1997; Mays, 2002).

However, while the general role of mechanical factors in producing directional bilateral asymmetry appears to be well established, it is also clear that different skeletal features exhibit variable degrees of asymmetry in response to the same mechanical environment. Specifically, several studies have found less asymmetry in lengths or articular dimensions than in diaphyseal breadths or cross-sectional dimensions of the same skeletal elements (Ruff and Jones, 1981; Trinkaus et al., 1994; Churchill and Formicola, 1997; Sakaue, 1998; but see Krahl et al., 1994). This finding appears to be consistent with experimental evidence for less environmental plasticity of bone length or epiphyseal size compared to cross-sectional diaphyseal morphology (Lanyon, 1980; Lieberman et al., 2001).

These observations, however, have been limited to particular populations and have not been tested in a large, geographically diverse sample of modern humans. In addition, possible associations between the magnitude and direction of asymmetry in different skeletal dimensions or between the upper and lower limbs have not been systematically tested. The purpose of this paper is to provide such comparisons with a large sample of modern human skeletal material in order to provide a general baseline for evaluating asymmetry in specific population samples, while addressing some of the factors (e.g., environment) influencing bilateral asymmetry of different skeletal features. We also provide some comparisons between (presumably) more physically active (pre-industrial) and less physically active (industrial) groups because there is reason to believe that more active humans should show greater asymmetry, at least in characteristics that are more strongly influenced by mechanical factors during life (Ruff, 2000). Similarly, we compare males and females. Although sex differences in bilateral asymmetry have been reported (e.g., Ruff and Jones, 1981; Steele, 2000), results are variable depending on skeletal element and sample, and this factor has not been investigated systematically in a large sample.

The dimensions considered here are lengths, articular or peri-articular breadths, and midshaft diaphyseal breadths of four major long bones (humerus, radius, femur, and tibia). The Appendix presents a summary of previous studies that have investigated bilateral asymmetry in these elements (both in linear dimensions and bone weights). Steele (2000) recently reviewed more general indicators of skeletal asymmetry (including arthritis and muscular attachments) in the human upper limb.

Methods

The sample and measurements

The skeletons of 780 adult Holocene humans (514 males, 266 females), spanning six continents and several dozen populations (Table 1), were measured. For the benefit of the reader and for certain later comparisons, the sample in Table 1 is also divided into broad and narrow regional/temporal groups

(following Auerbach and Ruff, 2004). All groups were pre-industrial, with the exception of two European samples (first-generation immigrants in the Hamann-Todd Osteological Collection and cadaveric remains from Syracuse, Sicily) and the modern Japanese sample (dated from the early 20th century and considered early industrial).

All individuals were measured bilaterally by one of us (BMA). Measurements were taken using Mitutoyo digital sliding calipers linked directly to a notebook computer, and a portable Paleo-tech Concepts osteometric board. Maximum lengths of humeri (HML), radii (RML), femora (FML), and tibiae (TML) were taken to the nearest 0.5 mm with the osteometric board using the methods described by Martin (1957); TML included the intercondyloid eminence (“spines”) and medial malleolus (comparable to Martin’s total length, M-1a). Three mediolateral (ML) peri-articular breadths were included: humeral epicondylar breadth (HEB), femoral epicondylar breadth (FEB), and tibial condylar breadth (TCB); these variables were measured to the nearest 0.5 mm with the osteometric board at their maximum diameters in the ML plane. Three articular breadths were included, all measured to the nearest 0.01 mm with the dial calipers: inferosuperior humeral head diameter (HHD), anteroposterior femoral head diameter (FHD), and the distal femoral ML articular breadth (FAB). All three articular measures were taken at their maximum breadths, and the FAB as it was observed distally. Diaphyseal midshaft locations on all four elements were determined from maximum lengths, and anteroposterior (AP) and ML breadths were measured to the nearest 0.01 mm using dial calipers. These ML and AP midshaft diameters were then averaged to yield the average diaphyseal midshaft diameters (HDB, RDB, FDB, and TDB) used in our analyses.

Thirty-six individuals were measured three times over a period of several weeks to test for measurement error; results are shown in Table 2. Measurement errors were calculated using the method outlined by White (2000), in which differences from the mean of the measurements are averaged and expressed as a percentage of the mean measure. Average measurement error is less than 1% for most dimensions, although closer to 2% for humeral and tibial diaphyseal breadths, as well as tibial condylar breadth.

Methods for sexing and adult determination are the same as those used previously in this (which we title as the Goldman) data set (see Auerbach and Ruff, 2004), relying mainly on pelvic traits for the former and epiphyseal fusion for the latter. Individuals exhibiting pathologies caused by disease or trauma on any elements under consideration were excluded from this study. Likewise, all individuals in which the association of bones was questionable or sex remained indeterminate were removed from the sample.

Statistical methods

As has been the convention in recent papers (Steele and Mays, 1995; Mays, 2002), data on asymmetry were converted into percentage directional asymmetries (%DA):

$$\%DA = (\text{right} - \text{left}) / (\text{average of left and right}) \times 100$$

Table 1
Populations sampled in this study

Broad group	Narrow group	Population (number of populations/sites)	<i>n</i> (males/females)	Source ¹
Andaman Islanders	Andaman Islanders	Great Andamanese, Jarawa (1)	12 (7/5)	AMNH; DC; NHM
Europeans ²	Neolithic European	Austrians (1), French (1)	5 (3/2)	MdH; NM
	Bronze Age European	Austrians (1), English (2), Italians (1)	35 (19/16)	DC; MNdAE; NM
	Iron Age European	Germans (1), English (1)	60 (33/27)	NHM; SfAP
	Early medieval European	Belgians (2), Germans (3), Scottish (1)	51 (32/19)	IRSN; NHM; SfAP
	Modern European	Early 20th century Cadaveric (2) ²	157 (134/23)	CMNH; MNdAE
Japanese	Edo Period Japanese	Early 20th century Cadaveric (2) ³	34 (20/14)	KU; MdH
	Jōmon	Middle and Late Shellmound sites (2)	13 (7/6)	KU
Madagascar	Madagascar	Merina (1)	11 (9/2)	MdH
Native Americans ⁴	Alaskan Inuit	Inupiat and Inuit (3)	51 (30/21)	AMNH; NMNH
		Several islands ⁵	28 (16/12)	NMNH
	Aleutian Islanders	Arikara (3)	19 (10/9)	NMNH
		Arkansas Hopewell (1)	2 (2/0)	AMNH
		Delaware (1)	9 (5/4)	NMNH
		Illinois Hopewell (1)	23 (15/8)	NMNH
		Indian Knoll (1)	52 (34/18)	WOAC
		Ketchipauan (1)	4 (2/2)	DC
		Peruvian (2)	24 (15/9)	MdH; MNdAE
		Santa Cruz Island (Channel Islands) (1)	6 (1/5)	NHM
		Toba (Patagonian) (1)	9 (6/3)	MdH; MNdAE; NHM
		Ute (2)	16 (13/3)	AMNH; NMNH
		Yamana (Terra del Fuego) (1)	7 (5/2)	MdH; MNdAE
		Chaco Canyon/Pueblo Bonito (1)	17 (10/7)	AMNH; NMNH
		Hawikuh (1)	21 (12/9)	NMNH
Pacific Northwest (1)	2 (1/1)	AMNH		
Puye (1)	4 (1/3)	NMNH		
Northeastern African	Egyptian	Pre-Dynastic to Middle Kingdom Egyptians (4)	40 (28/12)	AMNH; MdH; NM
	Nubian	Kerma and Sayala (2)	28 (16/12)	DC; NM
Oceania	Australian Aborigines ²	Several populations	21 (14/7)	AMNH; MdH; NHM; MNdAE; NMNH
	Solomon Islanders	Solomon Islanders (1)	3 (3/0)	MdH
Philippine Islands	Negrito	Not known ⁶	16 (11/5)	MdH
Total			780 (514/266)	

¹ **AMNH**, American Museum of Natural History, New York City, New York, USA; **CMNH**, Cleveland Museum of Natural History, Cleveland, Ohio, USA; **DC**, Duckworth Osteological Collection, Cambridge, England, United Kingdom; **IRSN**, Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium; **KU**, Kyoto University (Kyodai) Department of Anthropology, Kyoto, Japan; **MdH**, Musée de l'Homme, Paris, France; **MNdAE**, Museo Nazionale di Antropologia e Etnologia, Firenze, Italia; **NHM**, British Museum (The Natural History Museum), London, England, United Kingdom; **NM**, Naturhistorisches Museum, Wien, Österreich; **NMNH**, National Museum of Natural History (Smithsonian Institution), Washington, D.C., USA; **SfAP**, Staatssammlung für Anthropologie und Paläoanatomie, München, Deutschland; **WOAC**, Webb Osteology and Archaeology Collection, Lexington, Kentucky, USA.

² See Table 1 in Auerbach and Ruff (2004) for further details about populations and population designations.

³ These populations consist of one cadaveric sample measured at Kyoto University and one sample from Tokyo measured at Musée de l'Homme in Paris, both dating from the Edo period in Japan (late 19th and early 20th centuries).

⁴ Native Americans are divided into narrow groups based on general geographic location and group affinities. Because of uncertainty in the migrations of Asians into the Americas, and hence these groups' affinities to each other, this information is included only for referential purposes only.

⁵ Although the Aleutian Islanders were collected from the length of the Aleutian Island chain, and so some populations never directly interbred, the gene flow among these islands is assumed to be continuous enough to justify placing these populations in one group.

⁶ This Philippine Island population's origin was not positively ascertained from the museum accession records, although the individuals are unquestionably members of native upland tribes commonly called Negritos.

