

# Adult Proportionality in Small-Bodied Foragers: A Test of Ecogeographic Expectations

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**ABSTRACT** If predictable, ecogeographic patterning in body size and proportions of human populations can provide valuable information regarding human biology, adaptation to local environments, migration histories, and health, now and in the past. This paper evaluates the assumption that small-bodied Later Stone Age (LSA) foragers of Southern Africa show the adult proportions that would be expected of warm-adapted populations. Comparisons are also made with small-bodied foragers from the Andaman Islands (AI). Indices including brachial, crural, limb element length to skeletal trunk height, and femoral head and bi-iliac breadth to femoral length were calculated from samples of LSA ( $n = 124$ ) and AI ( $n = 31$ ) adult skeletons. Samples derived from the literature include those from high (Europe), middle (North Africa), and low (Sub-Saharan

Africa) latitude regions. The LSA and AI samples match some but not all expected ecogeographic patterns for their particular regions of long term habitation. For most limb length to skeletal trunk height indices the LSA and AI are most similar to the other mid-latitude sample (North Africans). However, both groups are similar to low latitude groups in their narrow bi-iliac breadths, and the AI display relatively long radii. Proportions of LSA and AI samples also differ from those of African pygmies. In regions like southern-most Africa, that do not experience climatic extremes of temperature or humidity, or where small body size exists through drift or selection, body size, and proportions may also be influenced by nonclimatic variables, such as energetic efficiency. *Am J Phys Anthropol* 136:28–38, 2008. © 2007 Wiley-Liss, Inc.

General patterns in animal body size, body proportions, and morphology relative to geographic gradients are described by biologists in terms of various ecogeographic rules. For example, Bergmann's (1847) and Allen's (1878) rules concern the ratio of body mass (BM) to surface area (SA). Since greater mass equals greater heat production from cellular activity, while relatively greater SA equals greater heat loss through radiation, convection, and evaporation, within species or closely related species, populations in cold climates tend to have larger BM (Bergmann's) and shorter limbs (Allen's) to increase the mass to SA ratio. The inverse is the case in warm environments.

Recent examinations of ecogeographic patterns in a wide variety of animal groups including mammals, birds, salamanders, turtles, and ants have predominantly supported the applicability of various ecogeographic rules (e.g., Cushman et al., 1993; Kaspari and Vargo, 1995; Ashton et al., 2000; Ashton 2002a,b; Ashton and Feldman, 2003; Meiri and Dayan, 2003; Meiri et al., 2004; Millien et al., 2006; Gaston et al., 1998). Lomolino et al. (2006) recently drew attention to the importance of these ecogeographical patterns as a factor in our understanding of the evolution and diversification of regional biotas. They note the unique opportunity that the regional morphological variation and migration history of *Homo sapiens* presents for exploring these patterns.

Roberts (1953) demonstrated that Bergmann's rule applies to humans when he found a negative relationship between mean annual temperature and body weight

in a worldwide sample of human populations. In a later study, Roberts (1973) found that populations from colder climates also had relatively short legs, as represented by relative sitting height, confirming that Allen's rule applies to humans as well. Subsequent studies have provided further evidence of ecogeographic patterns in the morphology of human populations (e.g., Hiernaux et al., 1975; Hiernaux and Froment, 1976; Trinkaus, 1981; Beals et al., 1984; Ruff, 1991, 1994). However, Katzmarzyk and Leonard (1998) have shown that the relationships between body size, relative sitting height and mean annual temperature are complex, in that these correlations have decreased in strength since Roberts' studies in the 1950s. Katzmarzyk and Leonard suggest that this is likely due to changes in lifestyle, health care, and nutrition, which have disproportionately affected

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populations in the tropics and subtropics; but their findings also support a genetic component to ecogeographic patterning in body size and proportions among human populations.

Given that human body size and proportions have been shown to conform to Bergmann and Allen's rules, important information regarding the biology, adaptation, and migratory history of a population can be derived from the study of body proportions preserved in the skeleton. Skeletal proportions of past populations have been studied as a means of exploring fossil hominin adaptation and migration (Trinkaus, 1981; Holliday and Falsetti, 1995; Holliday 1997; Ruff et al., 1997, 2002; Weaver, 2003). Most of this research has focused on the "hyper-arctic" body proportions of Neanderthals and the indications that the earliest anatomically modern humans in Europe were tropically adapted, as would be expected given a migration from Africa rather than a local evolution of modern humans within Europe.

Brachial (radius length/humerus length) and crural [tibial length/femoral length (FL)] indices are the most commonly studied aspects of physique found in the literature, due in part to the limited number of skeletal elements required for the calculations and the availability of those elements. Trinkaus (1981) found that brachial indices are more strongly correlated with mean annual temperature than are crural indices. However, Holliday (1995, 1997) argues that the broad range of values for both of these indices for any given sample means that comparisons between samples for ecogeographic patterning can be limited. Holliday instead notes that measures of skeletal trunk height (STH) to limb element ratios more aptly reflect geographic origin. Unfortunately, archaeologically-derived skeletal samples rarely have preservation of the complete or nearly complete thoracic to lumbar vertebral column that is needed for calculation of STH. Ruff (1994) utilizes BM to stature ratios, using skeletal proxies for mass and stature. His study demonstrates that "tropical" or low latitude groups have lower BM [as reflected in bi-iliac breadth (BIB) and femoral head size (FH)] relative to stature (reflected in FL) than do higher latitude samples. These BM to stature ratios using proxy skeletal elements are rarely used in the broader ecogeographic literature, although the reasons for this are unclear.

Ruff (1991, 1994) has also shown that absolute body breadth, as indicated by BIB, is strongly correlated with latitude (wide bodies in high latitudes, narrow bodies in low latitudes). BIB can be measured directly from the skeleton, if the full pelvis is preserved. On the basis of Ruff's cylindrical model of human body shape, only changes to body breadth result in different SA to BM (SA/BM) ratios, while changes to stature have no significant effect (Ruff, 1991, 1994). The short stature of the African pygmies makes them appear stocky relative to other low latitude populations because of their short femora; however since the critical determinant for SA/BM is BIB and they possess similar bi-iliac breadths to taller low latitude African populations, these pygmy populations still represent a warm climate adaptation (Ruff, 1994).

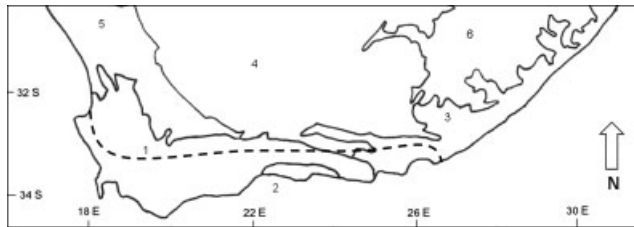
The archaeological skeletal remains of Later Stone Age (LSA) foragers from southern Africa have characteristically small skeletal dimensions (Smith et al., 1992; Wilson and Lundy, 1994; Sealy and Pfeiffer, 2000; Pfeiffer and Sealy, 2006). Studies of chronometrically dated LSA skeletal remains indicate consistency of small

body size throughout the Holocene, with a transient temporal pattern of further reduced adult body size (Sealy and Pfeiffer, 2000; Pfeiffer and Sealy, 2006). This small size presents challenges to accurate body size estimation since most prediction equations are based on reference samples of larger skeletal size and different proportions. Since body proportions are a central component of an individual's stature and mass, it is critical to match the skeletal proportions of the study sample to the reference sample that was used to generate the estimation formula which is to be applied (e.g., Auerbach and Ruff, 2004).

