The Ontogeny of Holocene and Late Pleistocene Human Postcranial Strength

Libby W. Cowgill*

Department of Anthropology, University of Central Florida, Orlando, FL 32816-1361

KEY WORDS growth; Neandertal; humerus; femur

ABSTRACT While a wide variety of studies have focused on population variation in adult cross-sectional properties, relatively little is known about population variation in postcranial robusticity in immature individuals. Furthermore, the age at which the population differences readily detected in adults manifest during growth is also unknown. This research addresses these gaps in our current understanding through the analysis of immature humeral and femoral long bone strength. Cross-sectional geometry was used to compare the developmental trajectories of diaphyseal strength in Late Pleistocene Neandertal and modern human subadults to a sample of immature humans from seven geographically diverse Holocene populations. Population differences in size-standardized cross-sectional properties appear to be systemic and develop very early in ontogeny in the Holocene sample. In many cases, these differences are present before one year of age. In general, the Late Pleistocene fossil samples fit within the range of recent human variation in long bone strength. Population differences detected here are likely related to a combination of factors including activity patterns, genetic propensities, and nutritional status. These results highlight the complex mosaic of processes that result in adult postcranial robusticity, and suggest that further exploration of the developmental interplay between intrinsic and extrinsic influences on skeletal robusticity will likely enhance our understanding of adult postcranial morphology. Am J Phys Anthropol 141:16–37, 2010.

Cross-sectional geometry has proven to be a valuable tool for reconstructing the activity patterns of both archaeological and paleontological human groups for over 30 years. Holocene and Late Pleistocene skeletal robusticity has been frequently investigated, and the range of variation of adult postcranial strength during these time periods is reasonably well established. Studies of adult remains have identified several consistent trends in postcranial strength that vary both temporally and spatially (Kimura and Takahashi, 1982; Ruff et al., 1993; Trinkaus, 1997; Churchill et al., 2000; Shackelford, 2005). These analyses have highlighted biobehavioral contrasts and similarities among Neandertals, early modern humans, and recent human populations in both habitual limb use and levels of populational mobility.

Although the body of research exploring ontogenetic acquisition of postcranial robusticity is relatively smaller than that focusing on adults, this slowly growing area of inquiry has contributed much to current understanding of the developmental processes underlying adult long bone strength (Van Gerven et al., 1985; Ruff et al., 1994; Sumner and Andriacchi, 1996; Trinkaus and Ruff, 1996; Nelson and Thompson, 2000; Kondo and Dodo, 2002a,b; Trinkaus et al., 2002a,b; Ruff, 2003a,b; Ramsay et al., 2005; Thompson and Nelson, 2005; Cowgill and Hagar, 2007; Cowgill et al., 2007; Robbins, 2007). While several studies have explored long bone strength in recent human children with important results (Van Gerven et al., 1985; Sumner and Andriacchi, 1996; Ruff, 2003a,b), few have looked at developmental variation in long bone strength in multiple populations. In addition, analyses of immature Late Pleistocene individuals have frequently been hampered by small sample sizes or limited to the analysis of a single individual. Nonetheless, Late Pleistocene immature postcrania follow patterns similar to those of adults: in general, many are relatively robust, with large cross-sectional areas and/or great torsional strength, but they tend to fall well within the range of recent human variation (Ruff et al., 1994; Trinkaus and Ruff, 1996; Odwak, 2000; Kondo and Dodo, 2002a; Trinkaus et al., 2002a,b; Cowgill et al., 2007).

These studies are of particular interest, as recently several researchers have suggested that mechanical loading before maturity may have a disproportionate effect on levels of adult postcranial strength (Lieberman et al., 2001; Lovejoy et al., 2002, 2003; Pearson and Lieberman, 2004). In an experimental study of diaphsyseal response to mechanical loading in sheep, Leiberman et al. (2001) detected significant differences in cross-sectional properties between exercised and control animals, but found that these differences occurred primarily in juveniles. In addition, Lovejoy et al. (2003) has suggested that adult bone structure is primarily a product of genetic background and subadult activities.

These critiques are certainly not without merit, given that human growth does not occur in a biomechanical

Grant sponsor: Leakey Foundation, Wenner-Gren Foundation. Grant sponsor: NSF; Grant number: BCS-0549925.

*Correspondence to: Libby W. Cowgill, Department of Anthropology, University of Central Florida, 4000 Central Florida Blvd., Howard Phillips Hall, 309 Orlando, FL 32816-1361, USA.
E-mail: lcowgill@mail.ucf.edu

Received 17 December 2008; accepted 23 April 2009

DOI 10.1002/ajpa.21107
Published online 15 June 2009 in Wiley InterScience (www.interscience.wiley.com).

TABLE 1. Sample description, size, and subsistance strategy

Sample	Location	Approx. time period	Subsistance	Humeri sample size	Femora sample size
California Amerindian	Northern California	500–4600 BP	Hunters and gatherers (semisedentary)	63	92
Dart	Johannesburg, South Africa	20th century	Mixed urban and rural	72	73
Indian Knoll	Green River, Kentucky	4143–6415 BP	Hunters and gatherers (semisedentary)	88	95
Kulubnarti	Batn el Hajar, Upper Nubia	Medieval	Agriculturalist	92	98
Luis Lopes	Lisbon, Portugal	20th century	Urban	27	47
Mistihalj	Bosnia-Herzegovina	Medieval (15th century)	Pastoralists	45	52
Point Hope	Point Hope, Alaska	300–2100 BP	Arctic hunters and gatherers	37	65

vacuum. It is unlikely that there is a developmental rubicon before which mechanical forces are not influential in shaping skeletal morphology, and they may even play a role in the earliest phases of limb morphogenesis (Henderson and Carter, 2002). Several studies have documented the effects of fetal immobilization on long bone growth, and suggested that normal osteological development is dependent on intermittent muscular contractions in utero (Hall, 1972; Rodríguez et al., 1988). Finite element models of ossification patterns in the cartilaginous fetal femur imply that diaphyseal shear stress is essential for the regulation of ossification during growth (Carter et al., 1987; Carter and Wong, 1988; Carter and Beaupré, 2001), further highlighting the fact that the relationship between bone and its mechanical environment is critical even prior to birth.