This method standardizes all raw asymmetric differences to percentages of directional asymmetry within elements, allowing for direct comparison of asymmetries in dimensions of different size. For example, a 3 mm difference between sides is a greater asymmetry for smaller dimensions (such as humeral head inferosuperior diameters) than for relatively larger dimensions (such as humeral maximum lengths). These results also translate into positive values for right-side asymmetries and negative values for left-side asymmetries. However, because %DA combines both the relative frequency of right

and left "dominance" with the absolute values of asymmetry within right and left dominant groups, for comparison we also calculated percent absolute asymmetries between sides as:

$$\%AA = (\text{maximum} - \text{minimum}) / (\text{average of maximum and minimum}) \times 100$$

This statistic describes the magnitude of "random" asymmetry in a given dimension. The majority of the analyses were conducted on %DA. As described below, we also determined

Table 2
Measurement errors for osteometrics included in this study ($n = 36$ individuals)

Measurement	Percentage of error		
	Left	Right	Average ¹
Humeral maximum length (HML)	0.23%	0.09%	0.16%
Humeral distal epicondylar breadth (HEB)	0.42	0.40	0.41
Humeral head SI diameter (HHD)	0.28	0.40	0.34
Humeral average 50% diaphyseal diameter (HAD)	1.95	1.80	1.88
Radial maximum length (RML)	0.10	0.08	0.09
Radial average 50% diaphyseal diameter (RAD)	0.91	1.00	0.96
Femoral maximum length (FML)	0.69	0.21	0.45
Femoral epicondylar breadth (FEB)	0.35	0.28	0.32
Femoral ML distal articular breadth (FAB)	0.74	0.94	0.84
Femoral AP head diameter (FHD)	0.16	0.14	0.15
Femoral average 50% diaphyseal diameter (FAD)	0.41	0.42	0.42
Tibial maximum length (TML)	0.58	0.41	0.50
Tibial condylar breadth (TCB)	1.80	1.76	1.78
Tibial average 50% diaphyseal diameter (TAD)	1.69	2.31	2.00

¹ Average percentage deviation of three measurements from their mean.

the frequency of right and left “dominant” individuals for each dimension.

Percentage data often violate the requirements of most parametric tests without arcsine transformation (Zar, 1999). All right-left and maximum-minimum differences, absolute and percentage, were non-normal in distribution according to a Lilliefors test. They were also highly leptokurtic, with many percentage values close to zero. Therefore, arcsine transformations did not produce normal distributions (Sokal and Rohlf, 1995) and most analyses were conducted using non-parametric tests on non-transformed data. For this reason,

we also emphasize median asymmetry values in our summary statistics, although we also include mean asymmetries for comparison with previous studies that employed this statistic (Ruff and Jones, 1981; Sakaue, 1998; Mays, 2002).

The %DAs and %AAs were examined first in the entire sample. The Wilcoxon signed-ranks test—the non-parametric equivalent of the paired t -test—was utilized to determine if right and left sides were significantly different for each dimension (Table 3). Sex differences in asymmetry were tested by applying the Mann–Whitney U -test—the non-parametric equivalent of the two-sample t -test—to percentage side differences (%DA and %AA). The same procedure was used to test for differences in asymmetry between broad groups within the sample and different dimensions within the same skeletal elements (i.e., length, diaphyseal breadth, and articular and/or peri-articular breadth). The Kruskal–Wallis test (the non-parametric ANOVA equivalent) was used to examine differences between three or more groups or dimensions. Post-hoc comparisons among groups found to be significant by the Kruskal–Wallis tests (i.e., among three groups significantly different from each other in a given dimension) were made using Mann–Whitney U -tests.

In addition to examining the Wilcoxon ranked sum tests to determine significant asymmetries, we also examined the percentage of the sample that exhibited laterality for each measure. Since many individual %DAs fall close to zero, and slight side biases may not be biologically significant as true directional asymmetry (i.e., instead of arising from measurement error or fluctuating asymmetry), we chose to categorize only individuals with greater than $\pm 0.5\%$ directional asymmetry. Based on this criterion, the number of right-biased and left-biased individuals were tallied and compared for equivalency (50:50 ratios) by a chi-square test; non-equivalent numbers indicated a population-level lateralization for a given dimension. This test was conducted on the overall sample and within males and females. Chi-square tests were also used to compare male and female right/left-biased proportions. Similar tests

Table 3
Medians and means of %DAs and %AAs for total pooled sample and by sex

Measure	Median %DA (mean %DA)			Median %AA (mean %AA)		
	Total	Males	Females	Total	Males	Females
Humeral maximum length (HML)	1.30* (1.27)	1.11* (1.11)	1.60* (1.60)	1.36 (1.50)	1.23 (1.38)	1.67 (1.74)
Humeral head SI diameter (HHD)	0.37* (0.49)	0.58* (0.73)	-0.10 (0.03)	1.59 (1.91)	1.64 (1.92)	1.49 (1.88)
Humeral distal epicondylar breadth (HEB)	1.61* (1.32)	1.60* (1.34)	1.71* (1.28)	1.83 (2.23)	1.77 (2.22)	1.90 (2.24)
Humeral average 50% diaphyseal diameter (HDB)	2.98* (3.19)	3.35* (3.55)	2.29* (2.50)	3.34 (4.02)	3.61 (4.34)	2.81 (3.40)
Radial maximum length (RML)	0.84* (0.80)	0.75* (0.67)	0.97* (1.05)	0.98 (1.20)	0.90 (1.10)	1.27 (1.39)
Radial average 50% diaphyseal diameter (RDB)	2.21* (2.31)	2.16* (2.33)	2.35* (2.27)	3.33 (3.95)	3.22 (3.90)	3.41 (4.06)
Femoral maximum length (FML)	-0.24* (-0.24)	-0.22* (-0.22)	-0.37* (-0.29)	0.66 (0.78)	0.63 (0.77)	0.71 (0.81)
Femoral head AP diameter (FHD)	0.11* (0.12)	0.17* (0.16)	0.01 (0.06)	1.02 (1.35)	0.97 (1.32)	1.12 (1.39)
Femoral epicondylar breadth (FEB)	0.00* (0.27)	0.00* (0.29)	0.00* (0.24)	1.22 (1.28)	1.20 (1.25)	1.36 (1.33)
Femoral distal articular breadth (FAB)	0.01 (-0.13)	0.05 (-0.09)	-0.12 (-0.20)	1.51 (1.91)	1.48 (1.91)	1.55 (1.90)
Femoral average 50% diaphyseal diameter (FDB)	-0.49* (-0.39)	-0.47* (-0.35)	-0.55* (-0.47)	1.78 (2.25)	1.73 (2.06)	1.89 (2.64)
Tibial maximum length (TML)	0.00 (0.01)	0.00 (0.04)	0.00 (-0.05)	0.55 (0.69)	0.55 (0.71)	0.57 (0.67)
Tibial condylar breadth (TCB)	0.00 (0.00)	0.00 (-0.03)	0.00 (0.07)	1.53 (2.02)	1.44 (1.97)	1.60 (2.12)
Tibial average 50% diaphyseal diameter (TDB)	-0.78* (-0.77)	-0.80* (-0.83)	-0.75* (-0.66)	2.52 (3.17)	2.49 (3.06)	2.60 (3.27)

*Right-left asymmetry is significant at $p < 0.05$ (Wilcoxon signed-ranks test). Bold indicates significant sexual dimorphism for given dimension.

considering individuals with any asymmetry (greater than 0%) and individuals with greater than $\pm 1\%$ asymmetry yielded similar right/left proportions and identical results from the chi-square tests.

Correlations between asymmetries of different dimensions within elements and within limbs were assessed by examining residuals of natural log-transformed raw measures (to reduce heteroscedasticity and size effects). Natural logs of right-side values for a given dimension were regressed on log-transformed left-side values using (ordinary) least squares regression. Residuals from these regressions were then subjected to a standard Pearson's correlation test. Because we ran a relatively large number of correlations for each group (overall, males, and females), we employed a Bonferroni correction to reduce the likelihood of making a type I error by reducing the alpha level by the number of comparisons made.

Crossed symmetry between upper and lower limbs was examined by a new test transforming the percentage asymmetries into dummy variables. Only similar properties (e.g., humeral maximum length with femoral maximum length) were tested between limbs, and only lengths and diaphyseal breadths were included since only these dimensions were measured on all skeletal elements. All positive %DAs were assigned a dummy value of 1, negative %DAs a value of -1 , and symmetrical %DAs were excluded. These dummy variables were then summed between limbs, thus yielding values of -2 or 2 for same-side asymmetries and 0 for crossed symmetries. All added values of 1, indicating that only one limb in a comparison exhibited asymmetry, were excluded from this test. Taking absolute values of the resultant summations, we compared frequencies of 2 and 0 to an expected frequency of 50:50 using a chi-square test. We tried this test first using a strict definition of symmetry ($\%DA = 0$) to be coded with a dummy variable of

0, and then more relaxed restrictions ($\%DA < 0.1\%$; $\%DA < 0.5\%$); all definitions produced the same results.

Results

Asymmetry in the total pooled sample

Median and mean %DAs and %AAs for the total sample and by sex are presented in Table 3. Figure 1 shows sex-specific box plots of %DAs of all measures taken over the total pooled sample. In the upper limb, all dimensions are significantly right-biased for the overall sample, with median asymmetries varying from 0.4% (humeral head) to 3% (humeral diaphyseal breadth). Lower limb measures are more variable in their directionality, are collectively closer to zero %DA than upper limb asymmetries, and (with the exception of femoral head diameter and the marginal exception of femoral epicondylar breadth) are left-biased when significantly asymmetric. Although FEB has a median of zero, the Wilcoxon signed-ranks test reveals that a significantly higher number of individuals have right-biased %DAs (352 right-biased versus 239 left-biased). Also, in contrast to the results of a previous study (Plochocki, 2004), femoral head diameters are significantly right biased in %DA, although the average asymmetry is quite small (0.1%). Table 4 shows the percentage of the sample (overall, male, and female) with greater than $\pm 0.5\%$ DA, with results that are consistent with all of these observations.