From roughly 20,000 to 2000 years ago, these LSA populations consisted exclusively of foragers subsisting by hunting small game, terrestrial foraging, and exploiting coastal marine resources (Deacon, 1993; Deacon and Deacon, 1999; Parkington, 2001; Mitchell, 2002; Stock and Pfeiffer, 2004). Around 2000 years ago, a pastoralist subsistence strategy was adopted by some of these populations, by as yet unknown mechanisms. Material culture, morphological characteristics and culture history link the prehistoric LSA foragers with the living hunter-gatherer groups of the Kalahari, collectively known as the Khoe-San (e.g., Lee, 1993; Crawhall, 2006). The average size of these living foragers, as documented by Truswell and Hanson (1976) (male mean stature = 161 cm, mass = 48 kg; female mean stature = 150 cm, mass = 40 kg), are consistent with the small body size indicated by skeletal dimensions of the LSA foragers. Nurse et al. (1985:116) describe both the "Khoi" and "San" as having short extremities compared to the body, or trunk, and a "tendency for the upper extremity to be rather short in comparison with the lower".

When the LSA populations and their modern Khoe-San descendants have been used in studies of ecogeographic patterning, they have generally been placed in "low latitude", "warm-adapted" groups with other populations from sub-Saharan Africa (e.g., Trinkaus, 1981; Holliday and Falsetti, 1995; Holliday, 1997, 2002; Pearson 2000a,b; Weaver, 2002, 2003). However, while evidence of LSA occupations during the Holocene has been found throughout southern Africa south of the Zambezi River, archaeological sites are most numerous from the coastal and near-coastal regions of South Africa, in the fynbos, forest, and savanna biomes (see Fig. 1). This coastal environment is typically more Mediterranean than tropical in climate. It lies at ~34° South, which is well beyond the low-high latitude cut-off of 30° South or North (as per Ruff, 1994). Similar to the Mediterranean region, the climate of this region of southern Africa is characterized predominantly by cold season rainfall (annual range 250–3000 mm), with warm-temperate shrubland and forests (Cowling and Hilton-Taylor, 1997; Schulze, 1997). Temperature maxima (warm season) and minima (cold season) range from 27 and 7°C in the west (Cape Town) to 26 and 10°C in the east (East London) (Anonymous, 2007).

The Andaman Islanders constitute a second small-bodied population of relatively isolated foragers. The Andaman Islanders, historically identified as the Great Andamanese, Jarawa and Onge, lived on a string of islands in the Bay of Bengal, at about 12° North, foraging and fishing in a region with a typical tropical monsoon climate. They exploited both marine and terrestrial food sources, and communally hunted wild pigs (Radcliffe-Brown, 1964). Stature data for living Onge, recorded by Cipriani in 1954, highlight their small size (male mean stature = 145 cm; female mean



**Fig. 1.** Biome map of southern Africa showing region from which Later Stone Age skeletal remains used in this study originate (coastal region delineated by dotted line). Biomes: 1) fynbos; 2) forest; 3) savanna; 4) Nama-Karoo; 5) succulent Karoo; 6) grassland (after Rutherford and Westfall, 1986; Morris, 1992).

stature = 139 cm) (Cipriani, 1966). Given the latitude of their home, ecogeographic patterning would predict a tropical physique.

Small-bodied populations are found in many regions of the world, but most commonly in tropical rainforests. There are a few models to explain this including minimizing internal heat production (Cavalli-Sforza, 1986), minimizing resource use in limited resource areas (i.e., the general “island rule” of mammalian body size) (Cavalli-Sforza, 1986) particularly in a stable, nonseasonal environment (Shea and Bailey, 1996), or as a life history response to high mortality (Migliano, 2005; Walker et al., 2006). However, as noted above, the LSA foragers from southern Africa were not tropical rainforest inhabitants, although the coastal region they inhabited, largely cut off from the interior of southern Africa by the Cape Fold Mountains, may have acted as an island-like environment.

This study assesses the proportions of the small-bodied LSA adult skeletal sample from an ecogeographic perspective. Specifically, we test whether the LSA foragers: 1) show a pattern of body proportions typical of hot environments, as is often assumed in the literature; 2) show a morphological pattern predicted by the Mediterranean-like environmental conditions within which they lived (i.e., are more similar to samples from North Africa); and/or 3) show a pattern similar to other small-bodied samples such as the Andaman Islanders or African Pygmies. Further, the proposition is explored that diminutive adults may show proportions that differ from those of larger-bodied adults, regardless of ecological region.

## MATERIALS AND METHODS

The LSA sample consists of archaeologically derived skeletons (male  $n = 59$ , female  $n = 65$ ) from the Southern, Southwestern, and Eastern Cape regions of South Africa, most with individual radiocarbon dates falling between 240 and 7853 years BP (uncalibrated). Sex and age at death estimates are based on traditional morphological indicators (e.g., Buikstra and Ubelaker, 1994). Data were also collected from a sample of proto-historic Andaman Islander forager skeletons (male  $n = 16$ ; female  $n = 15$ ). These skeletons are primarily from Great Andaman Island, which lies between 11 and 14° North latitude, and date from the time period following British settlement in 1858 (see Stock, 2002 for sample details). Additional comparative sample data representing populations from high (Europe: north and south), middle (North Africa) and low (Sub-Saharan Africa: East and West Africa, African pygmy, Khoe-San) latitude

regions were taken from published literature (Holliday, 1995, 1997).

The analysis of ecogeographic patterning in both samples was conducted by examining indices of body proportions as represented by skeletal elements. The measurements used in this analysis (M-numbers from Martin and Saller, 1957) are bicondylar femoral length (FL, M-2), superoinferior femoral head diameter (FH, M-18), tibial length measured to the lateral condyle (TL, M-1), maximum radial (RL, M-1) and humeral lengths (HL, M-1), BIB, and STH [sum of dorsal vertebral body heights of all thoracic and lumbar vertebrae and sacral ventral length (Franciscus and Holliday, 1992)]. For the LSA sample, maximum FL (M-1) was converted to bicondylar FL (M-2) using regression formula from Holliday (1995) to be comparable with the Andaman Islander sample and those taken from the literature utilized in this study. Although FH is included as a proxy for BM, it is important to note that Ruff and colleagues (Ruff, 1988; Ruff et al., 1993) have shown that the relationship between BM and FH is not isometric, and the effect would be amplified in small-bodied populations, such as those in this study.

Some individual skeletons (LSA  $n = 9$ , Andaman Islanders  $n = 16$ ) were missing vertebral elements. Following Franciscus and Holliday (1992) and Holliday (1995, 1997), STH was estimated for these individuals from those vertebral elements that were present using regression formulae that were generated using a large, mixed-population reference sample with complete thoraco-lumbar vertebral columns and sacra ( $n = 68$ ); including complete individuals from the study sample of LSA foragers ( $n = 18$ ), a sample of foragers from the Andaman Islands ( $n = 6$ ), and samples of European Americans ( $n = 19$ ) and Pecos Puebloans ( $n = 25$ ) from the Maxwell Museum collections (courtesy of T. Holliday). Auerbach (2007) found that relative proportions of vertebral heights (i.e., individual vertebral body height relative to total vertebral column length) did not differ significantly among the samples in his study. Comparisons of the four samples used in the current study for the mixed-population reference sample (results not shown) suggest that while some differences exist between the samples in relative vertebral height for specific elements, the seven vertebrae that show significant differences among the small- and large-bodied samples contribute an average total error of 2.2 mm in summed vertebral height. Further, using only the larger bodied samples (European American and Pecos Puebloans) for predicting STH in the LSA and Andaman Islander samples (results not shown) produces minimal error between predicted and measured STHs [range of mean percent prediction error for prediction equations = 0.3 – 2.0%, range of mean error (in mm) for prediction equations = 0.9 – 8.5 mm]. These findings support the use of a mixed-population sample, including both small-bodied and large-bodied samples for predicting STH in incomplete specimens. Regression formulae, and predicted STHs for incomplete LSA and Andaman Islander specimens using the mixed-population sample are provided in Table 1.

