

Patterns of clavicular bilateral asymmetry in relation to the humerus: variation among humans

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Abstract

Studies of directional asymmetry in the human upper limb have extensively examined bones of the arm, forearm, and hand, but have rarely considered the clavicle. Physiologically, the clavicle is an integrated element of the upper limb, transmitting loads to the axial skeleton and supporting the distal bones. However, clavicles develop in a manner that is unique among the bones of the upper limb. Previous studies have indicated that the clavicle has a right-biased asymmetry in diaphyseal breadth, as in humeri, radii, ulnae, and metacarpals, but unlike these other elements, a left-biased length asymmetry. Few studies have assessed how clavicular asymmetry relates to these other bones of the upper limb. Bilateral directional asymmetry of the clavicle is examined in relation to the humerus in a large, geographically diverse human sample, comparing lengths and diaphyseal breadths. Dimensions were converted into percentage directional (%DA) and absolute (%AA) asymmetries. Results indicate that humans have same-side %DA bias in the clavicles and humeri, and contralateral length %DA between these elements. Diaphyseal breadths in both clavicles and humeri are more asymmetric—both in direction and amount—than lengths. Differences in diaphyseal asymmetry are shown to relate to variation in physical activities among groups, but a relationship between activity and length asymmetry is not supported. This further supports previous research, which suggests different degrees of sensitivity to loading between diaphyseal breadths and maximum lengths of long bones. Differences in lateralized behavior and the potential effects of different bone development are examined as possible influences on the patterns observed among human groups.

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Introduction

Skeletal asymmetry is related to both exogenous (e.g., mechanical) and endogenous (e.g., genetic) factors (Auerbach and Ruff, 2006). Directional asymmetry best reflects variation among humans arising from lateralized behaviors (Stirland, 1993; Mays, 2002). (Directional asymmetry is defined as population-level deviations from bilateral symmetry that are unimodal and significantly different from symmetry.) This is especially found in structures related to the upper limb, as a consequence of its freedom from locomotor constraints (Trinkaus et al., 1994). The study of bilateral directional

asymmetry among human skeletal remains reveals both lateralized activity and the functional relationship of bones employed in those activities.

Previous studies of human bilateral directional asymmetry in the postcranial skeleton have focused on the limb bones (for a review of these studies, see Steele, 2000, and Auerbach and Ruff, 2006). Far fewer analyses have considered asymmetries in axial skeletal elements, namely the pelvic and shoulder girdles, and their relationship to appendicular bones. This is perhaps due to the more difficult interpretation of the biomechanical function of these elements (Harrington et al., 1993; Mays et al., 1999; Plochocki, 2002). This study addresses asymmetry in functionally related axial and appendicular bones by examining clavicular asymmetry in conjunction with asymmetry in the humerus.

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The relationship of humeral asymmetry to function and laterality has been one of the most studied aspects of directional bilateral asymmetry in the human skeleton (e.g., [Fresia et al., 1990](#); [Trinkaus et al., 1994](#); [Churchill and Formicola, 1997](#); [Steele, 2000](#); [Lazenby, 2002](#); [Auerbach and Ruff, 2006](#)), as have the connections between behavior and humeral morphology (e.g., [Stock and Pfeiffer, 2001](#); [Ruff, 2003](#); [Weiss, 2003](#); [Ruff, 2006](#)). Comparatively, the clavicle has been understudied ([Voisin, 2006](#)). Even fewer studies have examined the mechanical correspondence of the humerus and clavicle together. [Stock and Pfeiffer \(2001\)](#) demonstrated that, in comparisons among samples, strength (as measured using cross-sectional properties) in the clavicles followed the same patterns as those in humeri, reinforcing the functional relationship between these bones argued by clinical researchers ([Ljunggren, 1979](#)). However, [Stock and Pfeiffer \(2001\)](#) did not directly compare the strength of clavicles and humeri within individuals.

Despite functional relationships and developmental differences between the clavicle and humerus, none of the studies of clavicular bilateral asymmetry have examined both bones together.¹ Previous studies considering clavicles alone reported that length is asymmetrically biased to the left, while diaphyseal breadths are biased to the right ([Parsons, 1916](#); [Schultz, 1937](#); [Ray, 1959](#); [Huggare and Houghton, 1994](#); [Mays et al., 1999](#); [Voisin, 2001](#)). In contrast, mean humeral directional asymmetries are all right-biased among humans. Only [Parsons \(1916\)](#), [Mays et al. \(1999\)](#), and [Voisin \(2001\)](#) have offered explanations for resulting patterns of bilateral asymmetry among clavicles, invoking mechanical effects as primary factors. Despite the thoroughness of these authors, the relationship of lateralized behavior to aspects of clavicular directional asymmetries remains unresolved. It is assumed that, as the individuals studied are from groups that are right-side dominant in the upper limb, these clavicular patterns relate to the same factors that would be involved in the asymmetry of the upper-limb bones (i.e., humeri, radii, ulnae, and metacarpals) ([Roy et al., 1994](#); [Auerbach and Ruff, 2006](#)).

However, the factors implicated in upper-limb asymmetry are intertwined and complex; within the same appendicular bone, length asymmetries may be driven more by factors *other* than mechanical loading, while diaphyseal breadth asymmetry may be largely more sensitive to lateralized behavior ([Auerbach and Ruff, 2006](#)). Indeed, diaphyseal breadth has been demonstrated to change in response to mechanical loading throughout life, even after the cessation of primary longitudinal growth ([Ruff et al., 1994](#); [Kontulainen et al., 2001](#); [Bass et al., 2002](#)). Taking this difference into account, the interpretation of previously reported patterns of clavicular asymmetry solicits reconsideration.

This study investigates patterns of asymmetry in the clavicle in concert with patterns of asymmetry in the humerus. Assuming that the clavicle operates predominantly as

a functional element of the upper-limb unit, the patterns of clavicular asymmetry would be predicted to follow those of the appendicular bones, particularly the humerus (see [Auerbach and Ruff, 2006](#)). This should especially be the case for diaphyseal breadth asymmetry, but the predicted correspondence of asymmetry in clavicular diaphyseal breadth to humeral diaphyseal breadth is uncertain to some extent because of the dissimilar mechanical loading on each of the two bones. Given the developmental differences between the clavicle and the humerus, and evidence for some mechanical independence in longitudinal growth, length asymmetries of these two bones are expected to show less correspondence than those of diaphyseal breadths.