Both Table 3 and Fig. 1 reveal that diaphyseal breadth dimensions of all four elements exhibit the greatest systematic directional bias and total absolute (%AA; max-min) asymmetry. A higher percentage of the total sample has directional

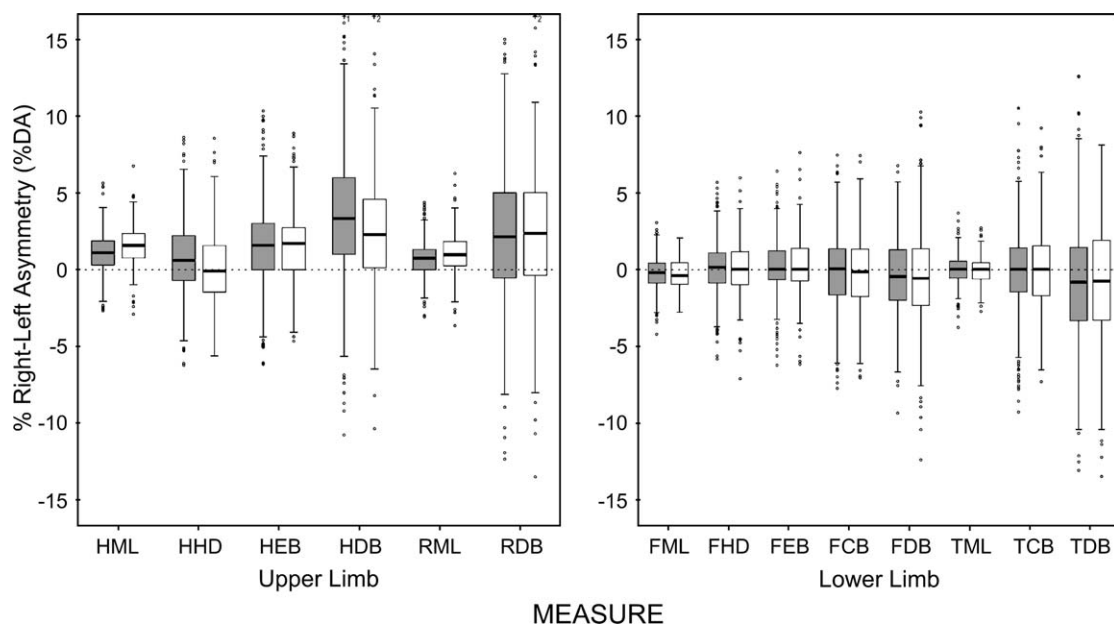


Fig. 1. Box-plots of directional asymmetries (%DA) for skeletal measures considered in this study (see Table 3 for abbreviations). Shaded boxes: males; open boxes: females. Numbers at the top of graphs refer to outliers.

Table 4
Percent of individuals with directional asymmetric bias

Measure	Overall Sample			Males			Females		
	+Left	< ±0.5%	+Right	+Left	< ± 0.5%	+Right	+Left	< ± 0.5%	+Right
HML	8%	18%	74%*	10%	21	69%*	5%	11	84%*
HHD	33	19	48*	29	19	52*	41	19	40
HEB	21	17	62*	21	15	64*	20	21	59*
HDB	14	10	76*	13	8	79*	17	13	70*
RML	13	28	59*	14	30	56*	11	24	65*
RDB	25	8	67*	26	8	66*	24	8	68*
FML	39*	41	20	36*	44	20	44*	35	21
FHD	35	23	42*	33	24	43*	38	23	39
FEB	31	24	45*	30	22	48*	32	28	40
FAB	41	20	39	40	21	39	44	18	38
FDB	50*	14	36	49*	15	36	51*	11	38
TML	29	44	27	27	44	29	31	46	23
TCB	40	17	43	40	17	43	39	19	42
TDB	53*	12	35	54*	11	35	52*	12	36

*Indicates significantly biased values based on chi-square test comparing only individuals with > 0.5% directional asymmetry ($p < 0.05$). Bold indicates significant sexual dimorphism in asymmetry frequencies (+Left and +Right only).

asymmetry in these dimensions as well (Table 4). Kruskal–Wallis tests with post-hoc Mann–Whitney U -tests comparing dimensions within sex and element further demonstrate that there are significantly greater amounts of absolute and directional asymmetry in diaphyseal breadth dimensions than in length, articular, or peri-articular measures ($p < 0.01$). Although asymmetries across elements but within the same limb are generally in the same direction (see below), the magnitudes of directional asymmetry of similar types of dimensions within a given limb (e.g., humeral and radial lengths) are significantly different in most cases. The exceptions are upper limb diaphyseal breadths in females and the two opposing knee breadths (FAB and TCB), which is expected given their integral functional morphology.

Individual variation in asymmetry, shown in Fig. 1, is greatest for upper limb diaphyseal breadths, with many individuals exceeding $\pm 10\%$ DA in these dimensions. Tibial diaphyseal breadth also exhibits high individual variation in asymmetry, with a number of individuals exceeding $\pm 10\%$ DA. The least variable asymmetries in both limbs are in bone lengths.

Significant sexual dimorphism in %DA and %AA is shown by bolded percentages in Table 3, the values of which may be directly compared to percentages within sex-specific samples in Table 4. In almost all cases, both sexes have the same directionality in asymmetries; the apparent difference observed in directionality for humeral head diameters (Table 3) may be misleading, as the median for female HHD %DA is non-significantly different from zero and almost equal numbers of females have left- and right-side biases in this dimension (Table 4). Males have significantly greater directional asymmetry in humeral head diameters, as well as greater %DA and %AA in humeral diaphyseal breadths. The proportion of males that are right-biased for humeral head and diaphyseal breadth is also larger than that for females (Table 4; near-significant [$p = 0.06$] for diaphyseal breadth). Females have significantly greater directional and absolute asymmetry in the maximum lengths of humeri and radii (Table 3) and a larger proportion of right-biased individuals for these dimensions

(Table 4; near-significant [$p = 0.07$] for the radius). Females also have higher %AAs (but not %DAs) for four lower limb dimensions (FML, FEB, FDB, and TCB) (Table 3). For both sexes and all comparisons, the least asymmetry occurs in knee articular dimensions and tibial length.

Asymmetry among geographic groupings

While these results are useful for summarizing asymmetries present in the total pooled sample, they do not indicate the degree of variation that may exist in these asymmetries among geographically diverse groups. In addition, it is possible that pooled results are unduly influenced by trends in the larger samples, i.e., North American Native Americans and Europeans (Table 1). The results presented above are therefore re-examined among more specific geographic subsamples. These correspond to the “narrow groups” listed in Table 1, except that, in order to somewhat limit the number of groups, pre-industrial (pre-“modern”) Europeans are grouped together, as are Alaskan Inuit and Aleutian Islanders, and Egyptians and Nubians. Only groups with at least five males and five females were included, thus eliminating the small Madagascar and Solomon Islander samples.

Table 5 gives the median directional asymmetries for nine subsamples, as well as the mean and median of these asymmetries. Results for the total pooled sample (Table 3) are also given for comparison. Box plots for the same samples are shown in Fig. 2 for upper limb dimensions. Since we found significant sexual dimorphism in magnitudes of asymmetry of some dimensions in the total pooled sample, data in Table 5 are presented by sex. The box plots in Fig. 2 are for pooled sexes; results here may be compared with those for the total pooled-sex sample in Table 3.

Average asymmetries derived from the subsample median asymmetries are generally quite similar to those in the total pooled sample, indicating that the total pooled sample results were not biased by the larger population samples. Subsamples vary in their degree of asymmetry for different dimensions;

Table 5
Medians of select broadly defined populations for directional asymmetries (%DA) in males (A) and females (B)