Indices calculated using these skeletal element measurements provide ways to compare relative lengths of distal with proximal limb elements [brachial index (radius length/humerus length  $\times 100$ ); crural index (tibial length/FL  $\times 100$ )], relative limb length to trunk height [indices of femoral, tibial, radial, and humeral lengths to STH (e.g., FL/STH  $\times 100$ )], and relative body breadth

TABLE 1. Regression formulae and predicted skeletal trunk heights (STH) for incomplete specimen

Specimen <sup>a</sup>	Missing vertebrae <sup>b</sup>	Predicted STH (mm)	Lower 95% CI	Upper 95% CI	SEE	%SEE	Regression formula (X = sum of vertebrae present)	R <sup>2</sup> (N = 68)
UCT 60	T11	450.8	448.2	453.4	1.3	0.3	STH = $X \times 1.05 + 1.08$	0.9992
UCT 331	T1, L4, L5	448.8	443.3	454.4	2.8	0.6	STH = $X \times 1.16 - 0.91$	0.9961
ALB 222	T6, T7, L3	419.3	414.8	423.8	2.3	0.5	STH = $X \times 1.17 - 3.55$	0.9974
ALB 244(1)	T12	459.3	456.9	462.1	1.3	0.3	STH = $X \times 1.06 - 0.55$	0.9992
ALB 305	T3, T7, T8	432.3	427.4	437.2	2.4	0.6	STH = $X \times 1.15 - 3.78$	0.9970
UCT 112	T3, T4, T5	485.8	480.7	490.9	2.6	0.5	STH = $X \times 1.15 - 7.63$	0.9967
ALB 354	L5	441.0	438.2	443.8	1.4	0.3	STH = $X \times 1.05 + 1.04$	0.9990
UCT 199	T6, T7	479.5	476.0	483.1	1.8	0.4	STH = $X \times 1.10 - 4.41$	0.9984
UCT 392	T5	456.7	454.8	458.5	0.9	0.2	STH = $X \times 1.05 - 3.58$	0.9996
AI 8035	SVL	458.1	437.8	478.3	10.1	2.2	STH = $X \times 1.17 + 40.79$	0.9476
AI 8301	SVL	425.6	405.3	446.0	10.2	2.4		
AI 8302	SVL	407.9	387.4	428.4	10.3	2.5		
AI 8303	SVL	431.6	411.2	451.9	10.2	2.4		
AI 8306	SVL	420.9	400.5	441.3	10.2	2.4		
AI 8308	SVL	402.2	381.6	422.7	10.3	2.6		
AI 8324	SVL	427.3	407.0	447.7	10.2	2.4		
AI 8325	SVL	435.1	414.8	455.4	10.2	2.3		
AI 8327	SVL	414.9	394.4	435.3	10.2	2.5		
AI 8329	SVL	400.6	380.0	421.1	10.3	2.6		
AI 8330	SVL	415.0	394.6	435.5	10.2	2.5		
AI 1861	T1, SVL	455.8	435.2	476.4	10.3	2.3	STH = $X \times 1.23 + 39.00$	0.9456
AI 8004	T1, SVL	419.5	398.8	440.2	10.4	2.5		
AI 1865	T12, L5	396.2	392.9	399.5	1.7	0.4	STH = $X \times 1.11 + 0.27$	0.9986
AI 8001	T12, L5	422.2	418.9	425.5	1.7	0.4		
AI 8328	T5, T12, SVL	419.6	399.5	439.7	10.1	2.4	STH = $X \times 1.35 + 36.50$	0.9491

<sup>a</sup> Specimen codes: Later Stone Age specimens = UCT (University of Cape Town), ALB (Albany Museum); AI = Andaman Islander (Natural History Museum).

<sup>b</sup> Letter indicates section of vertebral column (T = thoracic vertebra, L = lumbar vertebra), number indicates position of missing element. SVL = sacral ventral length (Franciscus and Holliday, 1992).

and BM to stature indices using skeletal proxies (BIB/FL; FH/FL). These indices were calculated for the LSA and Andaman Island samples males and females separately, and compared with indices from several samples collected from the literature. The indices available for the samples from the literature vary depending on which bone measurements are given. Since only summary statistics are available for the samples taken from the literature, *t*-tests were used to look for differences in mean index values between the LSA and other samples. A conservative alpha value was calculated using the Bonferroni method (Sokal and Rohlf, 1995) to control the overall experimentwise error rate for each index.

## RESULTS

Summary statistics for the brachial, crural, and limb element/STH indices are provided in Tables 2 and 3 (and Figs. 2–7), while BIB and the indices that represent BM/stature comparisons are given in Table 4 (and Figs. 8–10). The indices given in Table 4 are calculated from sample means for each variable for the samples, rather than mean indices for each sample. This was necessary because only mean measurement values for each variable are provided in the literature. The results of the *t*-tests are given in Table 5.

### Limb proportions

For most indices, the LSA foragers fall closest to those of the North African samples. There is little distinction among the samples for the crural index (see Fig. 2). Only the Europeans display an index significantly lower than the LSA sample. Brachial indices more clearly dis-

tinguish the samples (see Fig. 3). The LSA brachial indices fall between those of the Europeans and the North Africans for both sexes, although the difference in indices is not statistically significant for the comparison of male LSA and North African samples (Table 5). The limb segment/STH indices also show a clear distinction among the samples (Figs. 4–7), with the LSA generally falling between Europeans and North Africans, except for the humeral length/STH index. The LSA females and males are closer to the Northern and Southern Europeans for HL/STH than the other samples, although these differences are only significant for the East and West Africans.

Despite their low latitude setting, the Andaman Islanders display a pattern of lower limb indices that is similar to the LSA sample. It falls nearer the mid-latitude North Africans than the low latitude Sub-Saharan Africans. However, the relatively long radial lengths of the Andaman Islanders females and males are apparent in their high brachial and radial length/STH indices.

### Body shape

Body shape is represented by absolute body breadth (BIB), and the final two indices (Table 4, Figs. 8–10), which reflect body breadth and BM to stature ratios using proxy skeletal indicators. For BIB, the widest body breadths are found in Northern and Southern Europe (high latitude), followed by North Africa (mid-latitude), and then East and West Africa (low latitude). BIB is similar across all four small-bodied samples (i.e., African pygmy, Khoe-San, LSA and Andaman Islanders) with all four displaying narrower BIBs than all of the larger-bodied samples. The African Pygmy females have the widest

TABLE 2. Summary statistics for crural and brachial indices, sexes separate

Sample	Latitude	Crural				Brachial			
		Females		Males		Females		Males	
		N	Mean (SD)	N	Mean (SD)	N	Mean (SD)	N	Mean (SD)
N Europe <sup>a</sup>	59–48	122	82.5 (2.2)	213	82.5 (2.5)	112	74.3 (2.4)	181	75.6 (2.4)
S Europe <sup>a</sup>	45–43	39	83.8 (39)	60	83.9 (2.0)	38	73.7 (2.5)	58	75.4 (2.3)
N Africa <sup>a</sup>	30–20	61	84.7 (2.5)	72	85.2 (2.1)	61	78.2 (2.3)	75	78.9 (2.4)
W Africa <sup>a</sup>	5	4	86.5 (1.7)	16	85.8 (2.5)	5	80.1 (3.7)	16	81.4 (2.3)
E Africa <sup>a</sup>	2	19	86.1 (1.8)	27	86.3 (2.4)	19	78.5 (2.7)	27	79.3 (1.6)
Afr. Pygmy <sup>a</sup>	2	3	85.5 (2.5)	6	85.7 (1.2)	3	77.1 (4.3)	7	76.4 (1.7)
Khoe-San <sup>a</sup>	25	20	84.0 (2.6)	12	84.4 (2.2)	14	76.2 (2.7)	10	77.3 (2.4)
LSA <sup>b</sup>	34	53	85.4 (2.4)	37	86.1 (2.5)	46	76.5 (2.6)	43	78.8 (3.0)
AI <sup>b</sup>	12	13	84.7 (1.9)	15	85.7 (1.8)	15	80.3 (3.5)	15	81.6 (3.4)

<sup>a</sup> Sample data from Holliday (1995).<sup>b</sup> Current study sample.