Function and development of the clavicle

The functional anatomy of clavicles is multifaceted. As the only bony connection between the upper limb and axial skeleton, human clavicles are thought to function as struts that transfer upper-limb forces to the thorax, while helping to stabilize the glenohumeral joint by limiting motion of the scapula and anchoring the joint to the ribs and sternum through the sternoclavicular joint ([Ljunggren, 1979](#); [Harrington et al., 1993](#)). Thus, the clavicles could be modeled as responding to compressive (axial) and bending loads, resulting from weight and compression exerted by the upper limb on the glenoid. Clavicles are also attachment sites for half a dozen muscles in humans (pectoralis major, deltoid, sternocleidomastoid, sternohyoid, trapezius, and subclavius) and four force-transmitting and supporting ligaments. Together, these subject the bones to a variety of combined loads, including torsion and shear stresses ([Harrington et al., 1993](#); [Renfree and Wright, 2003](#); [Sellards, 2004](#)), and they may be responsible for the variation in the bone's double, or S-shaped, curvature ([Ljunggren, 1979](#)). Variation in the cross-sectional shape along the bone reflects this variety of mechanical loadings, supporting the multiple functional capacities experienced by clavicles. (For a more complete discussion of the anatomy and mechanics of clavicles, see [Inman and Saunders, 1946](#), [Harrington et al., 1993](#), and [Mays et al., 1999](#)).

Like their function, development of the clavicles is unique relative to that of other postcranial bones. Clavicles are the first bones to ossify in the upper-limb complex and are the only postcranial bones to develop, in part, from membranous (i.e., "dermal" cell layer) tissues, as opposed to chondral models ([Wirth and Rockwood, 1996](#); [Scheuer and Black, 2000](#)). Much of the clavicle's adult morphology is attained early in fetal growth, and its double-curved shape is achieved well before birth, leaving further growth to occur primarily at the ends, especially the medial epiphysis ([Corrigan, 1960](#)). Although much development occurs in utero, the clavicles are among the last bones to reach complete ossification of the epiphyses ([Webb and Suchey, 1985](#)). Thus, clavicles have a long period in which they may be sensitive to lateralized behavior, potentially by many more years after the cessation of primary growth in the humeri and radii.

¹ Although [Schultz \(1937\)](#) did examine claviculohumeral indices and found higher indices for the left side, it is not known if the variance in clavicular or humeral length contributed more to this difference between sides.

Methods

Sample and measurements

Osteometrics were taken on 509 adult humans (259 males, 250 females) dating throughout the Holocene. This sample, listed in Table 1, was further divided into “population” groups (generally defined by geographic and temporal associations), all of which were pre-industrial, except for the early twentieth century individuals from St. Louis, Missouri (the Terry Collection). Most of these pre-industrial samples represent indigenous populations from North America, with the exception of predynastic and dynastic Egyptians. These groups were also categorized into four broad subsistence categories as a proxy for general expected levels of activity: hunter-gatherers, horticulturalists, agriculturalists, and industrialists. The data used here are not the same as those employed in Auerbach and Ruff’s (2006) study of bilateral postcranial asymmetry (although some samples are shared in common), in which the Goldman data set, which lacks clavicular data, was employed.

Measurements were taken bilaterally by both authors, and these are listed in Table 2. Maximum lengths of the clavicle (CML) and humerus (HML) were taken in all instances using standard osteometric boards. Diaphyseal midshafts (50%) were determined from these maximum lengths for both bones. Clavicular diaphyseal midshaft diameters were measured perpendicular to the shaft of the bone (not the axis along

which the CML was measured) in the inferosuperior (IS) and anteroposterior (AP) orientations, using digital sliding calipers. These measurements were then averaged to yield the average clavicular midshaft diameter (CDB). Humeral midshaft diameters were measured in the mediolateral (ML) and AP directions, which were then averaged to obtain the average humeral midshaft diameter (HDB).

Measurement errors (Table 2) were calculated using the method described by White (2000). Intraobserver errors were obtained by BMA and MHR by taking three trials of measurements on subsets of their respective samples (Table 2). The measurement errors are reported in Table 2 using the total combined sample measured by both authors. A subset of the Egyptian sample was measured by both BMA and MHR to assess interobserver errors and thus comparability of results from their respective samples. In general, all of the measurements were assessed to be highly reliable, and all measurement errors were below 2.0%. Thus, the reported asymmetries were interpreted to reflect little biasing resulting from measurement error. Furthermore, the interobserver differences were minimal, assuring comparability of results.

Sex and age determination for the human archaeological specimens were performed by BMA and MHR using methods described previously for use by BMA in the Goldman data set (Auerbach and Ruff, 2004). Sexing relied primarily on pelvic traits, with additional use of cranial characteristics when the pelvis was ambiguous. Closure of epiphyseal sutures—especially

Table 1
Sample composition for this study

Population group (number of groups/sites)	Subsistence group	<i>n</i> (males/females)	Source(s) ¹ (observer) ²
Predynastic and dynastic Egyptians (6) ³	Agriculturalist	26 (13/13)	HPMAE; NMNH (MHR)
Terry Collection “whites” (1) ⁴	Industrialist	50 (25/25)	NMNH (MHR)
Terry Collection “blacks” (1) ⁴	Industrialist	50 (25/25)	NMNH (MHR)
Alutiq, Aleutian Islands (several) ⁵	Hunter-gatherer	43 (23/20)	NMNH (BMA)
Ipiutak, Point Hope, Alaska (1)	Hunter-gatherer	28 (15/13)	AMNH (BMA)
Tigara, Point Hope, Alaska (1)	Hunter-gatherer	33 (15/18)	AMNH (BMA)
Huari, Ancon, Peru (1)	Agriculturalist	29 (19/10)	FMNH (BMA)
Arikara, South Dakota (3)	Horticulturalist ⁶	35 (18/17)	NMNH (BMA)
Mississippian burials, Dickson Site, Illinois (1)	Agriculturalist	36 (18/18)	ISM (BMA)
Archaic burials, Eva Site, Tennessee (2)	Hunter-gatherer	23 (14/9)	MM (BMA)
Pueblo IV burials, Hawikuh, New Mexico (1)	Agriculturalist	31 (12/19)	NMNH (BMA)
Archaic burials, Indian Knoll, Kentucky (1)	Hunter-gatherer	49 (25/24)	WOAC (BMA)
Fort Ancient burials, Madisonville site, Ohio (1)	Agriculturalist	31 (15/16)	HPMAE (BMA)
Mississippian burials, Toqua site, Tennessee (1)	Agriculturalist	21 (9/12)	MM (BMA)
Cliff Dwellers, Glen Canyon, Utah (1)	Agriculturalist	24 (13/11)	AMNH (BMA)
Total sample		509 (259/250)	

¹ AMNH, American Museum of Natural History, New York City, New York; CMNH, Cleveland Museum of Natural History, Cleveland, Ohio; FMNH, Field Museum of Natural History, Chicago, Illinois; HPMAE, Harvard Peabody Museum of Anthropology and Ethnology, Cambridge, Massachusetts; ISM, Illinois State Museum, Springfield, Illinois; MM, Frank H. McClung Museum, Knoxville, Tennessee; NMNH, National Museum of Natural History (Smithsonian Institution), Washington, D.C.; WOAC, Webb Osteology and Archeology Collection, Lexington, Kentucky.