Population (<i>n</i>)	HML ¹	HHD	HEB	HDB	RML	RDB	FML	FHD	FEB	FAB	FDB	TML	TCB	TDB
A. Males														
Subarctic Native Americans (132)	0.63	0.90	1.72	6.11	0.60	3.15	-0.34	-0.14	0.00	-0.17	-0.57	-0.26	0.00	-1.20
Arctic Native Americans (46)	1.57	-0.43	0.85	3.28	0.32	2.45	0.12	0.43	0.00	-0.32	-0.55	0.29	0.00	-1.48
Australian Aborigines (14)	0.23	1.57	2.11	3.48	0.69	3.88	-0.40	-0.19	1.32	0.41	-0.76	0.20	1.38	-1.77
Northeastern Africans (44)	1.11	1.44	0.84	1.70	1.10	2.07	0.00	0.28	0.64	0.34	-0.50	0.26	0.00	0.00
Philippine Island "Negritos" (14)	0.74	0.34	1.96	2.52	1.28	1.26	-0.46	-0.01	0.00	0.25	-0.08	0.00	1.38	-2.89
Jōmon (7)	1.89	0.10	2.60	3.17	0.99	1.50	-0.01	-0.64	0.32	0.56	1.68	-0.15	0.39	-0.23
Pre-industrial Europeans (87)	1.75	0.81	0.84	3.20	0.56	3.21	-0.21	0.28	0.59	-0.68	-1.01	-0.13	0.00	0.43
Edo Period Japanese (20)	0.78	0.64	0.43	1.17	0.84	0.54	-0.24	0.33	0.28	-0.84	-0.35	0.00	0.34	-0.85
Industrial Europeans (134)	1.10	0.36	1.61	2.73	0.73	0.96	-0.13	0.34	0.58	0.27	-0.29	0.26	0.00	-1.07
Mean of medians	1.09	0.64	1.44	3.04	0.79	2.11	-0.19	0.08	0.41	-0.02	-0.27	-0.05	0.39	-1.01
Median of medians	1.10	0.64	1.61	3.17	0.73	2.07	-0.21	0.28	0.32	0.25	-0.50	0.00	0.00	-1.07
Pooled sample median ²	1.11	0.58	1.60	3.35	0.75	2.16	-0.22	0.17	0.00	0.05	-0.47	0.00	0.00	-0.80
Range of medians	1.66	2.00	2.17	4.94	0.96	3.34	0.52	1.07	1.32	1.40	1.69	0.55	1.38	3.32
B. Females														
Subarctic Native Americans (83)	1.36	-0.46	1.80	2.65	1.11	3.23	-0.38	-0.20	0.00	-0.44	-0.43	0.00	0.00	-1.65
Arctic Native Americans (33)	2.11	0.34	0.91	1.83	0.75	3.09	-0.53	0.05	0.00	-0.05	-0.57	-0.16	0.00	-1.50
Australian Aborigines (7)	0.00	0.00	0.00	6.25	1.18	6.94	-0.56	-0.76	0.00	-0.57	-0.68	0.00	0.00	-3.77
Northeastern Africans (24)	1.82	1.08	1.80	1.70	1.52	2.26	-0.64	0.04	0.00	-1.45	-0.50	-0.08	-1.63	0.25
Philippine Island "Negritos" (5)	0.37	2.20	2.20	5.00	-0.46	1.06	-0.71	0.03	0.00	0.21	0.35	-0.30	0.00	-1.26
Jōmon (6)	2.21	0.66	-0.99	2.65	0.75	0.61	0.00	-0.32	0.00	-0.76	-0.20	-0.46	0.00	0.82
Pre-industrial Europeans (64)	2.16	-0.09	1.71	2.24	1.34	2.09	0.00	1.01	1.33	0.61	-1.36	0.00	0.37	-0.12
Edo Period Japanese (14)	0.73	-0.14	0.85	1.06	0.51	1.30	-0.39	-0.19	0.00	-0.22	-0.80	-0.15	0.00	-1.54
Industrial Europeans (23)	1.44	-0.74	1.71	2.63	0.92	0.78	-0.37	0.17	0.00	-0.42	0.24	-0.60	0.00	-0.73
Mean of medians	1.36	0.32	1.11	2.89	0.85	2.37	-0.40	-0.02	0.15	-0.34	-0.44	-0.19	-0.14	-1.06
Median of medians	1.44	0.00	1.71	2.63	0.92	2.09	-0.39	0.03	0.00	-0.42	-0.50	-0.15	0.00	-1.26
Pooled sample median ³	1.60	-0.10	1.71	2.29	0.97	2.35	-0.37	0.01	0.00	-0.12	-0.55	0.00	0.00	-0.75
Range of medians	2.21	2.94	3.19	5.19	1.98	6.33	0.71	1.77	1.33	2.06	1.71	0.60	2.00	4.59

¹ See Table 3 for abbreviations.

² Derived from male pooled sample (see Table 3, third data column).

³ Derived from female pooled sample (see Table 3, fifth data column).

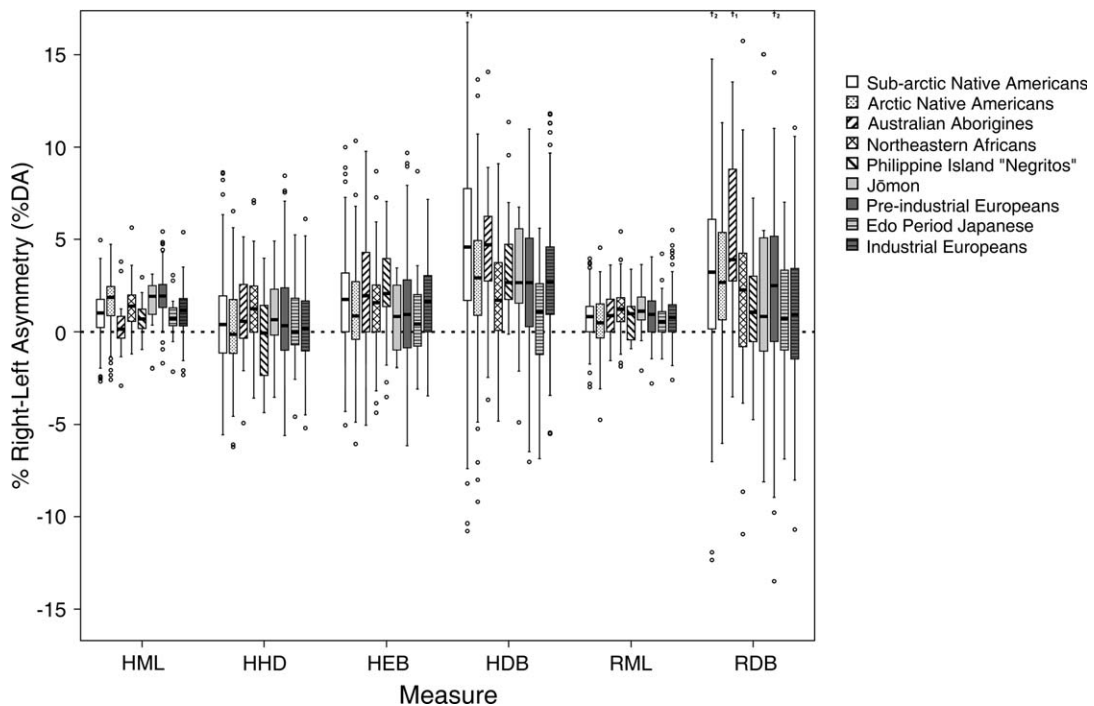


Fig. 2. Box-plots of upper limb directional asymmetries (%DA) in nine population samples (see Table 3 for abbreviations). Median asymmetries are given in Table 5. Numbers at the top of box plots refer to outliers.

however, the same general patterns observed in the total pooled sample are evident across groups. Except for HHD, all groups are directionally right-biased (have median %DAs above zero) in all upper limb dimensions, with the exception of HEB in one female group, the small ($n = 6$) Jōmon sample. Within bones, the largest asymmetries almost invariably occur in upper limb diaphyseal breadths (65 of 72 comparisons). Some average diaphyseal breadth asymmetries reach 5% or more, and many are over 3%, while average asymmetries in other dimensions are always less than 3%. The pattern of greater right-bias in males for HHD and HDB and greater right-bias in females for HML and RML observed in the total sample is also characteristic of most of the subsamples (6 of 9 in each case), although there are some notable exceptions, especially the very high asymmetry in upper limb diaphyseal breadths in female Australian Aborigines and in HDB in female Phillipine “Negritos” (both of which are small samples). Among geographically “matched” but temporally dissimilar samples, Edo Period Japanese generally have lower levels of upper limb asymmetry than Jōmon (10 of 12 comparisons), although the genetic discontinuity between these samples must be noted (Matsumara, 2001). Similarly, industrial European males (but not females) have less upper limb asymmetry (except in HEB and RML) than pre-industrial Europeans.

The great majority of subsamples demonstrate left-bias in lower limb diaphyseal breadths (29 of 36 samples) and FML (14 of 18 samples) but not in other dimensions. Variable FEB is more often right-biased in male subsamples (6 of 9 samples) but not in female subsamples. The largest lower limb asymmetries are found in tibial diaphyseal breadths in female Australian Aborigines (3.8%) and male Phillipine Island “Negritos” (2.9%), both of which are left-biased. As in the total pooled sample, variation within subsamples in asymmetry is greatest for diaphyseal breadths and least for bone lengths (Fig. 2). There is also more variation between subgroups in diaphyseal-breadth asymmetry than in other dimensions in both the upper and lower limbs, except for FDB in females (Table 5 and Fig. 2).

Sexual dimorphism in upper limb asymmetry is compared in the pre-industrial and industrial European samples in Table 6. (The Jōmon sample was considered too small to allow for meaningful comparisons of sexual dimorphism with modern Japanese.) Sexual dimorphism was calculated as the difference between male and female median asymmetries for each

property. Industrial Europeans consistently show less sexual dimorphism in asymmetry than pre-industrial Europeans. This is particularly true for humeral and radial diaphyseal breadths, where differences between the sexes are about 1% in the earlier group but only 0.1–0.2% in the later group.

Correlations of asymmetries within and between limbs

Table 7 gives the correlations between right-side and left-side regression residuals for measures within limbs for the total sample and by sex. Most of the correlations have poor explanatory power, although a number of them are significant. Noise arising from measurement error or variables not considered in this analysis (such as fluctuating asymmetry) may account for some of the low Pearson’s r -values (Palmer and Strobeck, 1986; Rittweger and Rauch, 2004). All significant correlations are positive, demonstrating that no inverse asymmetries occur within limbs. The highest correlations are between asymmetries in the two distal femoral dimensions (FEB and FAB), which is not surprising given their close functional and spatial relationship. The highest correlations in the upper limb are between humeral and radial diaphyseal breadths (total sample and males, but not females), and between humeral and radial lengths (both sexes). Femoral and tibial length asymmetries are significantly correlated in males, but not in females. Males show more significant correlations within both the upper and lower limbs than females. Within-limb asymmetries in maximum lengths and diaphyseal breadths are not significantly correlated in any of the comparisons.

Results of the chi-square tests for crossed symmetry between upper and lower limbs are reported in Table 8. The same table also shows comparisons between elements within limbs using the same test. Consistent with the results given above, comparisons within limbs using this test indicate ipsilateral (same-side or intermembral) symmetry, i.e., asymmetry in the same direction in both elements of the same limb. However, comparisons across upper and lower limbs demonstrate significant contralateral, or crossed, symmetry in several dimensions, including femoral length with humeral and radial lengths, femoral and tibial diaphyseal breadths with humeral diaphyseal breadth, and tibial diaphyseal breadth with radial diaphyseal breadth. These results support the existence of individual crossed symmetry within similar dimensions of upper limb and lower limb elements. In no case is there significant ipsilateral symmetry between the upper and lower limbs. The lack of crossed symmetry between the upper limb bone maximum lengths and tibial maximum length is not surprising given the lack of side bias in TML (Table 3).