TABLE 3. Summary statistics for limb element / skeletal trunk height indices, sexes separate

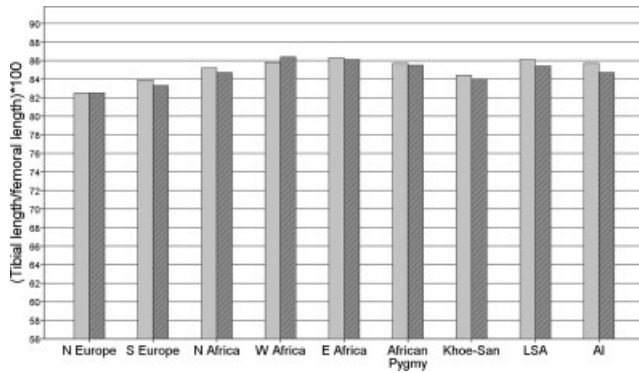
Sample	Latitude	FL/STH				TL/STH				HL/STH				RL/STH			
		Females		Males		Females		Males		Females		Males		Females		Males	
		N	Mean (SD)	N	Mean (SD)	N	Mean (SD)	N	Mean (SD)	N	Mean (SD)	N	Mean (SD)	N	Mean (SD)	N	Mean (SD)
N Europe <sup>a</sup>	59–48	32	86.0 (4.2)	37	88.9 (4.3)	32	71.2 (3.8)	34	72.7 (3.9)	33	61.6 (3.0)	37	64.2 (3.4)	33	46.6 (2.8)	37	48.7 (2.5)
S Europe <sup>a</sup>	45–43	24	89.2 (3.9)	29	90.9 (4.0)	25	74.3 (3.9)	30	76.1 (3.7)	25	64.2 (3.1)	28	64.8 (3.1)	25	47.7 (2.7)	28	49.1 (2.1)
N Africa <sup>a</sup>	30–20	33	93.4 (5.2)	30	95.2 (5.7)	32	78.9 (4.2)	28	80.8 (5.6)	32	65.2 (3.6)	30	66.9 (3.9)	32	50.9 (2.8)	30	53 (3.6)
W Africa <sup>a</sup>	5	3	97.7 (2.7)	13	103.7 (8.0)	3	84.8 (3.3)	13	88.7 (6.7)	3	69.4 (2.5)	13	72.4 (5.0)	3	54.1 (4.5)	13	58.6 (4.4)
E Africa <sup>a</sup>	2	16	96.1 (4.7)	11	99.3 (6.0)	16	82.8 (4.2)	11	85.7 (6.1)	16	68.5 (3.4)	11	70.2 (2.9)	16	53.8 (3.0)	11	55.8 (2.2)
Afr. Pygmy <sup>a</sup>	2	3	92.7 (8.4)	5	87.2 (2.4)	3	79.2 (5.7)	5	85.7 (2.4)	3	68.6 (3.4)	5	65.1 (1.4)	3	52.9 (4.5)	5	49.7 (1.5)
Khoe-San <sup>a</sup>	25																
LSA <sup>b</sup>	34	14	89.2 (3.8)	14	93.0 (5.7)	12	77.7 (3.3)	8	79.3 (4.8)	12	62.6 (3.4)	10	63.9 (5.2)	12	48.3 (3.3)	10	51 (3.4)
AI <sup>b</sup>	12	12	91.7 (5.8)	10	93.2 (6.0)	11	78.4 (4.3)	9	78.8 (5.3)	12	64.1 (4.5)	10	67.0 (5.2)	12	51.3 (3.5)	9	55.4 (3.8)

<sup>a</sup> Sample data from Holliday (1995).<sup>b</sup> Current study sample

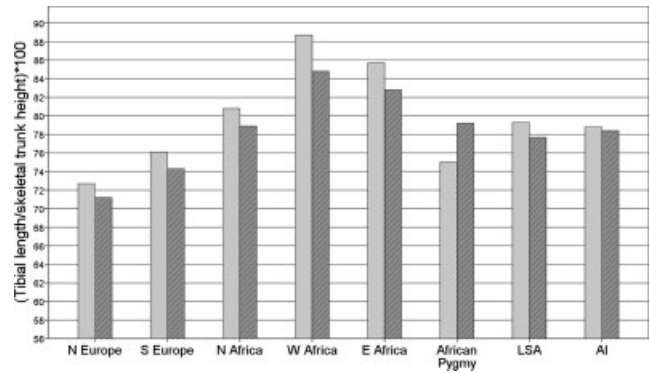
BIB of the small-bodied samples, although they are not significantly different from the LSA females.

The body shape ratios of the small-bodied samples exhibit an interesting pattern compared with the larger-bodied samples (Northern Europe through East Africa). Among the higher latitude and larger-bodied samples, BM (FH) is large, and body breadth is wide (BIB) relative to stature. These indicate the broader, more compact frame of the higher latitude samples versus the linear frame of the low latitude samples. The African pygmy males and females display high values for both indices, indicating high BM for stature (FH/FL) and wide bodies for stature (BIB/FL), when compared with the other low latitude samples. In both cases they appear more similar to the European samples. The Andaman Islanders also display relatively high FH/FL indices for both sexes,

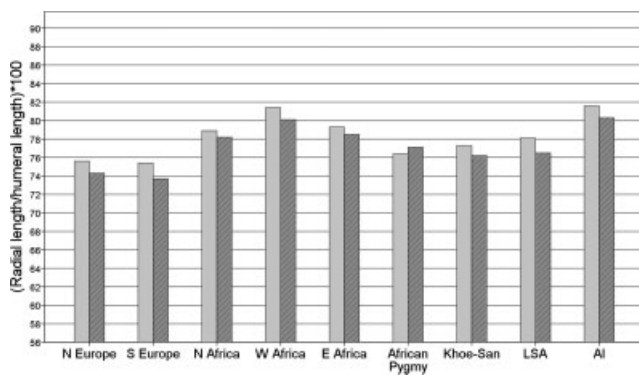
which is counter to their pattern of similarities to the North African and Sub-Saharan African samples for brachial, crural, and STH indices. Also, unlike the African pygmy samples, the Andaman Islander females and males display very narrow BIBs relative to FLs, as well as a different pattern of sexual dimorphism in this index (males > females) compared with the other samples. The LSA and Khoe-San females and males show similar values for both indices, although the FH/FL indices of the Khoe-San samples are lower (making them more similar to the other East and West African samples) and show an inverse pattern of sexual dimorphism (females > males). The FH/FL indices of the LSA samples follow the pattern of their limb indices in being similar to the North Africans. However, because of the nonisometric relationship between FH and BM, these FH/FL indices



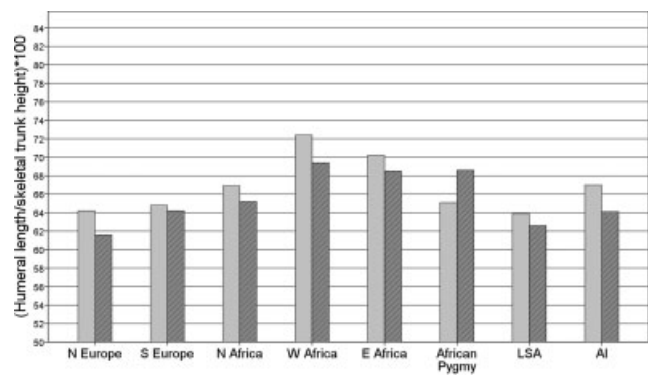
**Fig. 2.** Crural indices for the samples included in the analysis. Solid = males; Hatched = females. LSA = Later Stone Age foragers, AI = Andaman Islanders.



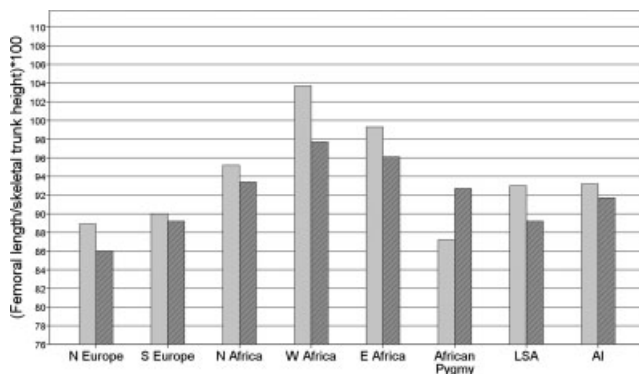
**Fig. 5.** Tibial length/STH indices for the samples included in the analysis. Solid = males; Hatched = females. Sample acronyms are as in Figure 2.