A variety of research on animal and human models supports the idea that elevated levels of mechanical loading in growing bone result in increased bone material and geometric properties (Woo et al., 1981; Biewener et al., 1986; McCulloch et al., 1992; Conroy et al., 1993; Grimston et al., 1993; Slemenda and Johnston, 1993; Biewener and Bertram, 1994; Kanuus et al., 1995; Mosley et al., 1997; Haapasalo, 1998; Haapasalo et al., 1998; Nordström et al., 1998; Schönau, 1998; Pettersson et al., 2000a,b; Söderman et al., 2000; Bass et al., 2002; Kontulainen et al., 2003). In fact, the combination of hormonal factors unique to the growth period may serve to make immature bone even more sensitive to mechanical loading than adult bone (Steinberg and Trueta, 1981; Raab et al., 1990). Steinberg and Trueta (1981) compared bone response to treadmill running in young and mature rats and found that while the bones of young rats had significantly greater bone density and cortical thickness as early as 1 week after the start of the experiment, the bone of mature rats showed no alterations. In clinical studies of human children, only very moderate levels of exercise were found necessary to elicit an osteogenic response (Bradney et al., 1998; McKay et al., 2000).

Lastly, the positive effects of exercise on bone mass during growth are long-lasting. In a study of retired dancers, self-reported hours of ballet class between the ages of 10 and 12 were positively correlated with bone mineral density in adults (Khan et al., 1998). Retired gymnasts, soccer players, weightlifters, and even recreational exercisers show similar benefits (Kriska et al., 1988; Teegarden et al., 1996; Bass et al., 1998; Micklesfield et al., 2003). The osteological benefits of mechanical loading during growth can be detected in retired adults for up to 20 years (Karlsson et al., 1995).

Despite the wealth of evidence that mechanical loading is instrumental in directing diaphyseal modeling during growth, it is highly unlikely that this single factor acts alone. Both genetic propensities and systemic nutritional factors likely play a complex role in cortical bone growth and maintenance by affecting bone metabolism and turnover and may alter mechanosensitivity to biomechanical stimulation (Adams, 1968; Kodama et al., 2000). The examination of the development of population-level differences in long bone strength over the course of growth may permit the exploration of the complex interchange among loading, genetics, and nutrition, providing further information about the intrinsic and extrinsic factors that influence cortical bone geometry over the life history of an individual.

RESEARCH OBJECTIVES

The goal of this research is to compare the development of femoral and humeral robusticity in a diverse sample of immature Holocene and Late Pleistocene remains in order to establish when population-level differences in postcranial strength develop during growth. Three research questions will be addressed:

1. Do populations differ in femoral and humeral strength before maturity?
2. If so, when do these differences emerge during ontogeny?
3. Do immature Late Pleistocene Neandertals and early modern humans differ from Holocene groups in their levels of humeral and femoral robusticity?

MATERIALS

The primary data for this analysis consist of right humeral and femoral cross-sectional properties from seven Holocene samples and a sample of Late Pleistocene Neandertals and early modern humans, all less than eighteen years of age.

Holocene samples

Cross-sectional properties from a total of 522 femora and 424 right humeri were collected from immature Holocene individuals. The seven Holocene samples were selected to represent the broadest possible range of time periods, geographic locations, and subsistence strategies. As such, these sampled populations vary in genetic background, daily activity levels, body proportions, and other intrinsic and extrinsic factors that may play a role in postcranial strength. In addition, diet and health was likely highly variable, with at least one sample (Kulub-

narti) showing clear indications of persistent nutritional deprivation (Van Gerven et al., 1995). Detailed descriptions of all of the Holocene samples are provided in the appendix. Table 1 includes samples sizes, locations, time periods, general subsistence strategies.

Late Pleistocene samples

The 75 immature Late Pleistocene specimens used in this analysis are presented in Table 2. While I collected the majority of the Late Pleistocene data from the original fossil specimens, data for this analysis were collected from plastic casts in three instances (Amud 7, Teshik Tash 1, and Balla 1, limited to measurements of total area only); from published sources for six individuals (Dederiyeh 1 and 2, Arene Candide 1, Dolní Vestonice 14, Lagar Velho 1, Yamashita-cho 1); and from previously unpublished data provided by Erik Trinkaus for six individuals (Kiik Koba 2, Krapina 168 and 177, Skhul 1, Sunghir 2 and 3).

While fetal material was generally excluded from the comparative sample, less stringent criteria were employed in the Late Pleistocene fossil group. At 68 and 63 mm, respectively, La Ferrassie 5 and Cro-Magnon 5D possess estimated femoral lengths that are small for a full-term infant (Fazekas and Kósa, 1978). However, given modern human variation in long bone length at birth and the difficulty with directly applying modern human standards to Late Pleistocene infants, La Ferrassie 5 and Cro-Magnon 5D are included in this analysis.

Late Pleistocene archaic humans. The geographic range for this sample spans sites in France (La Ferrassie, Le Moustier, Roc de Marsal), Germany (Ehringsdorf), Spain (Cova Negra), Italy (Buca del Tasso), Croatia (Krapina), Israel (Amud), Syria (Dederiyeh), Ukraine (Kiik Koba), and Uzbekistan (Teshik Tash). While the degree of precision with which this sample has been dated varies widely, the geological time frame of the archaic fossil group ranges from ~40,000 BP to 200,000 BP years.

Late Pleistocene early modern humans. The majority of the early modern human sample is from Europe and the Near East, although multiple individuals from North Africa (Taforalt) and one from east Asia (Yamashita-cho) are included. This sample includes sites from France (Abri Pataud, Cro-Magnon, Le Figuier, La Madeleine), Italy (Arene Candide, Barma Grande, Maritza, Romanelli), Portugal (Lagar Velho), Hungary (Balla), Czech Republic (Dolní Věstonice), Israel (El Wad, Skhul, Qafzeh), Russia (Sunghir), Japan (Yamashito-cha), and Morocco (Taforalt). The Taforalt sample is the only large immature Late Pleistocene sample, and includes the primarily isolated remains of 44 immature individuals from a Moroccan ossuary (Ferembach et al., 1962).

Early modern humans in this sample date between ~130,000 BP and 10,000 BP years. The sample of Late Pleistocene early modern humans has been divided into three temporal and cultural categories: Middle Paleolithic, Early Upper Paleolithic (~35–20 ky BP) and Late Upper Paleolithic (20–10 ky BP), following the approach of Shackelford (2005) and maintaining the distinction between Upper Paleolithic preglacial and postglacial maximum samples. While this division results in a small anatomically modern Middle Paleolithic sample, and a Late Upper Paleolithic sample dominated by individuals from Taforalt, it best preserves the behavioral and technological differences that are likely to affect postcranial strength.