Discussion

The patterns of long bone bilateral asymmetry documented in this study are similar to those reported previously by other researchers (summarized in the Appendix). However, this study is unique in comparing several different types of dimensions—lengths, diaphyseal breadths, and articular

Table 6
Sexual dimorphism in upper limb directional asymmetry (%DA) in pre-industrial Europeans and industrial Europeans, calculated as the difference between male and female median %DAs

Measures	Sexual dimorphism (male – female median %DA)	
	Pre-industrial Europeans (87♂, 64♀)	Industrial Europeans (134♂, 23♀)
HML	–0.41%	–0.34%
HHD	1.71	1.10
HEB	–0.87	–0.10
HDB	0.96	0.10
RML	–0.78	–0.19
RDB	1.12	0.18

Table 7
Correlations of asymmetry within limbs. Upper limb correlations are on the upper right; lower limb correlations are on the lower left. Bolded correlations are significant after Bonferroni correction ($p < 0.05$). See Table 3 for abbreviations

a. Overall sample ($n = 780$)

	HML	HHD	HEB	HDB	RML	RDB		
FML		0.182	0.064	0.050	0.227	0.083		
FHD	0.033		0.120	0.181	0.098	0.167		
FEB	0.145	0.043		0.207	0.057	0.127		
FAB	0.092	0.093	0.436		0.061	0.292		
FDB	0.015	0.120	0.096	0.104		0.119		
TML	0.228	-0.002	0.235	0.180	0.016			
TCB	0.042	0.042	0.203	0.220	0.154	0.103		
TDB	0.037	0.129	0.092	0.030	0.098	0.061	0.023	
FML		FHD	FEB	FAB	FDB	TML	TAB	TDB

b. Males ($n = 514$)

	HML	HHD	HEB	HDB	RML	RDB		
FML		0.208	0.106	0.124	0.214	0.106		
FHD	0.036		0.113	0.200	0.132	0.184		
FEB	0.117	0.030		0.224	0.106	0.124		
FAB	0.072	0.084	0.475		0.059	0.321		
FDB	-0.037	0.184	0.100	0.133		0.086		
TML	0.259	-0.009	0.231	0.205	0.032			
TCB	0.026	0.065	0.251	0.228	0.161	0.124		
TDB	0.052	0.183	0.099	0.011	0.153	0.068	0.054	
FML		FHD	FEB	FAB	FDB	TML	TAB	TDB

c. Females ($n = 266$)

	HML	HHD	HEB	HDB	RML	RDB		
FML		0.170	0.013	-0.064	0.246	0.070		
FHD	0.020		0.083	0.047	0.064	0.088		
FEB	0.196	0.058		0.103	-0.001	0.090		
FAB	0.123	0.090	0.360		0.107	0.168		
FDB	0.084	0.009	0.080	0.029		0.196		
TML	0.155	-0.001	0.239	0.107	-0.033			
TCB	0.062	-0.022	0.110	0.176	0.116	0.039		
TDB	0.001	0.020	0.069	0.025	-0.006	0.026	-0.067	
FML		FHD	FEB	FAB	FDB	TML	TAB	TDB

breadths—of both the upper and lower limb bones simultaneously within a large, diverse human sample. The sample (as a whole and divided into narrower subgroups) demonstrates a consistent right-biased asymmetry for all upper limb bone dimensions. There is a much weaker but still significant left-bias for lower limb diaphyseal breadths and femoral length, although some lower limb articular dimensions are very slightly right-biased. Upper limb dimensions also exhibit greater amounts of asymmetry—directional and overall—than the lower limbs. As noted by many authors, the latter result is likely due to the release of human upper limbs from locomotor constraints, which tend to produce more symmetric mechanical loading (and, for lengths, requirements for symmetry).

Both limbs also exhibit consistent differences in magnitudes of asymmetry for different structural features. Relative to other measures within elements, diaphyseal breadths consistently exhibit the most asymmetry, absolute and directional, followed by lengths and articular dimensions. In part, the increased asymmetry in external diaphyseal breadths may be due to the potential for continuing subperiosteal expansion of long bone cortices throughout life, after cessation of growth in length (and presumably articular size) (Garn et al., 1967; Lazenby, 1990; Heaney et al., 1997; Ahlborg et al., 2003). Thus, diaphyseal breadth asymmetry may increase in adults relative to length and articular asymmetry. It would be interesting to test this idea by comparing asymmetry of different bone features in older juveniles and adults from the same populations.

However, even among juveniles, a number of investigators have reported at least a partial decoupling between the growth of limb bone length and diaphyseal cross-sectional dimensions in response to mechanical stimuli (Biewener and Bertram, 1993, 1994; Bertram et al., 1997; Di Masso et al., 1998; Ruff, 2003). We found no significant correlations within individuals between asymmetry in bone lengths and asymmetry in diaphyseal breadths, supporting their relative independence. This suggests that lengths and diaphyseal breadths are “modular” in the sense of independent development, or perhaps simply that developmental integration of limb lengths and breadths is overridden to different extents by subsequent, stronger environmental effects on breadths (for a general discussion, see Hallgrímsson et al., 2002). It may be that, although limbs are potentially subject to the same perturbations during development, differing degrees of canalization (Hallgrímsson et al., 2002, 2003) may leave some bone dimensions more sensitive to these effects both in utero and after birth.

We did find some correlations between articular asymmetries and length and diaphyseal breadth asymmetries, indicating possible interdependence between these regions. As shown previously (Ruff et al., 1994), articulations follow a growth pattern that is more similar to that of bone length, and both articular size and bone length appear to be less responsive than cross-sectional diaphyseal dimensions to mechanical stimuli (i.e., they are more genetically canalized during growth [Lanyon, 1980; Biewener and Bertram, 1993, 1994; Lieberman et al., 2001; Ruff, 2003]). It is possible that the mechanisms governing articular growth are in some ways

finding in the total pooled sample of 14% (humerus) and 25% (radius) of individuals with left-biased diaphyseal breadths are broadly consistent with these behavioral observations. Although both international studies found significant geographic variation in handedness among the groups tested, there was no particular patterning to this variation, and different studies of the same general population sometimes obtained different percentages (possibly due to confounding socioeconomic or other effects), underscoring some of the problems in these types of studies. In addition, only one sample was “pre-industrial” (from Papua New Guinea). Interestingly, this sample had the highest frequency for left-handed throwing (20%) and hammering (15%) among studies that used actual performance assessments rather than questionnaires.

In contrast to the upper limb, behavioral studies of lower limb laterality seem to be in conflict with the bone structural data that we report here: behavioral studies consistently indicate higher frequencies of *right-footedness* (Peters and Durdling, 1979; Peters, 1988; Gentry and Gabbard, 1995; Bell and Gabbard, 2000; but see also Martin et al., 2004), although individuals have higher frequencies of mixed-footedness for different tasks compared to mixed-handedness (Gabbard and Iteya, 1996; Porac, 1996). This finding contrasts with the relatively modest yet significant *left-bias* for femoral and tibial diaphyseal breadths that we found here. However, interpretation of bilateral asymmetry in actual lower limb mechanical loadings is complicated by its weight-bearing nature. Foot preference in the behavioral studies was assessed as the foot utilized for object manipulation or other activities involving motor coordination—most commonly kicking, but also picking up objects, tracing or drawing with the foot, tapping, or stamping. As recognized by the original investigators (Peters, 1988; Gentry and Gabbard, 1995, and references therein), the contralateral “non-preferred” lower limb during such activities is used for “postural and stabilizing support,” (i.e., weight-bearing, and in the case of kicking, pushing off). Thus, in contrast to the upper limb, the “non-preferred” lower limb may actually be subjected to higher mechanical loads than the “preferred” limb. Interestingly in this regard, Faulkner and coworkers (1993) found slightly but significantly elevated bone mineral mass in the “non-dominant” lower limb in children (with “dominance” defined as the preferred limb used for kicking a ball). In terms of bipedal locomotion, one would expect very little directional asymmetry in lower limb bone lengths, and in fact this is the case: there is no directional asymmetry in tibial length, and only a 0.24% average directional asymmetry in femoral length (about 1 mm on average). In no sex/geographic subsample does average directional asymmetry in either femoral or tibial length exceed 0.71% (or about 2.5 mm), and very few individuals exceed 2% in either directional or absolute asymmetry in these dimensions.

We found support for the existence of crossed (contralateral) symmetries among maximum lengths and among diaphyseal diameters between the upper and lower limbs. Again, the behavioral literature at first seems mainly contradictory in that right-handed individuals are consistently right-footed, although left-handed individuals tend to show behavioral

crossed symmetry more often (Peters and Durdling, 1979; Porac et al., 1980b). However, following the argument above, our findings may actually be consistent with the levels of mechanical loading placed on the limbs if the “non-preferred” lower limb is the one used for stability and postural support (i.e., right-handed individuals may actually mechanically load their left lower limb to a greater degree). How or if these structural patterns relate to preferential turning behavior, or “spiral motion” (Schaeffer, 1928; Bracha et al., 1987; Day and Day, 1997), is not clear at present.