² Egyptians housed at the HPMAE were measured by both MHR and BMA to test interobserver error, though the measures employed in this study are MHR’s to ensure consistency of results for all Egyptians.

³ Egyptians represent samples from Giza, Lisht, Keneh, Kharga, Mesaeed, and Sheikh Fanag. Although these samples likely vary considerably due to their geographic and temporal ranges, the variation within the Egyptian sample is less than the variation observed among other population samples for the four measurements considered in this study.

⁴ These samples consist of a cadaveric sample amassed in St. Louis, Missouri, during the early and middle twentieth century.

⁵ As noted previously (Auerbach and Ruff, 2006), the Aleutian sample consists of individuals acquired from throughout the Aleutian Island chain, but are assumed to be genetically closely related and temporally similar enough to justify consolidating them into one group.

⁶ The Arikara are categorized as practicing a village hunter/horticultural subsistence (Wedel, 1983), but are listed here as “horticulturalists” for simplicity.

Table 2
Intraobserver and interobserver measurement errors for osteometrics included in this study

(A) Intraobserver measurement errors ($n = 24$)			
Measurement	Percentage of error		
	Left	Right	Average
Clavicular maximum length (CML)	0.20%	0.10%	0.15%
Clavicular average 50% diaphyseal diameter (CDB)	0.77	0.67	0.72
Humeral maximum length (HML)	0.40	0.04	0.23
Humeral average 50% diaphyseal diameter (HDB)	0.60	1.03	0.81
(B) Interobserver measurement errors ($n = 20$)			
Measurement	Percentage of error		
	Left	Right	Average
Clavicular maximum length (CML)	0.31%	0.22%	0.26%
Clavicular average 50% diaphyseal diameter (CDB)	1.78	1.91	1.85
Humeral maximum length (HML)	0.07	0.12	0.09
Humeral average 50% diaphyseal diameter (HDB)	1.15	1.35	1.24

the medial clavicle—was the primary determinant of adult status. Individuals deemed to exhibit pathologies (especially osteoarthritis) or healed trauma to humeri and/or clavicles were excluded from the analysis, as were humans whose sex was indeterminate.

Statistical methods

As described recently by Auerbach and Ruff (2006), the convention for examining directional asymmetry has been to convert the raw asymmetries into percent asymmetries to allow for direct comparison of dimensions of significantly different sizes. Two percentages were calculated, percent directional asymmetry (%DA) and percent absolute asymmetry (%AA):

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

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

Percent directional asymmetry describes the amount of directional asymmetry present in a given dimension, with positive values indicating right-biased asymmetries and negative values indicating left-biased asymmetries. Percent absolute asymmetry indicates the total amount of asymmetry present in any given dimension, standardized by the size of that dimension. The examination of %DA reveals the predominant *directional bias* of asymmetry and the magnitude of that bias, whereas the examination of %AA shows how much directional asymmetry occurs in a given dimension, regardless of directional bias.

Auerbach and Ruff (2006) outlined the use of and preference for nonparametric statistics to analyze percentage data, which again were employed in this study. Wilcoxon signed-ranks tests were performed on the total, sex-pooled sample to

determine significance of directional asymmetries. Additionally, a chi-square test for equivalency was employed to assess the number of individuals exhibiting $\geq 0.5\%$ bilateral asymmetry² for the four dimensions examined, both for the pooled-population sample and for each sex; significant non-equivalence of directional asymmetry indicated a population-wide lateralization in a dimension. A cutoff of $\geq 0.5\%$ DA was chosen to avoid including slight asymmetries that are not biologically significant or are the result of fluctuating asymmetry (Auerbach and Ruff, 2006). Sex and group differences among humans for %DA and %AA were examined using Mann–Whitney *U*-tests. Kruskal–Wallis tests were employed in exploring the differences among three or more human groups. The Nemenyi test (Zar, 1996), a nonparametric analog of the Tukey test, was used for post-hoc comparisons of significant Kruskal–Wallis results to determine which groups significantly differed from each other.

Comparisons of the patterns of asymmetry within and between the clavicles and humeri were examined using two methods: correlations of residuals and a test developed to assess “crossed symmetry” (Auerbach and Ruff, 2006). In the first method, natural-log-transformed right-side values for each dimension (lengths or breadths) were regressed against the natural-log-transformed left-side values, using ordinary least squares. Residuals from these regressions were subjected to Pearson correlation analyses to determine if directional asymmetries were significantly correlated among dimensions. In the second method, a chi-square test devised by Auerbach and Ruff (2006) to assess “crossed symmetry” (contralateral patterns of asymmetry between two dimensions [Schaeffer, 1928; Plochocki, 2004]) was utilized to examine the presence and significance of opposite-side asymmetries between two dimensions. The test for crossed symmetry involves converting directional asymmetry percentages into dummy variables for each individual, and then determining if the instances of same-side directional asymmetry significantly differ from instances of opposite-side asymmetry for any given pair of dimensions. One goal in using this chi-square test was to determine if the previously reported opposite directional length asymmetries for clavicles (left-biased) and humeri (right-biased) were present within individuals. As in its previous use by Auerbach and Ruff (2006), various definitions for symmetry ($>0\%$ DA, $\geq 0.5\%$ DA, $\geq 1\%$ DA) in coding dummy variables produced the same results; a criterion of $\geq 0.5\%$ DA was used for the results reported.

Results

Patterns of asymmetry in the total sample

Table 3 presents median and mean %DAs and %AAs for the total sample. Sex-specific box plots of %DAs and %AAs for the

² As explored in Auerbach and Ruff (2006), a cutoff of $\pm 0.5\%$ directional asymmetry was chosen after testing more relaxed ($\pm 0\%$) and strict ($\pm 1\%$) definitions of asymmetry. Results of these alternatives were comparable to the use of $\pm 0.5\%$ as a criterion for asymmetry, and chi-square results were identical.

Table 3
Median and mean %DA and %AA for total pooled sample and by sex

Measure	Median %DA (mean %DA)			Median %AA (mean %AA)		
	Total	Males	Females	Total	Males	Females
CML	-1.13* (-1.11)	-1.19* (-1.06)	-1.12* (-0.17)	1.99 (2.31)	1.94 (2.22)	2.08 (2.41)
CDB	2.41* (2.66)	2.80* (2.86)	2.22* (2.44)	3.76 (5.14)	4.18 (5.46)	3.50 (4.81)
HML	1.01* (1.02)	0.71* (0.73)	1.33* (1.32)	1.31 (1.37)	0.92 (1.20)	1.38 (1.55)
HDB	3.49* (3.64)	3.95* (4.08)	3.10* (3.19)	3.87 (4.55)	4.41 (5.06)	3.44 (4.03)

*Right-left asymmetry is significant at $p < 0.05$ using a Wilcoxon signed-ranks test. **Bold** indicates significant sexual dimorphism for a given dimension. See Table 2 for measurement abbreviations.

four measurements are presented in Fig. 1. All of the measurements exhibit significant directional asymmetry. Asymmetries in clavicular length are significantly *left*-biased (median 1.13%), while the other three measurements are significantly right-biased (CDB median, 2.41%; HML median, 1.01%; HDB median, 3.49%). These patterns of asymmetry are consistent when only the percent of individuals with directional

asymmetries of $\pm 0.5\%$ are examined (Table 4). Generally, lateral biases over 0.5% in asymmetry occur in at least 60% of the sample, and are significant.