TABLE 2. List of Late Pleistocene specimens included in this analysis

	Femur	Humerus	Age (years)
Neandertals			
Undescribed Amud[a]	X		neonatal[b]
Amud 7		X	0.34
Buco del Tasso 2[a]	X		7.8[b]
Cova Negra femur 1	X		3.7[b]
Dederiyeh 1	X	X	1.25
Dederiyeh 2	X		1.67
Ehringsdorf G		X	12.2[b]
Kiik-Koba 2		X	0.41[b]
Krapina 168		X	3.1[b]
Krapina 177		X	7.1[b]
La Ferrassie 4b	X		0.15
La Ferrassie 5	X		neonatal[b]
La Ferrassie 6	X		2.4[b]
Le Moustier 2	X	X	neonatal
Roc de Marsal 1[a]	X	X	2.5[b]
Teshik Tash 1	X		9.9
MP AMH			
Qafzeh 10	X	X	5.3
Skhul 1	X		3.3
Skhul 8	X		8.5[b]
Early UP AMH			
Abri Pataud 26.234A		X	13.3[b]
Arene Candide 1	X		16.4
Balla 1	X	X	1.5[b]
Barma Grande 3[a]		X	13.5
Cro-Magnon 5A		X	1.6[b]
Cro-Magnon 5B	X		neonatal[b]
Cro-Magnon 5C[a]	X		neonatal[b]
Cro-Magnon 5D[a]	X		neonatal[b]
Cro-Magnon 5E[a]	X		neonatal[b]
Dolní Věstonice 14	X	X	17.5
Lagar Velho 1	X		4.7
Sunghir 2	X	X	11.7
Sunghir 3		X	9.9
Yamashita-cho 1	X		6[b]
Late UP AMH			
Arene Candide 5b[a]	X	X	2.8
Arene Candide 8[a]	X	X	5.5
Arene Candide 11[a]	X	X	2.4[b]
Arene Candide 15	X	X	15.9
El Wad 10252	X	X	17.6
El Wad 10257		X	14.1
El Wad 10311	X	X	10.7
El Wad 10312	X		neonatal[b]
El Wad 10313	X	X	9.7[b]
El Wad 10314	X		6.3
El Wad 10315	X	X	10.0
Le Figuier 1		X	2.1
La Madeleine 4[a]	X	X	3.3
Maritza 1	X		7.0
Romanelli 3	X		0.9
Taforalt	26	14	N/A

[a] Indicates cross-sections reconstructed used the eliptical model method.
[b] Ages predicted from long bone length.

METHODS

Aging

The ages for all Late Pleistocene remains are shown in Table 2. Although these ages are likely to be inexact, these are the best point estimates that were used for the

TABLE 3. Comparative sample age prediction regression formulae by sample, and the percentage of each sample aged based on long bone length

Sample	Independant	Constant	Slope	R^2	SEE	% of sample
Dart						13
2 years and younger (n=34)	Femur	−2.5044	0.0299	0.918	0.261	
	Tibia	−2.6999	0.0379	0.902	0.286	
	Humerus	−3.2195	0.0452	0.895	0.296	
3 years and older (n=42)	Femur	−5.2839	0.0513	0.892	1.328	
	Tibia	−4.3335	0.0572	0.824	1.627	
	Humerus	−5.4632	0.0741	0.865	1.433	
Kulubnarti						4
2 years and younger (n=34)	Femur	−3.7339	0.0360	0.850	0.491	
	Tibia	−3.7180	0.0427	0.828	0.520	
	Humerus	−4.3860	0.0526	0.822	0.535	
3 years and older (n=61)	Femur	−5.8857	0.0526	0.807	1.622	
	Tibia	−5.9737	0.0620	0.796	1.621	
	Humerus	−7.2532	0.0811	0.820	1.569	
Mistihalj						8
2 years and younger (n=26)	Femur	−2.1673	0.0247	0.888	0.299	
	Tibia	−2.3164	0.0316	0.892	0.308	
	Humerus	−2.4260	0.0332	0.829	0.330	
3 years and older (n=29)	Femur	−9.2075	0.0613	0.871	1.569	
	Tibia	−8.8494	0.0744	0.877	1.558	
	Humerus	−10.5049	0.0918	0.882	1.554	
Indian Knoll						20
2 years and younger (n=19)	Femur	−3.0986	0.0312	0.662	0.545	
	Tibia	−2.8966	0.0355	0.579	0.602	
	Humerus	−3.7621	0.0462	0.556	0.626	
3 years and older (n=72)	Femur	−8.3439	0.0610	0.901	1.501	
	Tibia	−7.3568	0.0690	0.922	1.343	
	Humerus	−8.7387	0.0868	0.920	1.337	
California						50
2 years and younger (n=52)	Femur	−2.5538	0.0299	0.479	0.717	
	Tibia	−1.9406	0.0283	0.633	0.410	
	Humerus	−3.0874	0.0424	0.743	0.416	
3 years and older (n=70)	Femur	−7.6619	0.0583	0.928	1.241	
	Tibia	−6.1320	0.0642	0.906	1.396	
	Humerus	−7.9375	0.0833	0.926	1.248	
Point Hope						29
2 years and younger (n=8)	Femur	−2.9823	0.0308	0.903	0.279	
	Tibia	−3.0705	0.0396	0.843	0.350	
	Humerus	−3.9345	0.0470	0.819	0.480	
3 years and older (n=61)	Femur	−6.7552	0.0574	0.849	1.540	
	Tibia	−5.9412	0.0681	0.830	1.651	
	Humerus	−7.6418	0.0844	0.888	1.311	

purposes of this analysis. While reliable ages have previously been determined for many of the Late Pleistocene individuals used in this study, the following aging protocol was used to determine age in this analysis in order to maintain internally consistent ages.

Age estimation from dentition. With the exception of the Luis Lopes sample, age was unknown for all the samples used in this study, and crown and root formation evaluated from lateral mandibular radiographs was used whenever dental and postcranial remains were reliably associated. Crown and root formation was assessed following the developmental standards set by Smith (1991) for permanent dentition and Liversidge and Molleson (2004) for deciduous dentition. Each set of dentition was scored twice on two consecutive days, and individual teeth that produced different dental stage scores were evaluated a third time to resolve inconsistencies.