Ipsilateral correlations of asymmetry in length and, in the upper limb, diaphyseal breadth are significant within limbs, although they are of relatively low magnitude. Given the functional complex that the radius and humerus form and the likelihood that many behaviors would mechanically load both elements, their diaphyseal breadth asymmetry correlation is expected. Yet, by the same reasoning, we would also expect similar correlations between femoral and tibial diaphyseal breadth asymmetries in the same limb, but these are non-significant (although the chi-square test for ipsilateral symmetry is significant for tibial and femoral diaphyseal breadths). It is possible that load-sharing between the femur and tibia varies in some way that would reduce ipsilateral symmetry between these bones, or that there is variation in fibular asymmetry, not measured here, that affects tibial (but not femoral) asymmetry. Fibulae play a small but significant role in load-sharing in the leg (Yücel et al., 1986; Goh et al., 1992), and fibular/tibial cross-sectional proportions are not constant among individuals: in a sample of 29 matched pairs, fibular strength relative to tibial strength varied by a factor of four (unpublished data). Of course, forearm loading is also shared between the radius and ulna, but any variation in ulnar bilateral asymmetry (not measured in this study) apparently does not negate asymmetry correlations between the humerus and radius. The ipsilateral correlations of asymmetry in bone length in both the upper and lower limbs may relate to developmental mechanisms of control over bone length within limbs, although experimental support for this is equivocal (Hallgrímsson et al., 2002). Further investigations of modularity and morphological integration during development may elucidate the covariation of bilateral asymmetry between different types of traits and regions of the limbs and the interaction between genetic and environmental (particularly mechanical) influences on these associations.

Significant differences exist between the sexes in upper limb asymmetries. Males have a greater magnitude and directionality of asymmetry in humeral diaphyseal and head breadths, while humeral and radial maximum lengths are more asymmetrical in females. Females also have lower correlations among all asymmetries compared with males, both within and between elements. The greater male asymmetry in humeral diaphyseal breadths could be a result of generally greater mechanical loadings on the upper limb bones in males, related to greater muscular development during adolescence (Parker et al., 1990; Round et al., 1999) or possibly to more marked asymmetry in upper-limb-use among males (on average). Behavioral evidence for sex differences in upper limb preference are mixed, and potentially confounded by cultural factors

(Perelle and Ehrman, 1994; Raymond and Pontier, 2004). As noted earlier, almost none of the behavioral studies included pre-industrial samples that, perhaps, would make better models for the great majority of the samples in our study. We did find evidence for decreasing sexual dimorphism in upper limb lateralization in our industrial versus pre-industrial European samples, which could indicate more strongly defined sex-related differences in limb lateralized behavior in the earlier group.

The greater upper limb bone *length* asymmetry in females is interesting in that it runs counter to the humeral diaphyseal and head breadth asymmetry patterns. Greater humeral and radial length asymmetry in females has been reported previously in a few samples (Münter, 1936; Schultz, 1937; Sládek et al., submitted for publication). As cited above, there is evidence that longitudinal growth of the limbs is highly arbitrated by endogenous factors. A plethora of genes, hormones, and other intrinsic factors have been attributed to aiding or suppressing bone shape modification (Marcus, 1996), but only androgens, estrogen, and their receptors have been determined to be sexually dimorphic so far (Smith et al., 1994; Vanderschueren et al., 2004). How these factors could relate to asymmetric growth in bone length or the expression or timing of bone growth patterns is unknown. Almost no data exist on bilateral asymmetry in long bone growth or epiphyseal fusion. Kothari (1974: 256), in examining the radiographs of 204 boys and girls, noted that “there is no appreciable difference in the age of complete union of epiphyses on both right and left sides of the body,” but presented no statistical support for this assertion. The possible existence of endogenous, sex-linked traits that may relate to systematic bilateral asymmetry is an area that should be further explored, especially in the context of limb developmental mechanisms. At the very least, our results further support the relative independence of bone length and breadth dimensions during growth.

Conclusions

In summary, we find that general patterns of bilateral asymmetry in limb bones are present in a wide cross section of recent human groups. All asymmetries are more pronounced in the upper limb, favoring the right side. Most lower limb dimensions—especially those around the knee—have much less asymmetry, although a left-side bias for diaphyseal breadths is evident. Length asymmetries are less pronounced and less variable between and within populations than diaphyseal asymmetries, and articular and peri-articular asymmetries tend to be intermediate. The lack of correlation within individuals or between the sexes in length asymmetries and diaphyseal breadth asymmetries supports arguments that the factors affecting growth in these two types of dimensions may be relatively independent. Crossed symmetry in lengths and diaphyseal breadths between contralateral upper and lower limbs exists. Sexual dimorphism in asymmetry is present in some dimensions, especially those of the upper limb, and may implicate fundamental differences in both behavior and bone growth between males and females. Finally, more recent populations show a diminishing of the directionality and

magnitude of asymmetry and sexual dimorphism in asymmetry, probably reflecting changes in exogenous factors, such as division of labor. Earlier pre-Holocene humans show greater magnitudes of bilateral asymmetry in upper limb bone strength, but similar frequencies of right-bias, suggesting that, while the degree of stereotyped use of one limb or the other may change with specific behavioral patterns, the frequency of upper limb right-dominance has not changed among humans.

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Appendix. Past studies of limb long bone asymmetries in recent humans

Reference	Sample population(s)	Sample size (males/females) ¹	Overall results ²
Chhibber and Singh (1970)	Indian subcontinent cadavers	10	L Fe, T, Fi > R Fe, T, Fi (wts)
Churchill and Formicola (1997)	Barma Grande 2	1 (1/0)	Max-min asymmetry: H dbds > H abds, Ins;
	Paleolithic European	17 (17/0)	U dbds > U abds
	Aleut	24 (24/0)	Asymmetry in Paleolithic populations >
	Pueblo Amerindians	15 (15/0)	asymmetry in recent populations (H dbds)
Constandse-Westermann and Newell (1989)	Modern Euroamericans	25 (25/0)	
	Mesolithic northern Europeans	73 (41/32)	Right-left asymmetry: UL > LL (Ins, dbds)
			No correlation with age and lateralization Females > males in upper limb asymmetry Differences in UL laterality relate to environmental and cultural variation Higher social strata have less asymmetry

Appendix (continued)

Reference	Sample population(s)	Sample size (males/females) ¹	Overall results ²
Faulkner et al. (1993)	Modern Canadian children	224 juveniles (110/124)	UL bone mineral content and density higher in dominant limb for right-handed, equivalent between limbs for left-handed juveniles No significant difference in bone mineral density or content in LL
Fresia et al. (1990)	Georgia Coastal Amerindians (8 sites from 3 periods)	51 (26/25)	R H > L H (Ins, dbds) Temporal decline in H asymmetry: pre-agricultural > agricultural > contact populations
Hrdlička (1932)	Euroamericans Amerindians Black Americans	1350 (965/385) 301 (174/127) 82 (56/26)	R H > L H (Ins, dbds) Males H asymmetry > female H asymmetry L Fe > R Fe (Ins)
Huggare and Houghton (1994)	Maori (16th–18th century Polynesian) Prehistoric Thai (2000 yBP)	19 43	R H > L H (Ins) (Polynesians) R U > L U (Ins) (Polynesians) L Fe > L Fe (Ins) (Thais) R T > L T (Ins) (Polynesians)
Ingalls (1924)	Euroamericans	100 (100/0)	R Fe > L Fe (Ins, abds)
Ingalls (1931)	Euroamericans	100 (100/0)	R H > L H (wts) R R + U > L R + U (wts) R UL > L UL (wts) L Fe > R Fe (wts) R T + Fi > L T + Fi (wts) R LL > L LL (wts)
Ingelmark (1946)	Modern Germans (radiographs)	69 fetal 53 juveniles (24/29) 57 adolescents (32/25)	Majority of fetuses have Fe Ins = T Ins Amount of asymmetry in UL Ins increases with age Children have same-side UL and LL asymmetry Adolescents have crossed symmetry in UL and LL Handedness matches side with greater asymmetry
Latimer and Lowrance (1965)	Asians (affinities not specified)	105	R UL > L UL (wts, Ins) L LL > R LL (wts, Ins) Half of individuals exhibit crossed symmetry

Appendix (continued)

Reference	Sample population(s)	Sample size (males/females) ¹	Overall results ²
Laubach and McConville (1967)	Euroamericans	75 (75/0)	R UL > L UL (dbds)
Lowrance and Latimer (1957)			R H, R, U > L H, R, U (wts, Ins) L Fe, T > R Fe, T (wts, Ins) L Fi > R Fi (Ins) R Fi > L Fi (wts) Limited evidence supporting crossed symmetry
Münter (1936)	Archaeological English	326 (233/93)	Max-min asymmetry: H Ins > R Ins > Fe Ins > T Ins Male asymmetry > female asymmetry (except female R Ins)
Plochocki (2004)	Mississippian Missouri Amerindians	80 (39/41)	R H > L H (abds) R R > L R (abd) L Fe = R Fe (abds) R T AP ab > L T AP ab L T ML ab = R T ML ab
Ruff and Jones (1981)	Californian Coastal Amerindians	79 (30/39)	R H > L H (Ins, dbds) L T > R T (dbds)
Sakaue (1998)	Modern Japanese Jomon	63 (46/17) 40 (20/20)	R H > L H (Ins, dbds) (Jōmon) R H > L H (Ins, abds, dbds) (Modern) Male H > Female H (Ins, abds, dbds) (both groups)
Schell et al. (1985)	Euroamericans	135 adolescents (111/24)	R H > L H (abds, dbds)
Schultz (1926)	Euroamericans	100 fetal	R H > L H (Ins)
Schultz (1937)	Euroamericans Black Americans Amerindians	232 (122/110) 233 (122/111) 118 (64/54)	R H, R > L H & R (Ins) L Fe, T > R Fe, T (Ins) Asymmetry in UL Ins > asymmetry in LL Ins
	Alaskan Inuit Chinese Australian Aborigines	122 (73/49) 41 (39/2) 7 (4/3)	
Steele (2000)	Literature Review	N.A.	
Steele and Mays (1995)	10th–19th century English	14 infants 104 juveniles 153	R H > L H (Ins) (juveniles and adults) L H > R H (Ins) (infants) R R, U > L R, U (Ins) (infants, juveniles, adults)

(continued on next page)

Appendix (continued)