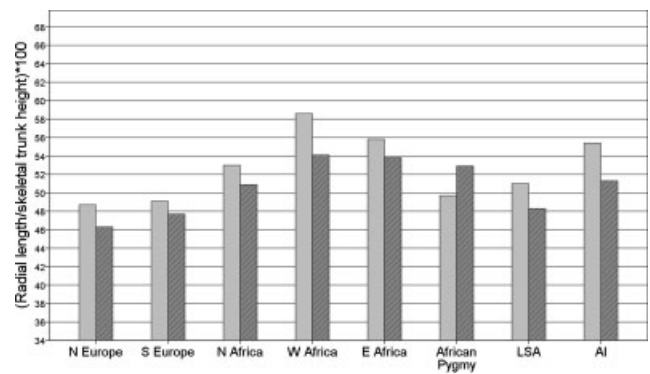
**Fig. 3.** Brachial indices for the samples included in the analysis. Solid = males; Hatched = females. Sample acronyms are as in Figure 2.



**Fig. 6.** Humeral length/STH indices for the samples included in the analysis. Solid = males; Hatched = females. Sample acronyms are as in Figure 2.



**Fig. 4.** FL/STH indices for the samples included in the analysis. Solid = males; Hatched = females. Sample acronyms are as in Figure 2.



**Fig. 7.** Radial length/STH indices for the samples included in the analysis. Solid = males; Hatched = females. Sample acronyms are as in Figure 2.

should be interpreted with caution. The BIB/FL indices of the LSA and Khoe-San, and those of the Andaman Islanders, are quite low, reflecting a narrow BIB relative to FL, compared with all other samples.

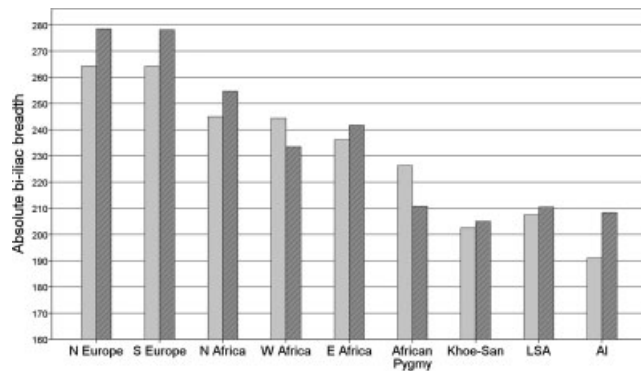
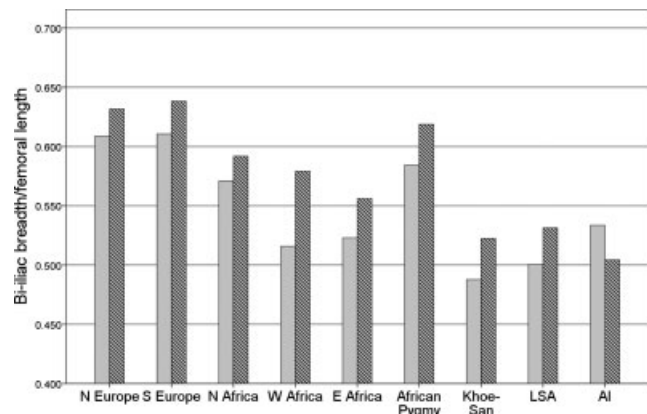
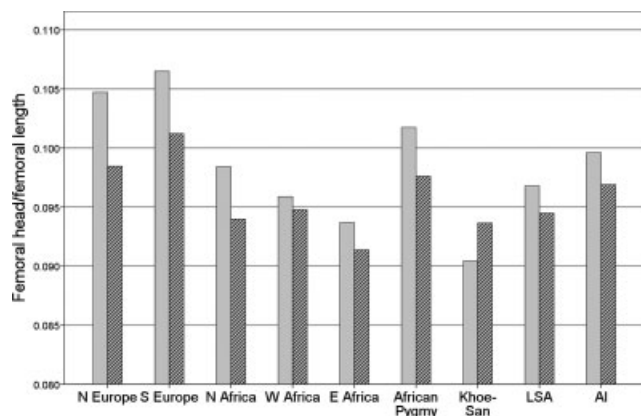
## DISCUSSION

On the basis of the previous research on ecogeographic characteristics of human skeletal samples, if hypothesis

1 is correct (LSA body proportions reflect a warm, low latitude environment) then the LSA foragers will display generally small body size, particularly BM with respect to stature, high crural and brachial indices (reflecting long distal limb segments), long arms and legs relative to trunk size, and narrow body breadths. If hypothesis 2 is correct (LSA body proportions reflect a mid-latitude, Mediterranean-like environment) then the LSA foragers will be more similar to the North African sample in gen-

TABLE 4. Summary statistics for femoral head, femoral length, and bi-iliac breadth (mm) by sample and indices representing body mass/stature ratios

Sample	Males								Females							
	Femoral head		Femoral length		Bi-iliac breadth		FH/FL	BIB/FL	Femoral head		Femoral length		Bi-iliac breadth		FH/FL	BIB/FL
	N	Mean (SD)	N	Mean (SD)	N	Mean (SD)			N	Mean (SD)	N	Mean (SD)	N	Mean (SD)		
N Europe <sup>a</sup>	80	47.9 (3.0)	251	457.4 (25.0)	75	278.5 (17.1)	0.105	0.609	60	41.2 (2.2)	131	418.4 (22.1)	54	264.3 (15.3)	0.098	0.632
S Europe <sup>a</sup>	54	48.5 (2.9)	60	455.4 (24.6)	52	278.1 (16.3)	0.106	0.611	38	41.9 (2.6)	40	413.9 (21.5)	35	264.2 (18.8)	0.101	0.638
N Africa <sup>a</sup>	73	43.9 (3.1)	75	446.0 (26.8)	61	254.7 (13.5)	0.098	0.571	61	38.9 (2.1)	63	413.9 (21.0)	46	245.0 (14.2)	0.094	0.592
W Africa <sup>a</sup>	16	43.4 (2.3)	16	452.6 (10.4)	15	233.5 (14.6)	0.096	0.516	5	40.0 (3.1)	5	422.0 (36.0)	5	244.4 (14.7)	0.095	0.579
E Africa <sup>a</sup>	27	43.3 (2.7)	27	462.2 (28.9)	27	241.7 (15.4)	0.094	0.523	19	38.8 (2.4)	19	424.6 (29.3)	19	236.1 (11.3)	0.091	0.556
Afr. Pygmy <sup>a</sup>	7	36.7 (2.0)	7	360.7 (17.2)	5	210.8 (11.8)	0.102	0.584	3	35.7 (1.9)	3	365.7 (19.3)	3	226.3 (7.4)	0.098	0.619
Khoe-San <sup>a</sup>	3	38.0 (1.3)	12	420.2 (23.3)	2	205.0 (2.8)	0.090	0.488	5	36.3 (0.9)	20	387.6 (19.3)	2	202.5 (16.3)	0.094	0.522
LSA <sup>b</sup>	31	40.7 (2.3)	48	420.5 (18.9)	25	210.5 (17.6)	0.097	0.501	29	36.9 (2.0)	59	390.5 (25.9)	30	207.5 (15.5)	0.094	0.531
AI <sup>b</sup>	16	38.9 (2.1)	16	390.5 (17.7)	5	208.4 (10.5)	0.100	0.534	15	36.7 (2.6)	15	378.7 (14.5)	4	191.0 (6.3)	0.097	0.504

<sup>a</sup> Sample data from Holliday (1995).<sup>b</sup> Current study sample.**Fig. 8.** Absolute BIB by sample. Solid = males; Hatched = females. Sample acronyms are as in Figure 2.**Fig. 10.** BIB/FL indices by sample. Solid = males; Hatched = females. Sample acronyms are as in Figure 2.**Fig. 9.** FH/FL indices by sample. Solid = males; Hatched = females. Sample acronyms are as in Figure 2.

eral body proportions, falling between the high latitude Europeans and the low latitude East and West Africans in body breadth, limb indices and body shape indices. Finally, if hypothesis 3 is correct (LSA display body proportions similar to the other small-bodied samples regardless of latitudinal differences among these samples) then the LSA foragers will show narrow body breadths, which appear stocky when examined using BIB to stature ratios only because of their short stature, and intermediate limb length indices and body shape indices. Since the LSA foragers inhabited coastal southern Africa at  $\sim 34^\circ$  South, we would expect, based on ecogeographic conditions, that they would be most similar to the middle latitude population from the Northern Hemisphere, the North Africans (i.e., hypothesis 2).