While several studies of tooth formation rates have suggested that Neandertal dental development was accelerated relative to both Upper Paleolithic and recent human populations (Ramerez Rossi and Bermudez de Castro, 2004; Smith et al., 2007), other analyses have found that Neandertal tooth formation rates are similar to those of modern humans (Guatelli-Steinberg et al., 2005; Macchiarelli et al., 2006). The lack of consensus on this issue necessitates that this study assume immature Neandertal and modern human development are approximately equivalent, and that they can be dentally aged based on the same criterion.

Age estimation from long bone length. When no dentition was directly associated with the postcranial remains, developmental age was predicted from within sample Least Squares regression of femoral, tibial, or humeral length on age for each of the comparative samples in order to maximize sample size (Table 3). By developing age-prediction equations specific to each sample, difficulties arising from the application of a formula developed on individuals differing in body size or proportions to an archaeological target sample are partially mitigated. The comparative samples were divided into two age categories to preserve linearity of the regression line.

Prediction of age in Late Pleistocene specimens using long bone length was necessary in order to include the

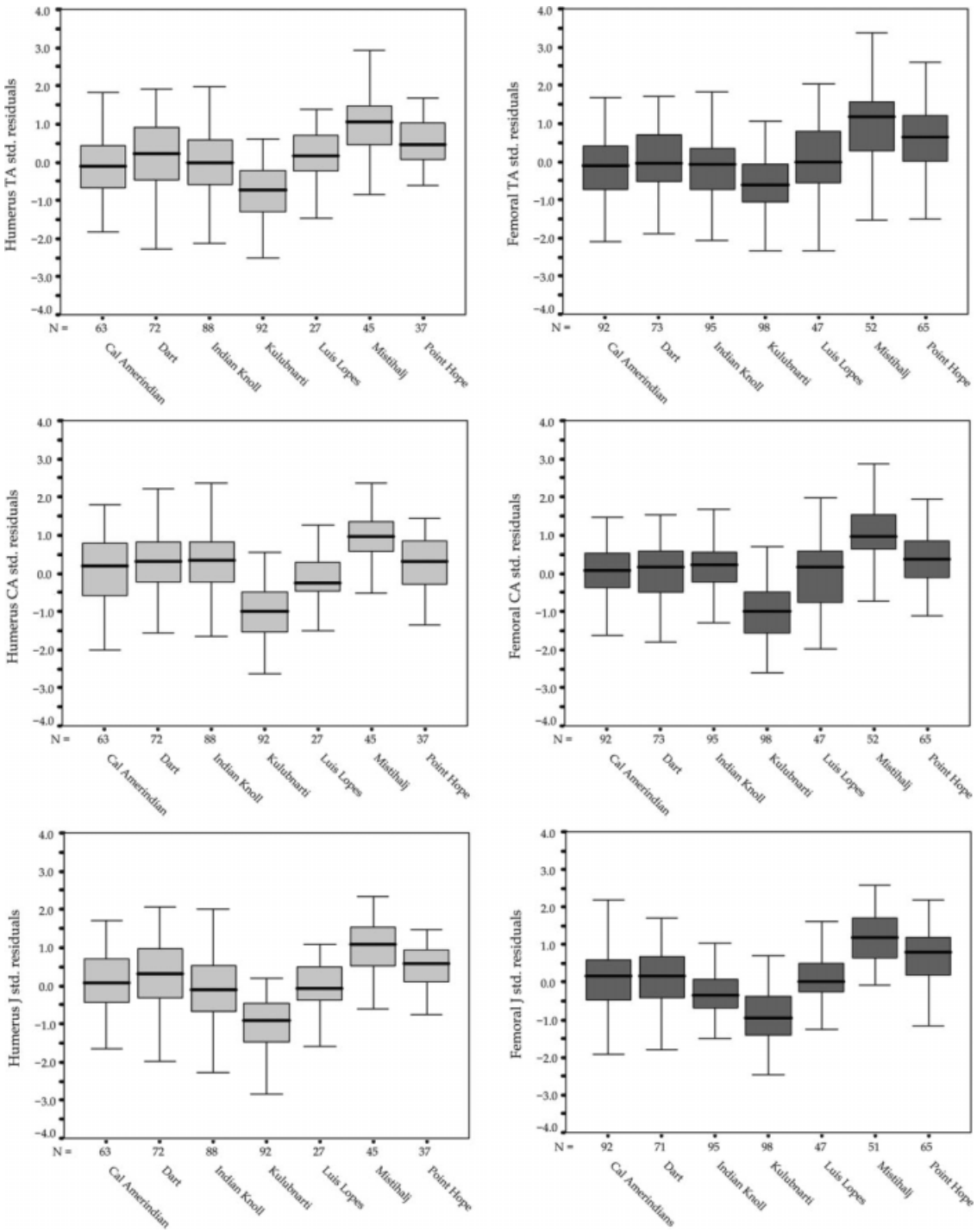

Fig. 1. Sample sizes and boxplots of population-specific residual medians for femoral and humeral properties (all ages).

numerous isolated elements in this sample. However, achieving accurate ages was methodologically challenging, given that, in most cases, Late Pleistocene sample size was not sufficiently large to generate sample-specific age prediction regression formulae. In these cases, formulae generated from the comparative sample were used to predict age. The appropriate regression formulae were selected primarily on the basis of possessing body size and body proportion characteristics analogous to the target Late Pleistocene sample. For individuals where dental age was known, age predicted from long bone length was compared to dental age to check for consistency.