Reference	Sample population(s)	Sample size (males/females) ¹	Overall results ²
Stirland (1993)	Late medieval English	100 (100/0)	Activity is correlated with amount of asymmetry, including abds and dbds. H In asymmetry may be augmented by usage differences
Tanaka (1999)	Modern Japanese	36 (36/0)	R H > L H (abds) Asymmetry in tubercular H region > asymmetry in H head
Trinkaus et al. (1994)	Euroamerican cadavers	38–48 (48/0)	Asymmetry in H dbds > H distal abds > H Ins
	Georgian Coastal Amerindians	37 (37/0)	Asymmetry in tennis players > other samples (dbds)
	Californian Coastal Amerindians	71 (71/0)	Asymmetry in UL > LL (dbds)
	Jōmon	24–25 (25/0)	Paleolithic populations have greater H asymmetry than modern human populations
	Professional tennis players	45 (45/0)	
	Paleolithic hominins	11 (11/0)	
Trotter and Gleser (1952)	Euroamericans	1433 (1370/63)	R H, R, U > L H, R, U (Ins)
	Black Americans	622 (455/177)	L Fe, T, Fi > R Fe, T, Fi (Ins)
Vettivel et al. (1992)	Indian subcontinent cadavers	100	R H > L H (intertubercular sulcus depth)
Watson (1973)	Modern (affinities not specified)	203 juveniles	H > R, U asymmetries (photon absorption), athletically utilized versus non-utilized side Asymmetry increases with age in children

¹ Numbers indicate adults unless otherwise specified.

² “>” indicates greater amounts of asymmetry in the given property. L and R indicate left and right, respectively. Abbreviations for elements are: H = humerus; R = radius; U = ulna; Fe = femur; T = tibia; Fi = fibula; UL = upper limb; LL = lower limb. Abbreviations for dimensions are: Ins = length metrics; ab/abds = articular metric breadths and circumferences; dbds = diaphyseal metric breadths and circumferences; wts = weights.

References

- Ahlborg, H.G., Johnell, O., Turner, C.H., Rannevik, G., Karlsson, M.K., 2003. Bone loss and bone size after menopause. *N. Engl. J. Med.* 349, 327–334.
- Auerbach, B.M., Ruff, C.B., 2004. Human body mass estimation: a comparison of “morphometric” and “mechanical” methods. *Am. J. Phys. Anthropol.* 121, 331–342.
- Bass, S.L., Saxon, L., Daly, R.M., Turner, C.H., Robling, A.G., Seeman, E., Stuckey, S., 2002. The effect of mechanical loading on the size and shape of bone in pre-, peri-, and postpubertal girls: a study in tennis players. *J. Bone Miner. Res.* 17, 2274–2280.
- Bell, J., Gabbard, C., 2000. Foot preference changes through adulthood. *Laterality* 5, 63–68.
- Bertram, J.E.A., Greenberg, L.S., Miyake, T., Hall, B.K., 1997. Paralysis and long bone growth in the chick: growth shape trajectories of the pelvic limb. *Growth Dev. Aging* 61, 51–60.
- Biewener, A.A., Bertram, J.E.A., 1993. Mechanical loading and bone growth *in vivo*. In: Hall, B.K. (Ed.), *Bone. Bone Growth—B*, vol. 7. CRC Press, Ann Arbor, pp. 1–36.
- Biewener, A.A., Bertram, J.E.A., 1994. Structural response of growing bone to exercise and disuse. *J. Appl. Physiol.* 76, 946–955.
- Bracha, H.S., Seitz, D.J., Otemaa, J., Glick, S.D., 1987. Rotational movement (circling) in normal humans: sex difference and relationship to hand, foot and eye preference. *Brain Res.* 411, 231–235.
- Chhibber, S.R., Singh, I., 1970. Asymmetry in muscle weight and one-sided dominance in the human lower limbs. *J. Anat.* 106, 553–556.
- Churchill, S.E., Formicola, V., 1997. A case of marked bilateral asymmetry in the upper limbs of an Upper Palaeolithic male from Barma Grande (Liguria) Italy. *Int. J. Osteoarchaeol.* 7, 18–38.
- Collins, E.H., 1961. The concept of relative limb dominance. *Hum. Biol.* 33, 293–317.
- Constandse-Westermann, T.S., Newell, R.R., 1989. Limb lateralization and social stratification in western European Mesolithic societies. In: Hershkovitz, I. (Ed.), *People and Culture in Change*. B.A.R., Oxford, pp. 405–433.
- Day, H.D., Day, K.C., 1997. Directional preferences in the rotational play behaviors of young children. *Dev. Psychobiol.* 30, 213–223.
- Di Masso, R.J., Celoria, G.C., Font, M.T., 1998. Morphometric skeletal traits, femoral measurements, and bone mineral deposition in mice with agonistic selection for body conformation. *Bone* 22, 539–543.
- Faulkner, R.A., Houston, C.S., Bailey, D.A., Drinkwater, D.T., McKay, H.A., Wilkinson, A.A., 1993. Comparison of bone mineral content and bone mineral density between dominant and nondominant limbs in children 8–16 years of age. *Am. J. Hum. Biol.* 5, 491–499.
- Fresia, A., Ruff, C.B., Larsen, C.S., 1990. Temporal decline in bilateral asymmetry of the upper limb on the Georgia coast. In: Larsen, C.S. (Ed.), *Archaeology of Mission Santa Catalina de Guale 2: Biocultural Interpretations of a Population in Transition*. Anthropological Papers of the American Museum of Natural History, vol. 68. American Museum of Natural History, New York, pp. 121–132.
- Gabbard, C., Itaya, M., 1996. Foot laterality in children, adolescents, and adults. *Laterality* 1, 199–205.
- Garn, S.M., Rohmann, C.G., Wagner, B., Ascoli, W., 1967. Continuing bone growth throughout life: a general phenomenon. *Am. J. Phys. Anthropol.* 26, 313–318.
- Gentry, V., Gabbard, C., 1995. Foot-preference behavior: a developmental perspective. *J. Gen. Psychol.* 122, 37–45.
- Goh, J.C.H., Lee, E.H., Ang, E.J., Bayon, P., Pho, R.W.H., 1992. Biomechanical study of the load-bearing characteristics of the fibula and the effects of fibular resection. *Clin. Ortho. Rel. Res.* 279, 223–228.
- Hallgrímsson, B., Múyake, T., Willmore, K., Hall, B.K., 2003. Embryological origins of developmental stability: size, shape and fluctuating asymmetry in prenatal random bred mice. *J. Exp. Zool.* 296B, 40–57.
- Hallgrímsson, B., Willmore, K., Hall, B.K., 2002. Canalization, developmental stability, and morphological integration in primate limbs. *Yearb. Phys. Anthropol.* 45, 131–158.
- Harris, L.J., 1990. Cultural influences on handedness: historical and contemporary theory and evidence. In: Coren, S. (Ed.), *Left-Handedness: Behavioral Implications and Anomalies*. Elsevier Science Publishers, New York, pp. 195–258.
- Heaney, R.P., Bargerlux, M.J., Davies, K.M., Ryan, R.A., Johnson, M.L., Gong, G., 1997. Bone dimensional change with age: interactions of genetic, hormonal, and body size variables. *Osteoporosis Int.* 7, 426–431.
- Hrdlička, A., 1932. The principal dimensions, absolute and relative, of the humerus in the white race. *Am. J. Phys. Anthropol.* 16, 431–450.
- Huggare, J., Houghton, P., 1994. Asymmetry in the human skeleton. A study on prehistoric Polynesians and Thais. *Eur. J. Morphol.* 33, 3–14.
- Ingalls, N.W., 1924. Studies on the femur. *Am. J. Phys. Anthropol.* 7, 207–255.
- Ingalls, N.W., 1931. Observations on bone weights. *Am. J. Anat.* 48, 45–98.