Results of a Kruskal–Wallis test with a Nemenyi post-hoc test reveal that CDB and HDB have greater directional-asymmetry (%DA) biases and absolute amounts of asymmetry (%AA) than CML and HML ($p < 0.01$), which exhibit less than half the percentage of asymmetry observed in diaphyseal breadths (Table 3). This is in concordance with trends previously reported for humans that indicate higher amounts of diaphyseal asymmetry throughout the skeleton when compared to other bone dimensions (Auerbach and Ruff, 2006). In addition, %DAs for HDB are significantly greater than those for CDB ($p < 0.01$), but not for %AAs ($p = 0.13$). CML absolute asymmetry is significantly greater than HML ($p < 0.01$).

Significant sexual differences in %DA and %AA are reported as bolded numbers in Tables 3 and 4. Interestingly, humans do not exhibit significant sexual dimorphism in the directional asymmetry of clavicular measures, although males have more overall asymmetry (%AA) than females in CDB. In contrast, human humeri are sexually dimorphic in both %DA and %AA, with females exhibiting more asymmetry in the maximum length and males displaying more in the diaphyseal breadths ($p < 0.01$). This is further reflected in the percent of the sample exhibiting asymmetries greater than 0.5%: significantly more females are right-biased in HML than males (Table 4). In all dimensions, both males and females share the same side bias in %DA.

Correlations of asymmetries within and between clavicles and humeri

Although the results above provide summaries of the degrees and types of asymmetries present in the clavicles and humeri, they do not explain the relationships of the dimensional asymmetries to each other. Table 5 gives the correlations between right- and left-side regression residuals for the total sample and by sex. Most of these correlations have low Pearson r -values, possibly in part due to “noise” resulting from measurement errors, fluctuating asymmetry, and other factors not considered (such as the effect of muscles common to both bones) (Palmer and Strobeck, 1986; Rittweger and Rauch, 2004). Among the overall and the male portion of the sample, there are significant positive correlations between the diaphyseal asymmetries of clavicles and humeri. Females, but not males, also show a significant inverse asymmetry in CML and CDB.

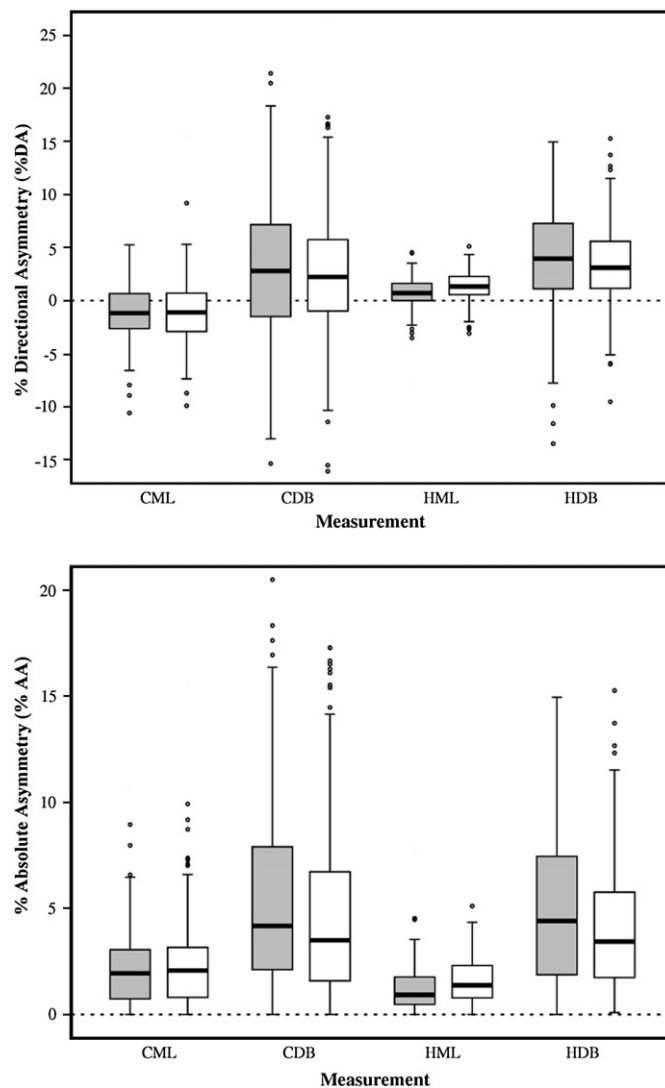


Fig. 1. Box plots of percentage directional asymmetries (%DA) and percentage absolute asymmetries (%AA) of the four dimensions considered in the study. See Table 2 for abbreviations. Shaded boxes: males; open boxes: females.

Table 4
Percent of individuals with bilateral asymmetric bias

Measure	Total sample (<i>n</i> = 509)			Males (<i>n</i> = 259)			Females (<i>n</i> = 250)		
	+Left	<±0.5%	+Right	+Left	<±0.5%	+Right	+Left	<±0.5%	+Right
CML	62.5*	10.0	27.5	60.6*	10.8	28.6	64.4*	9.2	26.4
CDB	28.7	7.6	63.7*	30.5	7.7	61.8*	26.8	7.6	65.6*
HML	11.4	21.8	66.8*	15.1	27.4	57.5*	7.6	16.0	76.4*
HDB	15.3	5.3	79.4*	13.9	5.4	80.7*	16.8	5.2	78.0*

*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).

These trends are further explored with the test for crossed symmetry, the results of which are reported in Table 6. The chi-square test for crossed symmetry is used to determine if the directions of asymmetries are the same (i.e., ipsilateral) for the four dimensions considered within individuals. Humeral and clavicular diaphyseal breadths exhibit same-side asymmetries, as do humeral length and clavicular diaphyseal breadth ($p < 0.01$). Contralateral symmetry is characteristic of humeral and clavicular lengths, and humeral diaphyseal breadth and clavicular length.

Asymmetry among human groups

The overall trends reported for the total sample may mask the variation in patterns of asymmetries among geographically diverse groups engaging in substantially different activities.