The specific fossil individuals for which age was estimated from long bone length are marked with asterisks in Table 2. The Point Hope age prediction regression was used to predict age of immature Neandertals. Comparisons between dental ages and ages predicted from long bone length in the cases where both were available revealed that in all cases except one (Dederiyeh 1), the

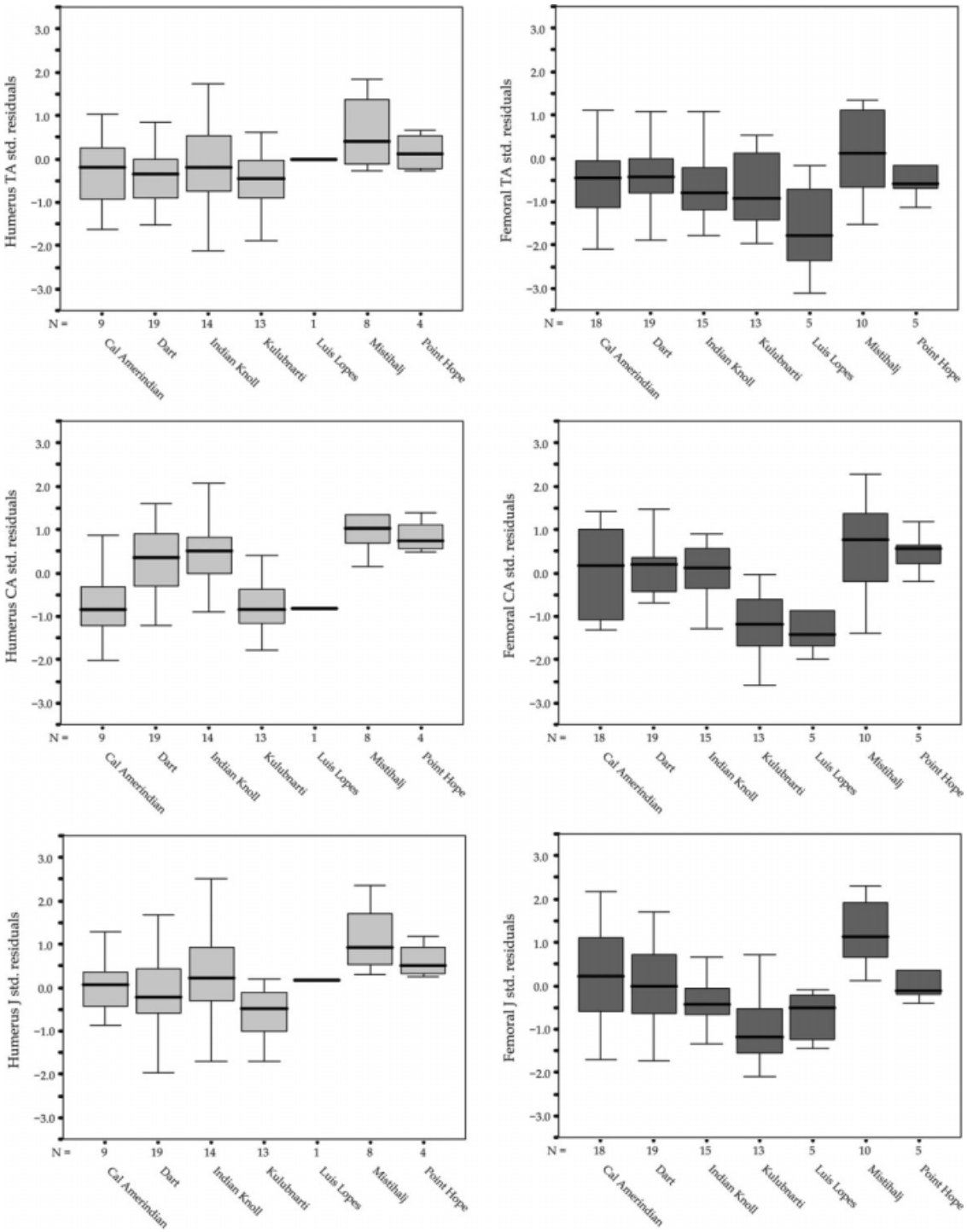

Fig. 2. Sample sizes and boxplots of population-specific residual medians for femoral and humeral properties (<1 year).

Point Hope regression formulae underestimated the dental age. Therefore, a correction factor of 6 months was added to the Neandertal ages estimated using the Point Hope regression formulae. The fact that this was necessary suggests that Neandertals, even relative to a cold-adapted population of short stature such as Point Hope, were very small bodied for their age during growth (or, perhaps, that dental development was relatively advanced).

Given the relatively tall statures and Nilotic body proportions from Middle Paleolithic and Early Upper Paleolithic modern human populations (Formicola and Giannecchini, 1999; Holliday, 1999), an ideal developmental reference sample would possess both these characteristics. However, comparison of the known dental ages to ages predicted from long bone length indicates that none of the comparative sample regression formulae are a particularly good match for these fossil groups, due to the