- Ingelmark, B.E., 1946. Über die Längenasymmetrien der Extremitäten und ihren Zusammenhang mit der Rechts-Linkshändigkeit. *Upsala Lakareforenings Forhandlingar* 52, 17–82.
- Jones, H.H., Priest, J.D., Hayes, W.C., Tichenor, C.C., Nagel, D.A., 1977. Humeral hypertrophy in response to exercise. *J. Bone Joint Surg.* 59, 204–208.
- Kontulainen, S., Kannus, P., Haapasalo, H., Sievanen, H., Pasanen, M., Heinonen, A., Oja, P., Vuori, I., 2001. Good maintenance of exercise-induced bone gain with decreased training of female tennis and squash players: a prospective 5-year follow-up study of young and old starters and controls. *J. Bone Miner. Res.* 16, 195–201.
- Kontulainen, S., Sievanen, H., Kannus, P., Pasanen, M., Vuori, I., 2002. Effect of long-term impact-loading on mass, size, and estimated strength of humerus and radius of female racquet-sports players: a peripheral quantitative computed tomography study between young and old starters and controls. *J. Bone Miner. Res.* 17, 2281–2289.
- Kothari, D.R., 1974. Age of epiphyseal union at elbow and wrist joints in Marwar region of Rajasthan. *J. Indian Med. Assoc.* 63, 252–256.
- Krahl, H., Michaelis, U., Pieper, H.G., Quack, G., Montag, M., 1994. Stimulation of bone-growth through sports—a radiologic investigation of the upper extremities in professional tennis players. *Am. J. Sport Med.* 22, 751–757.
- Lanyon, L.E., 1980. The influence of function on the development of bone curvature. An experimental study on the rat tibia. *J. Zool.* 192, 457–466.
- Latimer, H.B., Lowrance, E.W., 1965. Bilateral asymmetry in weight and in length of human bones. *Anat. Rec.* 152, 217–224.
- Laubach, L.L., McConville, J.T., 1967. Notes on anthropometric technique: anthropometric measurements—right and left sides. *Am. J. Phys. Anthropol.* 26, 367–370.
- Lazenby, R.A., 1990. Continuing periosteal apposition. I: Documentation, hypotheses, and interpretation. *Am. J. Phys. Anthropol.* 82, 451–472.
- Lazenby, R.A., 2002. Skeletal biology, functional asymmetry and the origins of “handedness”. *J. Theor. Biol.* 218, 129–138.
- Lieberman, D.E., Devlin, M.J., Pearson, O.M., 2001. Articular area response to mechanical loading: effects of exercise, age, and skeletal location. *Am. J. Phys. Anthropol.* 116, 266–277.
- Lowrance, E.W., Latimer, H.B., 1957. Weights and linear measurements of 105 human skeletons from Asia. *Am. J. Anat.* 101, 445–459.
- Marcus, R., 1996. Endogenous and nutritional factors affecting bone. *Bone* 18, 11S–13S.
- Martin, R., 1957. *Lehrbuch der Anthropologie in Systematischer Darstellung mit Besonderer Berücksichtigung der Anthropologischen Methoden. Zweiter Band: Kraniologie Osteologie*, third edition. Verlag von Gustav Fischer, Stuttgart.
- Martin, W.L.B., Machado, A.H., Paixão, C.B., 2004. Footedness across the age span among Brazilian right- and left-handers. *Percept. Motor Skill* 99, 999–1006.
- Matsumara, H., 2001. Differentials of Yayoi immigration to Japan as derived from dental metrics. *Homo* 52, 135–156.
- Mays, S., 2002. Asymmetry in metacarpal cortical bone in a collection of British post-mediaeval human skeletons. *J. Archaeol. Sci.* 29, 435–441.
- McGrew, W.C., Marchant, L.F., 1997. On the other hand: current issues in and meta-analysis of the behavioral analysis of the behavioral laterality of hand function in nonhuman primates. *Yearb. Phys. Anthropol.* 40, 201–232.
- Münter, A.H., 1936. A study of the lengths of the long bones of the arms and legs in man, with special reference to Anglo-Saxon skeletons. *Biometrika* 28, 258–294.
- Palmer, A.R., Strobeck, C., 1986. Fluctuating asymmetry: measurement, analysis, patterns. *Annu. Rev. Ecol. Syst.* 17, 391–421.
- Parker, D.F., Round, J.M., Sacco, P., Jones, D.A., 1990. A cross-sectional survey of upper and lower-limb strength in boys and girls during childhood and adolescence. *Ann. Hum. Biol.* 17, 199–211.
- Perelle, I.B., Ehrman, L., 1994. An international study of human handedness: the data. *Behav. Genet.* 24, 217–227.
- Peters, M., 1988. Footedness: asymmetries in foot preference and skill and neuropsychological assessment of foot movement. *Psychol. Bull.* 103, 179–192.
- Peters, M., Durdin, B.M., 1979. Footedness of left- and right-handers. *Am. J. Psychol.* 92, 133–142.
- Plato, C.C., Fox, K.M., Garruto, R.M., 1984. Measures of lateral functional dominance: hand dominance. *Hum. Biol.* 56, 259–275.
- Plochocki, J.H., 2004. Bilateral variation in limb articular surface dimensions. *Am. J. Hum. Biol.* 16, 328–333.
- Porac, C., Coren, S., Duncan, P., 1980a. Life-span age trends in laterality. *J. Gerontol.* 35, 715–721.
- Porac, C., Coren, S., Steiger, J.H., Duncan, P., 1980b. Human laterality: a multidimensional approach. *Can. J. Psychol.* 34, 91–96.
- Porac, C., Coren, S., 1981. *Lateral Preferences and Human Behavior*. Springer-Verlag, New York.
- Porac, C., Lees, L., Buller, T., 1990. Switching hands: a place for left hand use in a right hand world. In: Coren, S. (Ed.), *Left-Handedness: Behavioral Implications and Anomalies*. Elsevier Science Publishers, New York, pp. 259–290.
- Porac, C., 1996. Hand and foot preference in young and other adults: a comment on Gabbard and Iteya. *Laterality* 1, 207–213.
- Rafferty, K.L., Ruff, C.B., 1994. Articular structure and function in *Hylobates*, *Colobus*, and *Papio*. *Am. J. Phys. Anthropol.* 94, 395–408.
- Raymond, M., Pontier, D., 2004. Is there geographical variation in human handedness? *Laterality* 9, 35–51.
- Rittweger, J., Rauch, F., 2004. What is new in neuro-musculoskeletal interactions? *J. Musculoskel. Neuron. Interact.* 4, 227–230.
- Round, J.M., Jones, D.A., Honour, J.W., Nevill, A.M., 1999. Hormonal factors in the development of differences in strength between boys and girls during adolescence: a longitudinal study. *Ann. Hum. Biol.* 26, 49–62.
- Roy, T.A., Ruff, C.B., Plato, C.C., 1994. Hand dominance and bilateral asymmetry in the structure of the second metacarpal. *Am. J. Phys. Anthropol.* 94, 203–211.
- Rutherford, S.L., 2000. From genotype to phenotype: buffering mechanisms and the storage of genetic information. *Bioessays* 22, 1095–1105.
- Ruff, C.B., 1987. Sexual dimorphism in human lower-limb bone-structure: relationship to subsistence strategy and sexual division of labor. *J. Hum. Evol.* 16, 391–416.
- Ruff, C.B., 2000. Biomechanical analyses of archaeological human skeletal samples. In: Katzenburg, M.A., Saunders, S.R. (Eds.), *Biological Anthropology of the Human Skeleton*. Alan R. Liss, New York, pp. 71–102.
- Ruff, C.B., 2003. Ontogenetic adaptation to bipedalism: age changes in femoral to humeral length and strength proportions in humans, with a comparison to baboons. *J. Hum. Evol.* 45, 317–349.
- Ruff, C.B., Jones, H.H., 1981. Bilateral asymmetry in cortical bone of the humerus and tibia—sex and age factors. *Hum. Biol.* 53, 69–86.
- Ruff, C.B., Walker, A., Trinkaus, E., 1994. Postcranial robusticity in *Homo*. III: Ontogeny. *Am. J. Phys. Anthropol.* 93, 35–54.
- Sakaue, K., 1998. Bilateral asymmetry of the humerus in Jōmon people and modern Japanese. *Anthropol. Sci.* 105, 231–246.
- Schaeffer, A.A., 1928. Spiral movements in man. *J. Morphol.* 45, 293–398.
- Schell, L.M., Johnston, F.E., Smith, D.R., Paolone, A.M., 1985. Directional asymmetry of body dimensions among white adolescents. *Am. J. Phys. Anthropol.* 67, 317–322.
- Schmitt, D., Churchill, S.E., Highlander, W.L., 2003. Experimental evidence concerning spear use in Neandertals and early modern humans. *J. Archaeol. Sci.* 30, 103–114.
- Schultz, A.H., 1926. Variations in man and their evolutionary significance. *Am. Nat.* 60, 297–323.
- Schultz, A.H., 1937. Proportions, variability and asymmetries of the long bones of the limbs and the clavicles in man and apes. *Hum. Biol.* 9, 281–328.
- Sládek, V., Berner, M., Sosna, D., Sailer, R. Human manipulative behavior in the central European late Neolithic and early Bronze Age: humeral bilateral asymmetry (submitted for publication).
- Smith, E.P., Boyd, J., Frank, G.R., Takahashi, H., Cohen, R.M., Specker, B., Williams, T.C., Lubahn, D.B., Korach, K.S., 1994. Estrogen resistance caused by a mutation in the estrogen-receptor gene in a man. *New Engl. J. Med.* 331, 1056–1061.
- Sokal, R.R., Rohlf, F.J., 1995. *Biometry*. W.H. Freeman and Company, New York.

- Steele, J., 2000. Handedness in past human populations: skeletal markers. *Lateralality* 5, 193–220.
- Steele, J., Mays, S., 1995. Handedness and directional asymmetry in the long bones of the human upper limb. *Int. J. Osteoarchaeol.* 5, 39–49.
- Stirland, A.J., 1993. Asymmetry and activity-related change in the male humerus. *Int. J. Osteoarchaeol.* 3, 105–113.
- Tanaka, H., 1999. Numerical analysis of the proximal humeral outline: bilateral shape differences. *Am. J. Hum. Biol.* 11, 343–357.
- Trinkaus, E., Churchill, S.E., Ruff, C.B., 1994. Postcranial robusticity in *Homo*. II: Humeral asymmetry and bone plasticity. *Am. J. Phys. Anthropol.* 93, 1–34.
- Trotter, M., Gleser, G.C., 1952. Estimation of stature from long bones of American whites and Negroes. *Am. J. Phys. Anthropol.* 52, 463–514.
- Vanderschueren, D., Vandenput, L., Boonen, S., Lindberg, M.K., Bouillon, R., Ohlsson, C., 2004. Androgens and bone. *Endocr. Rev.* 25, 289–425.
- Vettivel, S., Indrasingh, I., Chandi, G., Chandi, S.M., 1992. Variations in the inter-tubercular sulcus of the humerus related to handedness. *J. Anat.* 180, 321–326.
- Watson, R.C., 1973. Bone growth and physical activity in young males. In: Mazess, R.B. (Ed.), *International Conference on Bone Measurements*. DHEW Pub No NIH 75-683, Washington, D.C., pp. 380–385.
- White, T.D., 2000. *Human Osteology*. Academic Press, New York.
- Yücel, M., Gadiel, H.E., Scharf, H.-P., 1986. In vitro-Untersuchungen zur Tragfunktion der Membrana Interossea und Fibula im Hinblick auf die Gesamtbelastbarkeit des Unterschenkels. *Z. Orthop. DE* 124, 273–277.
- Zar, J.H., 1999. *Biostatistical Analysis*, fourth edition. Prentice Hall, New York.