Table 5
Correlations of asymmetry among clavicular and humeral measurements, calculated from regression residuals

CDB	HML	HDB	
-0.072 (O)	-0.032 (O)	-0.003 (O)	CML
-0.006 (M)	-0.026 (M)	-0.052 (M)	
-0.172 (F)	-0.089 (F)	0.063 (F)	
	0.058 (O)	0.199 (O)	CBD
	0.055 (M)	0.272 (M)	
	0.028 (F)	0.108 (F)	
		0.054 (O)	HML
		0.112 (M)	
		-0.010 (F)	

Gray boxes indicates correlations of comparable dimensions between the two elements. Bolded correlations are significant ($p < 0.05$). Abbreviations are follows: O = total sample; M = male; F = female; see Table 2 for abbreviations.

The results presented in Table 3 are re-examined by population group (as defined in Table 1) in Table 7. Figure 2 presents box plots for these results, with boxes shaded to correspond with generalizations of subsistence patterns, which are proxies for activity differences among groups. As some measurements exhibit sexual dimorphism in the total sample, all analyses at the population-group level are reported for males and females separately.

Patterns of directional asymmetry from Fig. 2, as well as the medians reported in Table 7, are generally the same as those reported for the total sample. In comparisons among subsistence groups using Kruskal–Wallis tests with Nemenyi post-hoc analyses, it is evident that, in both sexes, all pre-industrial subsistence groups have greater amounts of diaphyseal breadth asymmetry for clavicles and humeri ($p < 0.01$), as well as greater asymmetry in humeral maximum length ($p < 0.01$), than the industrial Terry samples. Comparisons between broadly defined hunter-gatherers and cultivators (the horticulturalist Arikara and agriculturalist groups) indicate greater asymmetry in CDB among male hunter-gatherers, but not in HDB. Conversely, female comparisons indicate that HDB asymmetry is significantly greater ($p < 0.01$) among hunter-gatherer females, while CDB does not significantly differ between hunter-gatherer and cultivator groups. No significant difference in maximum lengths occurs between these pre-industrial groups. Some of the median diaphyseal breadth directional asymmetries within groups are as great as approximately 10% among the males and females, whereas length asymmetries are never greater than 3% (%DA or %AA) for any group.

The box plots in Fig. 2, however, show that there is much variation within subsistence groups. For example, both male and female hunter-gatherers from the Eva and Indian Knoll sites present significantly greater right-biased asymmetry in

Table 6
Test for common directionality in asymmetry among measures within individuals¹

	HML	HDB
CDB	=	=
CML	X	X

¹ Assessed using test for crossed symmetry (Auerbach and Ruff, 2006), with results tested with a chi-square test for equivalency. Significance was determined at $p < 0.05$; =, same-side asymmetry; X, contralateral asymmetry. See Table 2 for abbreviations.

Table 7
Median (bolded text) and mean (normal text) asymmetries for “population” groups

[Group #] Population group (<i>n</i>)	%DA				%AA			
(A) Males	CML ¹	CDB	HML	HDB	CML	CDB	HML	HDB
[1] Aleutian (23)	−2.05	3.53	1.22	2.71	2.15	5.36	1.57	4.64
	−1.98	3.34	1.12	2.83	2.57	5.84	1.52	4.53
[2] Ipiutaq (15)	−0.74	0.29	1.23	2.93	1.50	3.66	1.72	3.58
	−1.01	1.39	1.03	2.01	2.35	5.04	1.75	3.81
[3] Tigara (15)	−1.61	0.31	1.75	2.38	1.70	2.36	1.76	3.06
	−2.05	0.88	1.60	1.93	2.81	3.77	1.84	2.92
[4] Indian Knoll (25)	−2.11	8.71	0.86	9.32	2.25	9.78	1.20	9.32
	−1.88	8.05	0.63	9.34	2.60	9.98	1.13	9.34
[5] Eva (14)	−1.21	3.91	0.75	7.97	2.13	4.66	1.01	7.97
	−1.02	4.11	0.79	6.25	2.37	5.42	1.25	6.95
[6] Arikara (18)	0.97	7.32	1.76	6.65	1.57	7.56	1.76	7.51
	1.46	6.79	1.95	5.86	1.96	8.42	1.95	6.69
[7] Ancón (19)	−0.98	2.94	0.83	6.46	1.58	3.84	0.83	6.80
	−0.87	2.19	1.03	5.19	1.71	3.96	1.20	6.20
[8] Dickson Mounds (18)	−2.30	0.62	0.32	3.98	2.30	5.95	0.32	4.69
	−2.22	1.72	0.63	3.84	2.55	6.50	0.68	5.38
[9] Hawikuh (12)	−2.03	0.69	0.90	3.16	2.77	1.89	1.02	3.16
	−1.56	2.55	0.73	2.73	2.70	5.30	1.31	3.39
[10] Madisonville (15)	−0.32	3.44	0.49	2.66	0.96	4.63	1.31	2.77
	−0.10	3.23	0.67	2.69	1.67	5.20	1.23	3.66
[11] Toqua (9)	−0.93	2.82	0.33	5.45	1.30	3.01	0.62	5.45
	−0.74	2.12	0.50	5.43	1.26	3.96	0.78	5.47
[12] Utah Cliff Dwellers (13)	−2.01	3.60	0.32	8.22	2.52	4.18	0.49	8.22
	−0.97	3.04	0.30	7.78	2.38	5.47	0.84	7.88
[13] Egyptians (13)	0.00	−0.42	1.00	2.53	1.45	2.67	1.00	3.98
	−1.01	−1.46	1.03	1.11	1.91	4.07	1.17	3.83
[14] Terry “whites” (25)	−1.29	0.43	0.00	1.69	1.94	2.74	0.58	2.19
	−1.02	0.31	0.09	2.97	2.05	3.40	0.75	3.36
[15] Terry “blacks” (25)	−0.65	2.11	0.00	1.09	1.94	3.14	0.58	1.88
	−0.49	1.99	−0.41	1.09	2.02	3.66	0.81	2.36
Mean of medians	−1.15	2.69	0.78	4.48	1.87	4.36	1.05	5.01
Median of medians	−1.21	2.82	0.83	3.16	1.94	3.84	1.01	4.64
Range of medians	3.27	9.12	1.76	8.24	1.82	7.89	1.44	7.44
[Group #] Population group (<i>n</i>)	%DA				%AA			
(B) Females	CML ¹	CDB	HML	HDB	CML	CDB	HML	HDB
[1] Aleutian (20)	−1.96	3.57	1.90	2.86	2.12	4.19	1.93	2.86
	−1.68	3.87	1.54	3.07	2.12	5.05	1.77	3.38
[2] Ipiutaq (13)	−2.15	3.98	1.69	2.93	2.15	4.62	1.69	2.93
	−1.91	4.15	1.49	3.61	2.44	5.77	1.60	3.71
[3] Tigara (18)	−2.53	−1.18	2.45	2.61	2.57	2.64	2.45	3.16
	−2.12	−1.55	2.40	1.91	2.89	3.64	2.40	2.93
[4] Indian Knoll (24)	−1.76	4.04	1.05	7.08	2.12	4.29	1.23	7.08
	−1.37	3.80	0.78	6.57	2.10	4.60	1.38	7.00
[5] Eva (9)	−1.46	0.35	0.33	9.22	1.96	1.88	0.89	9.22
	−1.00	0.26	0.43	7.85	2.35	2.80	1.01	9.17
[6] Arikara (17)	−0.73	1.87	2.56	3.64	2.57	3.94	2.56	3.64
	−0.94	2.09	2.66	3.32	2.77	4.67	2.66	3.83
[7] Ancón (10)	−1.33	−0.45	1.59	2.27	2.09	3.42	1.59	3.16
	−1.65	0.67	1.62	1.98	2.25	3.52	1.62	4.25
[8] Dickson Mounds (18)	−0.68	2.96	0.97	4.29	1.63	3.80	0.97	4.29
	0.91	1.65	0.99	4.48	2.77	7.05	1.15	4.82
[9] Hawikuh (19)	−1.45	0.51	1.54	3.25	2.75	2.84	1.54	3.25
	−1.96	1.00	1.67	3.24	3.37	4.41	1.71	4.04
[10] Madisonville (16)	−2.08	4.45	1.77	1.87	2.08	5.60	2.00	2.23
	−1.71	2.77	1.58	1.79	2.35	6.04	1.83	2.73
[11] Toqua (12)	−1.28	2.11	1.18	3.85	1.50	2.74	1.18	4.19
	−1.33	3.72	1.40	3.67	1.83	4.21	1.51	4.36