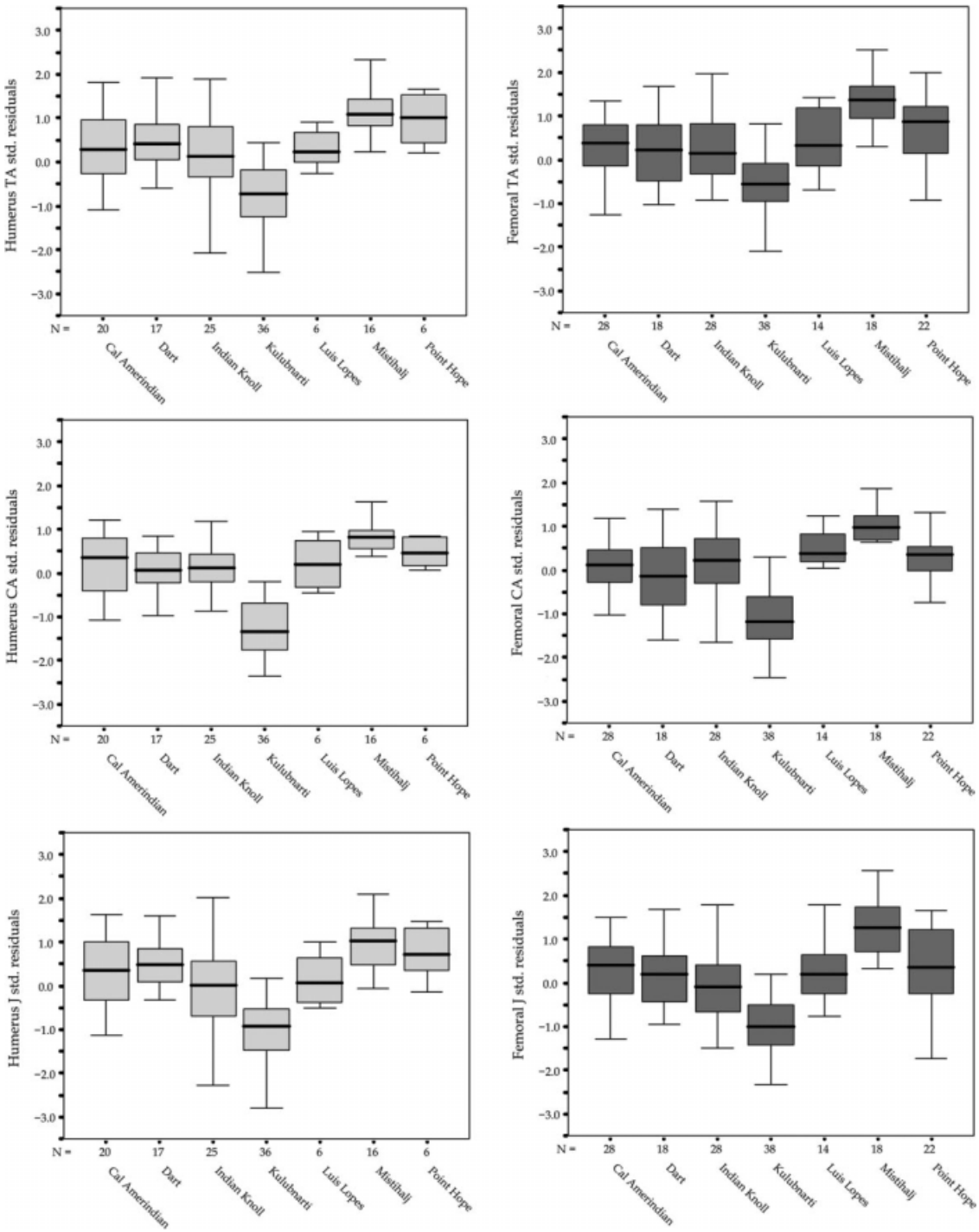

Fig. 3. Sample sizes and boxplots of population-specific medians for femoral and humeral properties (1.0–5.9 years).

relatively greater stature of the Middle and early Upper Paleolithic immature individuals. Therefore, despite small sample sizes, the best solution was to predict age for the earliest modern humans based on a regression of long bone biomechanical length on dental age within this group. Age was estimated for individuals in the Late Upper Paleolithic using formulae from the Mistihalj sample, which provided the best "match" in terms of moderate body size and temperate body proportions (Churchill et al., 2000).

Age categories. The samples were analyzed in four age groups: birth to 0.9 years, 1.0–5.9 years, 6.0–11.9 years, and 12.0–17.9 years. The first age category is restricted to the first year of life in order to explore very early differences in long bone strength; subsequent categories are somewhat broader, but are sufficiently narrow to determine if the patterns detected in the first age category are maintained consistently throughout growth. Population-specific sample sizes for each age group are included with Figures 1–6.

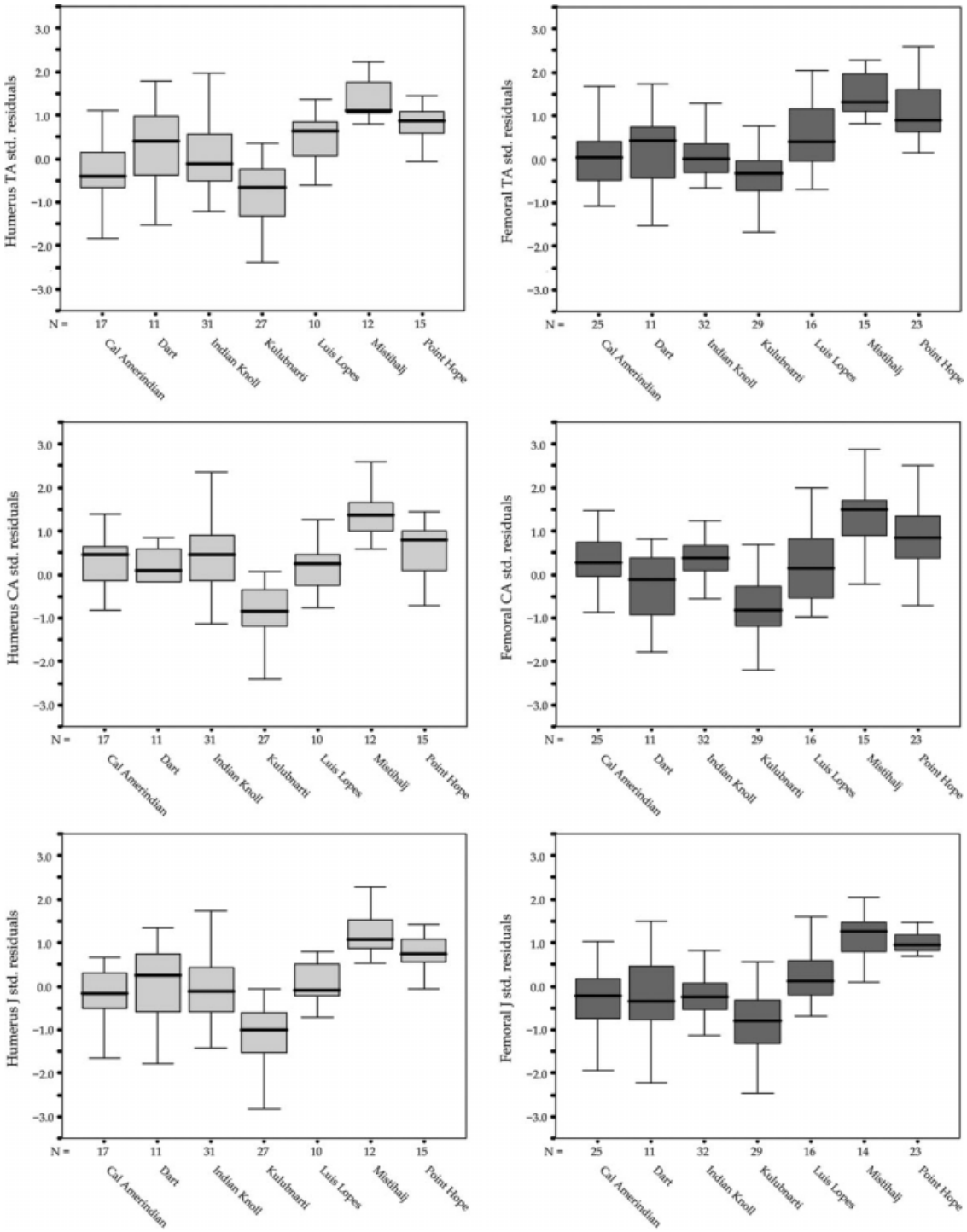

Fig. 4. Sample sizes and boxplots of population-specific medians for femoral and humeral properties (6.0–11.9 years).