The skeletal proportions of the LSA foragers and the previously published Khoe-San samples show these sam-

TABLE 5. The *t*-test results for intralimb and limb element/skeletal trunk height indices comparing LSA sample to other geographical samples, sexes separate

Index	LSA vs.	Females		Males	
		<i>P</i> -value	Sample with larger mean index	<i>P</i> -value	Sample with larger mean index
Crural <sup>a</sup>	N Europe	<0.006	LSA	<0.006	LSA
	S Europe	<0.006	LSA	<0.006	LSA
	N Africa	ns		ns	
	W Africa	ns		ns	
	E Africa	ns		ns	
	Afr. Pygmy	ns		ns	
	Khoe-San	ns		ns	
	AI	ns		ns	
Brachial <sup>a</sup>	N Europe	<0.006	LSA	<0.006	LSA
	S Europe	<0.006	LSA	<0.006	LSA
	N Africa	<0.006	N Africa	ns	
	W Africa	ns		<0.006	W Africa
	E Africa	ns		ns	
	Afr. Pygmy	ns		ns	
	Khoe-San	ns		ns	
	AI	<0.006	AI	<0.006	AI
FL/STH <sup>b</sup>	N Europe	ns		ns	
	S Europe	ns		ns	
	N Africa	ns		ns	
	W Africa	<0.007	W Africa	<0.007	W Africa
	E Africa	<0.007	E Africa	ns	
	Afr. Pygmy	ns		ns	
	AI	ns		ns	
TL/STH <sup>b</sup>	N Europe	<0.007	LSA	<0.007	LSA
	S Europe	ns		ns	
	N Africa	ns		ns	
	W Africa	<0.007	W Africa	<0.007	W Africa
	E Africa	<0.007	E Africa	ns	
	Afr. Pygmy	ns		ns	
	AI	ns		ns	
HL/STH <sup>b</sup>	N Europe	ns		ns	
	S Europe	ns		ns	
	N Africa	ns		ns	
	W Africa	<0.007	W Africa	<0.007	W Africa
	E Africa	<0.007	E Africa	<0.007	E Africa
	Afr. Pygmy	ns		ns	
	AI	ns		ns	
RL/STH <sup>b</sup>	N Europe	ns		ns	
	S Europe	ns		ns	
	N Africa	ns		ns	
	W Africa	ns		<0.007	W Africa
	E Africa	<0.007	E Africa	<0.007	E Africa
	Afr. Pygmy	ns		ns	
	AI	ns		ns	
Bi-iliac Breadth <sup>a</sup>	N Europe	<0.006	N Europe	<0.006	N Europe
	S Europe	<0.006	S Europe	<0.006	S Europe
	N Africa	<0.006	N Africa	<0.006	N Africa
	W Africa	<0.006	W Africa	<0.006	W Africa
	E Africa	<0.006	E Africa	<0.006	E Africa
	Afr. Pygmy	ns		ns	
	Khoe-San	ns		ns	
	AI	ns		ns	

<sup>a</sup> *P*-values < 0.006 considered significant in order to control experimentwise error at an alpha of 0.05 using the Bonferroni method. ns = not significant.

<sup>b</sup> *P*-values < 0.007 considered significant in order to control experimentwise error at an alpha of 0.05 using the Bonferroni method. ns = not significant.

ples to be more similar in crural and FH to FL indices to samples from mid-latitude regions (Northern Africa), than to low latitude populations of Africa and Melanesia. This distinction is even more evident with the STH ratios, where the relatively short limb elements of the LSA sample contrast with the long limbs and short trunks of the Sub-Saharan Africans. The LSA brachial indices for both sexes also fall between the North African and European samples; however they are most similar to the brachial indices of the African pygmy sample. These

findings indicate that the common practice of grouping all African populations located south of the Sahara into a “tropical” or “warm-adapted” ecogeographic category does not reflect adaptive characteristics of physique. The southern African LSA people, who lived mainly in a mid-latitude, coastal, and Mediterranean-like environment, do not fit this pattern.

However, the LSA sample also differs in its body proportions from other mid-latitude samples. The relatively narrow BIBs of the LSA females and males, as reflected



in their BIB to FL ratios and absolute BIBs are lower than all of the other samples, except for the Khoe-San. A narrow BIB in human populations, regardless of stature (as reflected in FL) has been shown by Ruff (1991, 1994) to indicate a warm-climate (low latitude) adaptation for body heat loss through radiation. Therefore, in body breadth characteristics, the LSA foragers and the Khoe-San both are consistent with low latitude morphologies and the morphologies of the other small-bodied samples. It is interesting that BIB/FL ratios of the LSA, Khoe-San, and Andaman Islanders are unlike that of the African pygmies, that is, they do not possess their stocky physique. Finally, following Bergmann's rule, the overall small body size (both stature and mass) of the LSA foragers, as indicated by the small size of their skeletal elements (and see body size estimations in Pfeiffer and Sealy, 2006), could be interpreted as a warm climate adaptation. Thus, when all dimensions are considered together, the LSA and Khoe-San samples represent distinctive characteristics that match some but not all of the predictions for body proportions based on traditional ecogeographic patterning.

The Andaman Islanders also present a pattern of body proportions and shape that do not match ecogeographic predictions in some characteristics. The Andaman Islanders inhabit islands at low latitude, and their body proportions, small body size, and high brachial and radial length/STH indices in some ways reflect this. However, the other limb indices for the Andaman Islander sample are similar to the mid-latitude North African and LSA samples. Like the LSA foragers, the Andaman Islanders are also characterized by high BM (FH) for stature (FL), more similar to high latitude samples, and narrow bodies (BIB) for stature, suggesting low latitude adaptation.

The discordant LSA, Andaman Islander, Khoe-San and African pygmy BM and BIB to stature indices are problematic for interpreting climatic adaptation. Although these indices have been used to examine body shape and climatic adaptation (e.g., Ruff 1991, 1994), when body size is particularly small as is the case with these samples, the relationship between these indices and climate appears to fall apart. This reflects the fact that body breadth (e.g., BIB) is a critical attribute of climatic adaptation (Ruff, 1991, 1994), as opposed to stature. However, the interesting, though unexplained pattern among the small-bodied groups in these physique indices is that both indices differ so greatly between the African pygmies and the LSA foragers, Andaman Islanders, and Khoe-San. These results have implications for hominin morphology in light of the small body size characteristic of many hominin species.

These results suggest that the small-bodied samples included in this study (LSA, Khoe-San, Andaman Islanders, and African Pygmies) may have met the selective pressures of climate in their respective regions in somewhat different ways relative to larger-bodied populations. It may be that these small bodied populations already possess high SA/BM ratios because of their absolutely narrow body breadths, and therefore the relatively long distal limb segments of low latitude large-bodied populations, as reflected in intralimb and limb element to trunk height indices, are not required to meet thermoregulatory selective pressures (Ruff, personal communication). As well, these small-bodied samples differ from one another in body proportions (contra hypothesis 3), indicating that they have each met climatic selective

pressures in different ways and/or been subject to different additional selective pressures on body proportions.