(continued on next page)

Table 7 (continued)

[Group #] Population group (n)	%DA				%AA			
	CML ¹	CDB	HML	HDB	CML	CDB	HML	HDB
(B) Females								
[12] Utah Cliff Dwellers (11)	-0.70	4.90	0.69	1.45	0.76	4.90	0.69	1.72
	-1.14	5.11	0.92	1.14	2.08	5.45	0.92	2.93
[13] Egyptians (13)	-0.65	0.14	1.33	-0.27	2.12	2.61	1.40	2.13
	-1.18	0.77	0.94	0.49	2.70	3.71	1.61	2.51
[14] Terry “whites” (25)	-1.39	3.08	0.97	3.47	1.50	3.56	0.98	3.47
	-1.19	5.04	0.98	3.03	2.07	6.66	1.15	3.41
[15] Terry “blacks” (25)	0.00	2.03	0.33	1.69	2.20	2.41	0.91	2.42
	-0.03	1.68	0.55	1.61	2.05	3.14	1.00	2.85
Mean of medians	-1.34	2.16	1.36	3.35	2.01	3.56	1.47	3.72
Median of medians	-1.39	2.11	1.33	2.93	2.12	3.56	1.40	3.16
Range of medians	2.53	6.08	2.24	9.49	1.99	3.72	1.87	7.50

¹ See Table 2 for abbreviations.

humeral diaphyseal breadth than the three Alaskan hunter-gatherer groups. Yet, these two southeastern United States groups have among the lowest directional-asymmetry values for humeral maximum length. Note that Indian Knoll site males also exhibit more %DA in clavicular diaphyseal breadth than the other hunter-gatherers. It is also noteworthy that the Arikara—namely the males—have greater asymmetry in their diaphyseal breadths and HML than most agriculturalists.

Sexual dimorphism within groups is reported for %AAs in Table 8. Positive values indicate male-biased sexual dimorphism, and negative values reflect higher asymmetry values among females. Males in nearly all cases have greater humeral diaphyseal breadth asymmetries compared to females, while females have greater HML asymmetry in all but two instances. Contrastingly, a third of the groups' females have greater CDB asymmetries than their respective males (6 of 15 comparisons), as well as greater amounts in over half of the CML asymmetries (8 of 15 comparisons), though not in the same groups. Males from Indian Knoll, Eva, and the Arikara sites have considerably greater amounts of clavicular diaphyseal breadth asymmetry relative to females than other groups considered. It is curious that Eva females, however, have more humeral diaphyseal breadth asymmetry. Not all hunter-gatherers exhibit greater amounts of sexual dimorphism in asymmetry; the three Arctic maritime groups in fact have considerably lower amounts of %AA asymmetry differences between the sexes than the temperate hunter-gatherers and even some agriculturalists (Table 8). Furthermore, Egyptians and the modern United States samples exhibit low amounts of sexual dimorphism in all of the dimensions, especially when compared with many of the nonindustrial groups.

Discussion

The patterns of clavicular asymmetry reported in this study are similar to those found in previous studies (Parsons, 1916; Schultz, 1937; Ray, 1959; Huggare and Houghton, 1994; Mays et al., 1999; Voisin, 2001), as are the patterns of humeral asymmetry (for a review, see Auerbach and Ruff, 2006). The

total sample exhibits a left-biased clavicular length asymmetry and right-biased clavicular diaphyseal asymmetry (in the total pooled sample and most of the subgroups). As noted, the humeri are right-biased in asymmetry for both length and average mid-diaphyseal diameters. However, this study adds a unique set of results to these former analyses, in that this is the first time patterns of asymmetry in the clavicle have been compared with another bone of the upper-limb complex, while also using a diverse sample.

Following trends noted elsewhere in the human appendicular skeleton (Trinkaus et al., 1994; Auerbach and Ruff, 2006), the diaphyseal breadths of clavicles have significantly greater magnitudes of asymmetry for both %DA and %AA than found for clavicular lengths. An ipsilateral asymmetry pattern for the clavicular and humeral diaphyseal breadths is demonstrated with the test for crossed symmetry and significant (albeit low) correlations, and a majority of individuals used in the total sample have contralateral asymmetry for clavicular and humeral maximum lengths. As diaphyseal breadths are most likely more responsive to loading than lengths (Trinkaus et al., 1994; Biewener and Bertram, 1994; Ruff, 2003; Auerbach and Ruff, 2006), closer concordance of diaphyseal breadth asymmetries would be expected in elements experiencing similar magnitudes of loading, a result supported by the test for crossed symmetry. The presence of these similar trends between the clavicles and humeri supports the assertion that the clavicle acts as a functional component of the upper limb (Mays et al., 1999), despite its separate developmental origin and different loading pattern when compared to the humerus and more distal elements (Renfree and Wright, 2003).