Reconstruction of cross-sectional properties

The primary data for this analysis consist of the midshaft total areas, cortical areas, and polar second moment of areas of immature femora and right humeri. All cross-sectional properties in the comparative collection and the vast majority of the fossil sample were collected using a method similar to O'Neill and Ruff's (2004) "latex cast method" (LCM) and the method used by Sakaue (1998), which rely on anteroposterior and mediolateral radiographs and silicone molding putty. However, external contour molds were not possible in 11 cases due to fossil fragility, museum protocol, or extremely small long bone diaphyses (see Table 2). For these individuals, cross-sectional properties were calculated using the "ellipse model method" (EMM), which

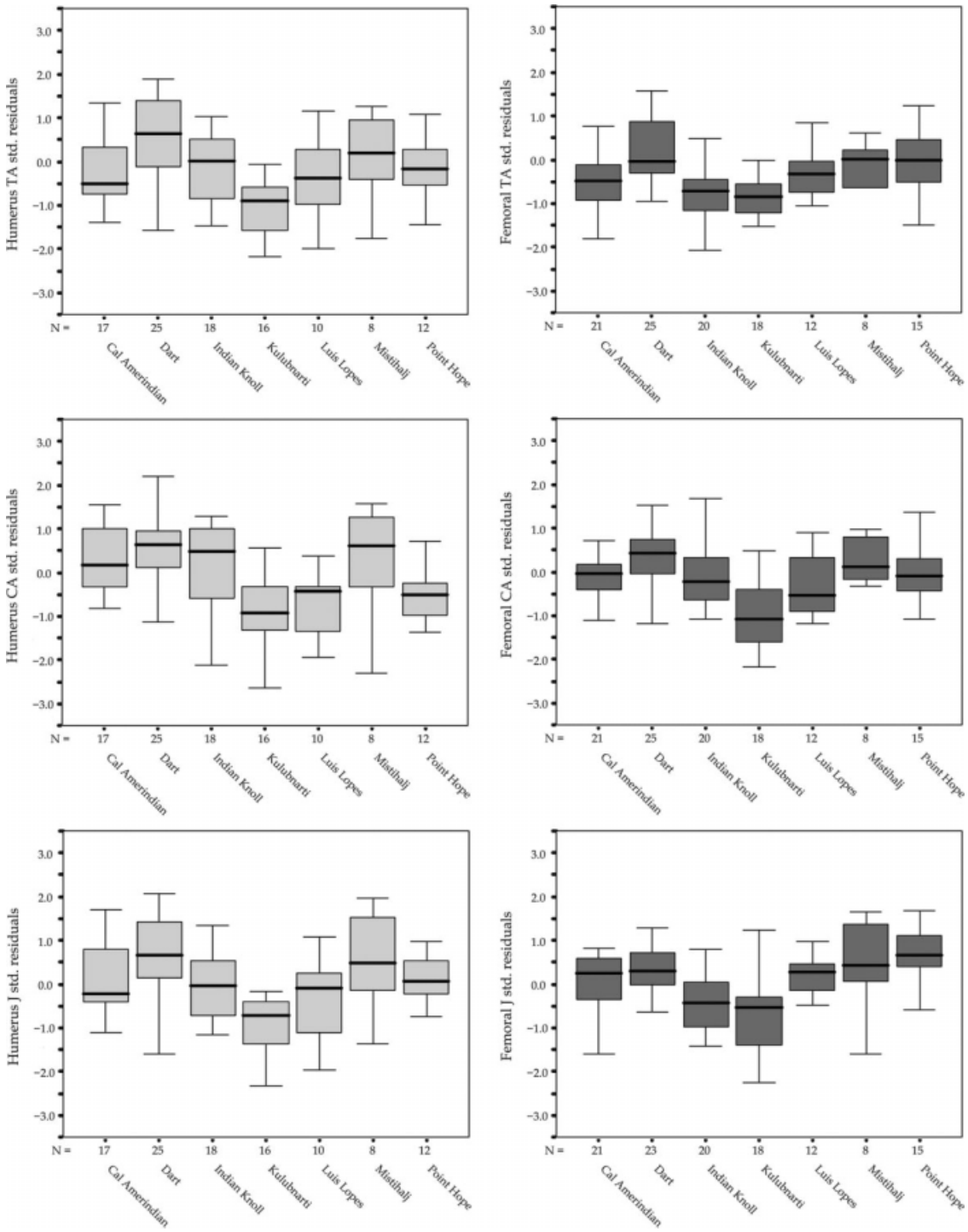

Fig. 5. Sample sizes and boxplots of population-specific medians of femoral and humeral properties (>12 years).

relies on biplanar radiography alone (O'Neill and Ruff, 2004). When compared with the LCM, the EMM tends to overestimate cross-sectional properties in adults, and a formula has been calculated to correct EMM femoral cross-sections for this error (O'Neill and Ruff, 2004). However, since the amount of error increases as the cross-section deviates from an elliptical shape, individuals in this analysis were not corrected using this formula, as immature long bone cross-sections frequently approximate an ellipse (Ruff, 2003a,b). In addition, published data were available for several individuals (Trinkaus and Ruff, 1996; Holt, 1999; Kondo and Dodo, 2002a,b; Trinkaus et al., 2002a,b, 2006), and the Kiik-Koba 2 humerus had a fracture located near mid-shaft, where cross-sectional properties were reconstructed directly from scaled photographs of the exposed diaphyseal break.

Biomechanical length for unfused humeri and femora were measured following Trinkaus et al. (2002a,b).