Climatic factors influencing body size and proportions may not be equally strong in all environments. Climate extremes, particularly cold climates (Rodríguez et al., 2006; but see Ashton et al., 2000), may have more of a selective influence on body proportions than the climates of middle latitude regions. Situated at  $\sim 34^\circ$  South, the LSA forager population in this study may have been less constrained by climatic factors such as temperature (since latitude is used as a proxy for mean annual temperature) influencing body proportions when compared with other factors, such as resource availability or terrain.

Life history parameters may also influence body size among human populations. A recent study of body size among the Aeta pygmies of the Philippines suggests that high rates of mortality select for earlier reproduction and cessation of growth (Migliano, 2005; Migliano et al., in press). Subsequent analyses provide additional evidence that life history parameters influence body size among foragers and small-scale societies (Walker et al., 2006). Studies have also suggested that factors such as disease and nutrition can affect both linear growth (stature) and relative limb length (Tanner et al., 1982; Bogin et al., 2002). These environmental factors may result in relatively short limbs in short-statured individuals. Ruff (1994) has shown that these environmental factors do not affect absolute body breadth to the same degree. Small-body size may also be linked to limited resource availability in a restricted and nonseasonal environment (Cavalli-Sforza, 1986; Shea and Bailey, 1996). These additional selective factors acting on body size and proportions may help account for the unique body proportion patterns seen in the three small-bodied samples included in this analysis (e.g., African pygmy, Andaman Islanders, and LSA and Khoe-San). However, in the case of the LSA foragers, there is little skeletal evidence of nutritional deficiency diseases or signs of stress (e.g., linear enamel hypoplasias, growth arrest lines, porotic hyperostosis). Further, while restricted in area by the Cape Fold Mountains, the coastal region of southern Africa exhibits more seasonality than tropical low latitude rainforests.

Mayr (1953) argued that exceptions to the ecogeographic "rules" do not prove the rule invalid since an animal's phenotype is determined by means of compromise between many often competing factors. Therefore the physiological constraints of body size and proportions in relation to heat loss or conservation are not the sole determinants (see also Millien et al., 2006). Finally, support for flexibility in ecogeographic patterns of human populations comes from the demonstration by Katzmarzyk and Leonard (1998) that the relationship between body proportions and climate in human populations has weakened since the early studies of Roberts (1953, 1973).

## CONCLUSIONS

The region inhabited by most LSA foragers in coastal southern Africa during the Holocene is at  $\sim 34^\circ$  South in latitude, and the climate is cooler and dryer than the climate characterizing tropical regions. This study investigated the accuracy of including these foragers into a larger Sub-Saharan, low latitude, or warm-adapted group for the purpose of exploring human ecogeographic patterning, as is often done in human ecogeographic literature. The results indicate that the body proportions of this LSA sample are more similar in brachial and

limb-to-trunk indices to northern mid-latitude populations, such as those from North Africa, than they are to low latitude African samples. This is not unexpected, given that the northern and southern coasts of Africa lie at similar distances from the equator, and therefore at similar mid-latitude regions. On the other hand, absolute BIB and the BIB to FL ratio of the LSA group is the lowest of all of the samples, lower even than the East and West African samples. The adaptive relevance of the BIB/FL ratio in relation to climate is questionable. As well, the overall small body size characteristic of the LSA foragers and the historic Khoe-San is more consistent with a low latitude region as per Bergmann's rule. Although the Andaman Islanders show limb proportionality that is consistent with their tropical environment, they too show inconsistencies in trunk-to-limb or BM measures. One particularly interesting finding is that while the LSA, Khoe-San and Andaman Islander groups have very narrow BIBs, they do not appear as stocky as the African pygmy group when BIB to FL ratios are examined. One would expect a stocky physique given the short stature of all of these groups.

The possibility arises that climatic factors play a less important role in body size and proportions outside of climatic extremes, or that life history or other factors also play a role in determining body size and proportions. Additionally, it may be that small body size itself, as is characteristic of the LSA, Khoe-San, Andaman Islander, and African pygmy groups results in different responses to climatic factors. When the new information from LSA and Andaman Islander samples are combined with published data on African pygmies and Khoe-San, it appears that small-bodied populations in many ways meet ecogeographic body proportion expectations for the particular regions they inhabit. However, they may meet these thermoregulatory selective pressures in ways that are slightly different from those of larger-bodied populations. Each small-bodied sample has its own distinctive proportional features. The applicability of current body size estimation methods from skeletal remains continues to be problematic for samples like that of the LSA because of the scarcity of not only mid-latitude reference samples, but also of reference samples with diminutive body size ranges, needed to validate estimations of stature and BM.

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## LITERATURE CITED

- Anonymous. 2007. National weather [Internet]. South African Weather Service. Available at <http://www.weathersa.co.za>  
 Allen JA. 1878. The influence of physical conditions in the genesis of species. *Radic Rev* 1:108–140.

- Ashton KG. 2002a. Patterns of within-species body size variation in birds: strong evidence for Bergmann's rule. *Global Ecol Biogeogr* 11:505–523.  
 Ashton KG. 2002b. Do amphibians follow Bergmann's rule? *Can J Zool* 80:708–716.  
 Ashton KG, Feldman CR. 2003. Bergmann's rule in nonavian reptiles: turtles follow it, lizards and snakes reverse it. *Evolution* 57:1151–1163.  
 Ashton KG, Tracy MC, de Queiroz A. 2000. Is Bergmann's rule valid for mammals? *Am Nat* 156:390–415.  
 Auerbach BM. 2007. Human skeletal variation in the New World during the Holocene: effects of climate and subsistence across geography and time. Ph.D. dissertation, Johns Hopkins University School of Medicine.  
 Auerbach BM, Ruff CB. 2004. Human body mass estimation: a comparison of "morphometric" and "mechanical" methods. *Am J Phys Anthropol* 125:331–342.  
 Beals KL, Smith CL, Dodd SM. 1984. Brain size, cranial morphology, climate, and time machines. *Curr Anthropol* 25:301–330.  
 Bergmann C. 1847. Über die Verhältnisse der Wärmeökonomie der Thiere zu ihren Grösse. *Göttinger Studien* 1:595–708.  
 Bogin B, Smith P, Orderi AB, Varela Silva MI, Loucky J. 2002. Rapid change in height and body proportions of Maya American children. *Am J Hum Biol* 14:753–761.  
 Buikstra JE, Ubelaker DH. 1994. Standards for data collection from human skeletal remains. Fayetteville, Arkansas: Arkansas Archaeological Survey. Report number 44.  
 Cipriani L. 1966. The Andaman Islanders. Weidenfeld and Nicolson: London.  
 Cavalli-Sforza LL. 1986. African Pygmies: an evaluation of the state of research. In: Cavalli-Sforza LL, editor. *African Pygmies*. Orlando: Academic Press. p 361–426.  
 Cowling RM, Hilton-Taylor, C. 1997. Phytogeography, flora and endemism. In: Cowling RM, Richardson DM, Pierce SM, editors. *Vegetation of Southern Africa*. Cambridge: Cambridge University Press. p 43–61.  
 Crawhall, N. 2006. Languages, genetics and archaeology: problems and the possibilities in Africa. In: Soodyall H, editor. *The prehistory of Africa*. Johannesburg: Jonathan Ball. p 109–124.  
 Cushman JH, Lawton JH, Manly BFJ. 1993. Latitudinal patterns in European ant assemblages: variation in species richness and body size. *Oecologia* 95:30–37.  
 Deacon H. 1993. Planting an idea: an archaeology of stone age gatherers in South Africa. *S Afr Archaeol Bull* 48:86–93.  
 Deacon H, Deacon J. 1999. Human beginnings in South Africa. Cape Town: David Philip.  
 Franciscus RG, Holliday TW. 1992. Hindlimb skeletal allometry in Plio-Pleistocene hominids with special reference to AL-288-1 ("Lucy"). *Bull Mem Soc Anthropol Paris* 22:1–16.  
 Gaston KJ, Blackburn TM, Spicer JJ. 1998. Rapoport's rule: time for an epitaph? *Trends Ecol Evol* 13:70–74.  
 Hiernaux J, Froment A. 1976. The correlations between anthropobiological and climatic variables in sub-Saharan Africa: revised estimates. *Hum Biol* 48:757–767.  
 Hiernaux J, Rudan P, Brambati A. 1975. Climate and the weight/height relationship in sub-Saharan Africa. *Ann Hum Biol* 2:3–12.  
 Holliday TW. 1995. Body size and proportions in the Late Pleistocene Western Old World and the origins of modern humans. Ph.D. dissertation, University of New Mexico.  
 Holliday TW. 1997. Postcranial evidence of cold adaptation in European neandertals. *Am J Phys Anthropol* 104:245–258.  
 Holliday TW. 2002. Body size and postcranial robusticity of European upper Paleolithic hominins. *J Hum Evol* 43:513–528.  
 Holliday TW, Falsetti AB. 1995. Lower limb length of European early modern humans in relation to mobility and climate. *J Hum Evol* 29:141–153.  
 Kaspari M, Vargo E. 1995. Does colony size buffer environmental variation? Bergmann's rule and social insects. *Am Nat* 145:610–632.  
 Katzmarzyk PT, Leonard WR. 1998. Climatic influences on human body size and proportions: ecological adaptations and secular trends. *Am J Phys Anthropol* 106:483–503.