Two crucial insights are provided by this study: the existence of these groupwide patterns of asymmetry within individuals, and variation in the magnitude of these patterns of asymmetry among human groups. Although the aforementioned research has shown that there are general patterns for contralateral directional asymmetry in length between the clavicle and the humerus, this study shows that this is generally universal among a diverse sample of humans, with a few, notable exceptions (see Fig. 2). The ipsilateral pattern of diaphyseal asymmetry between the clavicle and humerus

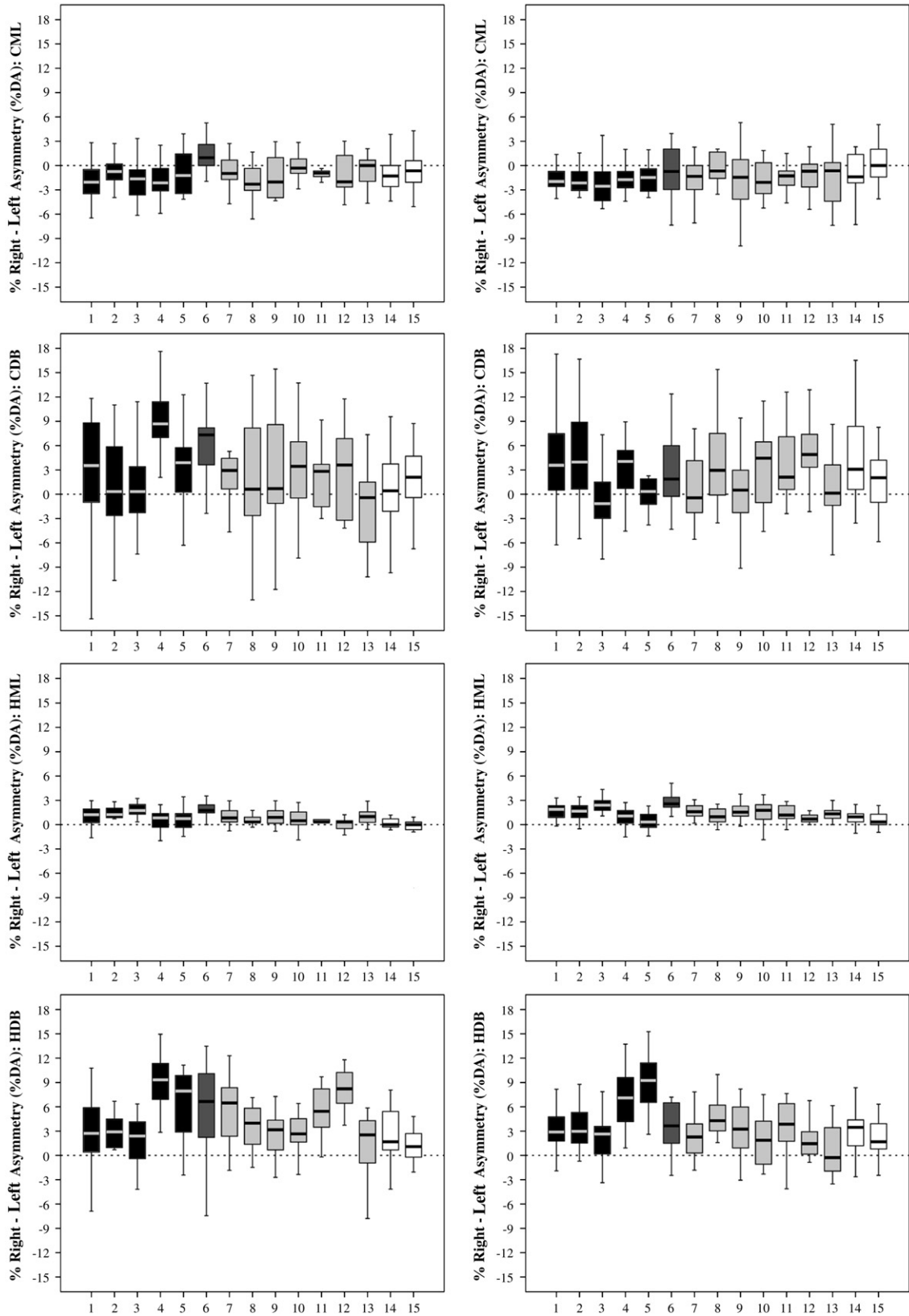


Fig. 2. Box plots of percentage directional asymmetries (%DA) for males and for females in the 15 “population” groups (see Table 2 for abbreviations for dimensions). Table 7 gives median and mean asymmetries, a key to coded group numbers, as well as sample sizes for groups compared. Box shading corresponds with subsistence-mode classifications: black, hunter-gatherer; dark gray, horticulturalist; light gray, agriculturalist; white, industrialist.

Table 8
Percent sexual dimorphism in %AA for “population” groups¹

[Group #] Population group	CML ²	CDB	HML	HDB
[1] Aleutian	0.03	1.17	-0.36	1.78
[2] Ipiutaq	-0.65	-0.96	0.03	0.65
[3] Tigara	-0.87	-0.28	-0.69	-0.10
[4] Indian Knoll	0.13	5.49	-0.03	2.24
[5] Eva	0.17	2.78	0.12	-1.25
[6] Arikara	-1.00	3.62	-0.80	3.87
[7] Ancón	-0.51	0.42	-0.76	3.64
[8] Dickson Mounds	0.67	2.15	-0.65	0.40
[9] Hawikuh	0.02	-0.95	-0.52	-0.09
[10] Madisonville	-1.12	-0.97	-0.69	0.54
[11] Toqua	-0.20	0.27	-0.56	1.26
[12] Utah Cliff Dwellers	1.76	-0.72	-0.20	6.50
[13] Egyptians	-0.67	0.06	-0.40	1.85
[14] Terry “whites”	0.44	-0.82	-0.40	-1.28
[15] Terry “blacks”	-0.26	0.73	-0.33	-0.54

¹ Calculated as (male median %AA – female median %AA).

² See Table 2 for abbreviations.

is also generally universal among human groups, though this exhibits more variation (as exhibited by comparing %DA and %AA amounts reported in Table 7). This latter result is illuminating, as it further supports a previous assertion that there may be less canalization or developmental constraint on diaphyseal breadths than on long-bone lengths (Auerbach and Ruff, 2006), and that this applies to bones both of intramembranous and endochondral developmental origin.

The differences in degrees of directional bias and total amounts of asymmetry—especially in diaphyseal breadths—among the groups studied are likely related to behavioral differences (Perelle and Ehrman, 1994; Raymond and Pontier, 2004; Sládek et al., 2007). Significant differences among the broad subsistence categories support the conclusion that activity differences play a significant role: nonindustrial groups tend to have significantly higher amounts of asymmetry and more directional bias than the two industrial samples in diaphyseal breadths. Moreover, the hunter-gatherers and Arikara generally exhibit greater asymmetry in their diaphyseal breadths, which indicates a greater amount of high-strain unimanual tasks among members of these groups. Yet, comparisons among the five groups composing the hunter-gatherer category reveal distinctions among the hunter-gatherers; marine populations have considerably lower amounts of directional and total asymmetry in CDB and HDB dimensions than the inland Archaic hunter-gatherers from the Green and Tennessee river valleys (Indian Knoll and Eva). The Arctic marine groups’ subsistence depended on some rowing activities (Hrdlička, 1945; Larsen and Froelich, 1948), and these results indicate that these tasks were largely bimanual. As pointed out by Stock (2004), the greatest impact of rowing may be on the forearms, but the entire upper-limb musculoskeletal complex—including the clavicle—is involved, which is demonstrated in the patterns of asymmetry reported. By inference, the South-eastern Archaic groups’ activities involved more unimanual tasks, especially among males. Similarly high amounts of and directional bias in diaphyseal breadth asymmetry among the Arikara undoubtedly relates, in part, to the semiannual bison-

hunting parties that supplemented their largely horticulturalist subsistence pattern (Wedel, 1983).