- Lee RB. 1993. The Dobe Ju/'hoansi. Fort Worth: Harcourt Brace College Publishers.
- Lomolino MV, Sax DF, Riddle BR, Brown JH. 2006. The island rule and a research agenda for studying ecogeographical patterns. *J Biogeogr* 33:1503–1510.
- Martin R, Saller K. 1957. *Lehrbuch der Anthropologie*. Stuttgart: Gustav Fischer Verlag.
- Mayr E. 1953. *Animal species and evolution*. Cambridge, Mass: Harvard University Press.
- Meiri S, Dayan T. 2003. On the validity of Bergmann's rule. *J Biogeogr* 30:331–351.
- Meiri S, Dayan T, Simberloff D. 2004. Carnivores, biases and Bergmann's rule. *Biol J Linn Soc* 81:579–588.
- Migliano AB. 2005. Why are Pygmies small? Ontogenetic implications of life history evolution, Ph.D. dissertation, University of Cambridge, Cambridge.
- Migliano AB, Vinicius L, Lahr MM. Life history trade-offs explain the evolution of human pygmies. *Proc Natl Acad Sci USA*, in press.
- Millien V, Lyons K, Olson L, Smith FA, Wilson AB, Yom-Tov Y. 2006. Ecotypic variation in the context of global climate change: revisiting the rules. *Ecol Lett* 9:853–869.
- Mitchell PJ. 2002. *The archaeology of Southern Africa*. Cambridge, UK: Cambridge University Press.
- Morris AG. 1992. A master catalogue: holocene human skeletons from South Africa. Johannesburg: Witwatersrand University Press.
- Nurse GT, Weiner JS, Jenkins T. 1985. *The peoples of Southern Africa and their affinities*. Oxford: Clarendon Press.
- Parkington JE. 2001. Mobility, seasonality and Southern African hunter-gatherers. *S Afr Archaeol Bull* 173/174:1–7.
- Pearson OM. 2000a. Activity, climate, and postcranial robusticity: implications for modern human origins and scenarios of adaptive change. *Curr Anthropol* 41:569–607.
- Pearson OM. 2000b. Postcranial remains and the origin of modern humans. *Evol Anthropol* 9:229–247.
- Pfeiffer S, Sealy J. 2006. Body size among Holocene foragers of the Cape Ecozone, Southern Africa. *Am J Phys Anthropol* 129:1–11.
- Radcliffe-Brown AR. 1964. *The Andaman Islanders*. New York: The Free Press.
- Roberts DF. 1953. Body weight, race and climate. *Am J Phys Anthropol* 11:533–558.
- Roberts DF. 1973. Climate and human variability. An Addison-Wesley module in anthropology, Vol. 34. Reading, MA: Addison-Wesley.
- Rodríguez MA, López-Sañudo IL, Hawkins BA. 2006. The geographic distribution of mammal body size in Europe. *Global Ecol Biogeogr* 15:173–181.
- Ruff CB. 1988. Hindlimb articular surface allometry in Hominoidea and Macaca, with comparisons to diaphyseal scaling. *J Hum Evol* 17:687–714.
- Ruff CB. 1991. Climate and body shape in hominid evolution. *J Hum Evol* 21:81–105.
- Ruff CB. 1994. Morphological adaptation to climate in modern and fossil hominids. *Am J Phys Anthropol* 37:65–107.
- Ruff CB, Trinkaus E, Holliday TW. 1997. Body mass and encephalization in Pleistocene *Homo*. *Nature* 387:173–176.
- Ruff CB, Trinkaus E, Holliday TW. 2002. Body proportions and size of Lagar Velho 1. In: Zilhao J, Trinkaus E, editors. *Portrait of the artist as a child. The Gravetian human skeleton from the Abrigo do Lagar Velho and its archaeological context*. Lisbon: Instituto Portugees de Arqueologia. p 365–391.
- Ruff CB, Trinkaus E, Walker A, Larsen CS. 1993. Postcranial robusticity in *Homo*, I: temporal trends and mechanical interpretation. *Am J Phys Anthropol* 91:21–53.
- Rutherford MC, Westfall RH. 1986. Biomes of Southern Africa: an objective categorization. *Mem Bot Surv S Afr* 54:1–98.
- Schulze RE. 1997. Climate. In: Cowling RM, Richardson DM, Pierce SM, editors. *Vegetation of Southern Africa*. Cambridge: Cambridge University Press. p 21–42.
- Sealy J, Pfeiffer S. 2000. Diet, body size and landscape use among Holocene peoples in the Southern Cape. *South Africa. Curr Anthropol* 41:642–655.
- Shea BT, Bailey RC. 1996. Allometry and adaptation of body proportions and stature in African Pygmies. *Am J Phys Anthropol* 100:311–340.
- Smith P, Horwitz LK, Kaplan E. 1992. Skeletal evidence for population change in the Late Holocene of the south-western Cape: a radiological study. *S Afr Archaeol Bull* 47:82–88.
- Sokal RR, Rohlf FJ. 1995. *Biometry*. New York: W. H. Freeman.
- Stock JT. 2002. Climatic and behavioural influences in postcranial robusticity among Holocene foragers, Ph.D. dissertation, Toronto, University of Toronto.
- Stock JT, Pfeiffer SK. 2004. Long bone robusticity and subsistence behaviour among Later Stone Age foragers of the forest and fynbos biomes of South Africa. *J Archaeol Sci* 31:999–1013.
- Tanner JM, Hayashi T, Preece MA, Cameron N. 1982. Increase in length of leg relative to trunk in Japanese children and adults from 1957 to 1977: comparison with British and with Japanese Americans. *Ann Human Biol* 9:411–423.
- Trinkaus E. 1981. Neanderthal limb proportions and cold adaptation. In: Stringer CB, editor. *Aspects of human evolution*. London: Taylor and Francis. p 187–224.
- Truswell AS, Hansen JDL. 1976. Medical research among the Kung. In: Lee RB, De Vore I, editors. *Kalahari Hunter-gatherers: studies of the Kung San and their neighbors*. Cambridge, Mass: Harvard University Press. p 166–194.
- Walker R, Gurven M, Hill K, Migliano A, Chagnon N, de Souza R, Djurovic G, Hames R, Hurtado AM, Kaplan H, Kramer K, Oliver W, Vaeggia C, Yamauchi T. 2006. Growth rates and life histories in twenty-two small-scale societies. *Am J Hum Biol* 18:295–311.
- Weaver TD. 2002. A multi-causal functional analysis of hominid hip morphology, Ph.D. dissertation, Stanford, CA, Stanford University.
- Weaver TD. 2003. The shape of the Neandertal femur is primarily the consequence of a hyperpolar body form. *Proc Natl Acad Sci USA* 100:6926–6929.
- Wilson ML, Lundy JK. 1994. Estimated living statures of dated Khoisan skeletons from the south-western coastal region of South Africa. *S Afr Archaeol Bull* 49:2–8.