It is interesting that, despite a variety of farming methods, most of the agriculturalists show comparatively (and often significantly) lower %DA and %AA in the diaphyseal breadths of either the clavicle or humerus. Other researchers have demonstrated that agriculturalists have lower overall bone strength as a result of decreased activity (e.g., Ruff, 2006), which may relate to the observed pattern of asymmetry reported here; in addition to more bilaterally equivalent activity in the upper limb, these agriculturalists may have been generally less active early in life to produce the higher amounts of asymmetry observed among the Archaic inland groups. That is, even if these agriculturalists had engaged in some unimanual tasks, these activities did not produce the strains on the upper limb that the tasks in which the Archaic groups engaged. The Utah Cliff Dwellers and Huari Empire males from Ancón are exceptions to this pattern, namely in humeral diaphyseal breadths, that as of yet cannot be explained. However, they add a note of further caution about generalizing patterns of asymmetry or activity within broad subsistence categories. Finally, lower amounts of diaphyseal breadth asymmetry for the Egyptians could also result from less manual labor or other behavioral laterality among the individuals sampled, who were entombed mummies (and thus might bias the sample against individuals who were laborers).

Perhaps the most important conclusion from these various comparisons is the lack of a consistent pattern among subsistence groups in the magnitude of clavicular or humeral length asymmetries compared to diaphyseal breadth asymmetries. The amounts of asymmetry in maximum bone lengths are no greater among the groups that were likely more biased in unimanual tasks. For instance, the median CML %AA for Indian Knoll males was 2.25%, compared with a median of 2.30% among Dickson Mound males, and compared with CDB %AA values of 9.78% and 5.95%, respectively. The same patterns are found contrasting humeral dimensions. That the overall patterns of directionality were similar may indicate an underlying genetic influence on length asymmetries, but an apparent decoupling of the magnitude of length asymmetries relative to diaphyseal breadth asymmetries within and among population groups furthers the argument for limited influence from activity on the development of long-bone length.

In general, decreased amounts of sexual dimorphism in asymmetry—namely diaphyseal breadth—among the marine hunter-gatherers, agriculturalists, and industrialists may be attributed to more similarities in the activities of the sexes within these groups in comparison to the Archaic hunter-gatherers or Arikara. Although this does not argue for shared identical tasks among males and females within these various population groups, it does indicate that females were involved in more similar activity patterns as males than had existed among the populations represented by Indian Knoll, Eva, or the Arikara sites. Again, the Utah and Ancón samples do not follow the same pattern as the other groups within the agriculturalist subsistence category, possibly signifying a greater difference in habitual behaviors between the sexes.

One curious result is the overall lack of sexual dimorphism in the dimensions of the clavicle, especially the lack of a difference in directional-asymmetry bias in the maximum clavicular length. Both the humerus and radius have significantly higher right-biased asymmetries among females in almost all modern human groups observed (Auerbach and Ruff, 2006; Auerbach, 2007), which contrasts to a higher %DA in the diaphyseal breadths of these bones among males. The lack of significant sexual dimorphism in CML argues for some developmental decoupling of the clavicle from the humerus, as long-bone lengths, noted previously, may be more developmentally constrained. Given the left-side directional asymmetry bias in the CML, this conclusion has tentative support.

The significantly left-biased directional asymmetry for clavicular lengths found among almost all groups entreats further explanation (e.g., Mays et al., 1999; Voisin, 2001). The consensus from previous studies is that clavicular growth is retarded as a result of repeated axial compression from the upper limb during loading throughout primary growth. Experimental evidence for the slowing of longitudinal growth due to compressive loading is generally lacking, however, and implies that abnormally high-intensity loading is necessary to affect epiphyseal growth (Forwood and Burr, 1993). There is also an internal contradiction to this explanation, also noted by Mays et al. (1999), as asymmetry in humeral length (though loaded differently from the clavicle) is significantly contralateral to clavicular length asymmetry. It is possible that differences in loading patterns do create opposite effects on the epiphyses of endochondrally versus intramembranously ossified bone, though there is no experimental evidence to support this idea. Another option is that asymmetry in the development of the thorax, especially in lung size, placement of the heart, and vasculature (i.e., the arch of the aorta and related arteries), could also contribute to the left bias in clavicular length asymmetry by introducing visceral constraints to the bony anatomy. This explanation, however, is at best conjecture. An alternative to these explanations would be that the partially different developmental origins and periods of growth for clavicles and humeri may be one of the dominant causes for the different directions for length directional asymmetries in humans. The discontinuity of sexually dimorphic length-asymmetry patterns in the clavicle when compared with those of the humerus and radius (see Auerbach and Ruff, 2006)—despite evidence that the clavicle is a functional component of the upper limb—further supports this possibility. The specific mechanisms involved are unknown, so this solution remains speculative, but it would be interesting to examine developmental differences between humeri and clavicles simultaneously in experimental models, especially in terms of longitudinal growth, as well as compare patterns of asymmetry among juveniles.

Conclusions

Human clavicular asymmetry is significantly left-biased in length and right-biased in diaphyseal breadth. This length asymmetry is contralateral to the length asymmetry observed in humeri in the same sample, though clavicles and humeri

have same-side directional asymmetry in diaphyseal breadths. This pattern provides more support for the notion that the clavicle is an integral functional element of the upper-limb complex. As in previous research of all the major long bones of the postcranium, diaphyseal breadths were found to exhibit greater amounts of asymmetry than long-bone lengths. Despite some variation, these patterns are universal among all modern humans sampled. Females have significantly greater directional asymmetry in humeral length, whereas males have significantly more directional humeral diaphyseal asymmetry, but this sexual dimorphism is not evident in the clavicle.

Results further suggest that different regions of the bones react dissimilarly to behavior (i.e., mechanical loading) and/or genetic influences. The clavicle, although a functional component of the upper limb, has a developmental pathway that is different from the humerus, which therefore results in some discontinuity in shared patterns of asymmetry between these bones. Diaphyseal breadths, however, continue to exhibit greater sensitivity to loading than lengths of long bones. Comparisons of groups that had different patterns of activity and loading behaviors emphasize the observable effects of these differences among patterns of asymmetry. Future research examining longitudinal-growth samples among humans will better elucidate these patterns.

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