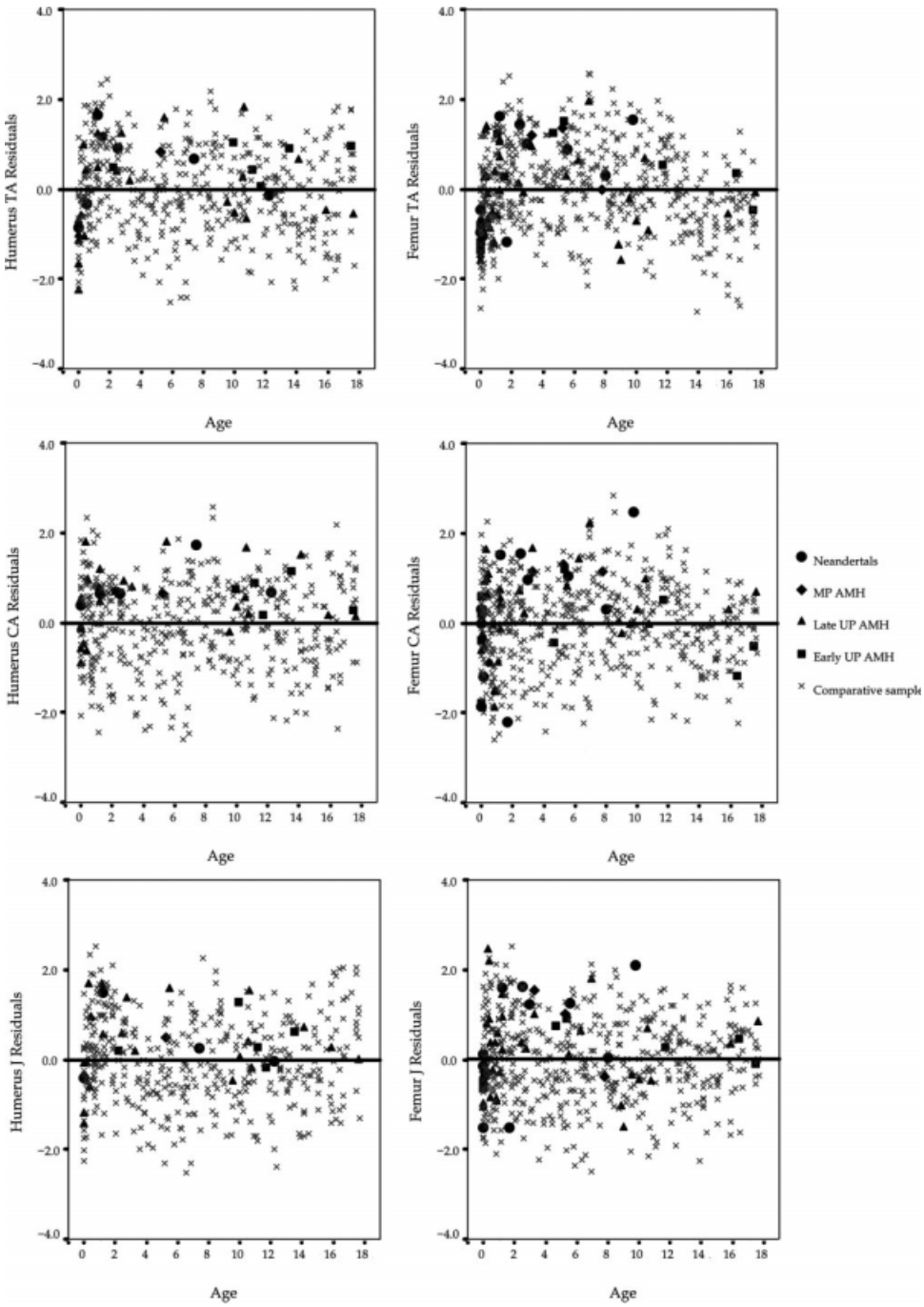

Fig. 6. Scatterplots of standardized residuals from both Late Pleistocene and comparative samples on age.

Cross-sectional levels were chosen to best approximate the 50% section level in fused elements. For humeri, 50% of intermetaphyseal biomechanical length was used, as the proximal and distal epiphyses contribute about equally in length to the measurement of biomechanical length in fused elements (Ruff, personal communication). In immature femora, however, the 50% level was calculated as 45.5% of femoral intermetaphyseal length, as this measurement best corresponds to the location of the 50% level in individuals with fused distal femoral epiphyses due to the relatively larger contribution of the distal epiphysis to biomechanical length in fused femora (Ruff, 2003b).

To reconstruct the femoral and humeral cross-sectional properties, the external surface of the diaphysis was molded with Cuttersil Putty Plus™ silicone molding putty. Anterior, posterior, medial and lateral cortical bone widths were measured with digital calipers, and measurements were corrected for parallax distortion by comparing external breadths measured on the radiograph with external breaths measured on the element at each section level. Once corrected for parallax, the four

TABLE 4. Sample sizes, means, and confidence intervals for body mass/leg length residuals

Sample	N	Mean	CI Upper bound	CI Lower bound
Dart	72	−0.4684	−0.2055	−0.7313
Indian Knoll	89	−0.3665	−0.1891	−0.5440
Kulubnarti	90	−0.2243	−0.0725	−0.3761
Cal Amerindian	69	0.3408	0.5302	0.1515
Point Hope	49	0.3761	0.6618	0.0905
Mistihalj	44	0.4938	0.7286	0.2589
Luis Lopes	44	0.5194	0.9092	0.1296

cortical bone measurements were plotted onto the two-dimensional copy of the original mold, and the endosteal contours were interpolated by using the subperiosteal outline as a guide. The resultant sections were enlarged on a digitizing tablet, and the endosteal and periosteal contours digitized. Cross-sectional properties were computed from the sections in a PC-DOS version of SLICE (Nagurka and Hayes, 1980; Eschman, 1992). All elements in the fossil sample were digitized twice and averaged in order to minimize tracing error.

Size standardization

Body mass prediction. Despite continued discussion of appropriate scaling factors for humeral diaphyseal robusticity (Churchill, 1994; Ruff, 2000a), both humeral and femoral cross-sectional properties were standardized by body mass or body mass and beam length^2 in this analysis. Body mass was predicted based on formulae developed specifically for immature individuals, which predict body mass from femoral distal metaphyseal M-L breadth and femoral head size (Ruff, 2007; personal communication). Within the comparative sample, the femoral metaphyseal breadth measurement was not available for ~17% of younger individuals possessing one lower limb element, and in these cases femoral metaphyseal breadth was predicted from proximal tibial metaphyseal M-L breadth (r^2 = 0.925, all comparative samples under 13.5 years). In addition, body mass prediction regression formulae in Ruff's original study (2007) did not attain significance for infants under 4 months of age or 15-year-old. Therefore, within sample interpolation and extrapolation was necessary to provide body masses for these age groups in this analysis.

In the 2007 paper, where Ruff developed the regression formulae for body mass prediction in juveniles, he cautioned that his formulae had not been tested on immature individuals from different populations. While these formulae have since been used on other samples (Sciulli and Blatt, 2008), it is still not entirely clear if these formulae are capable of producing body mass estimates which reflect ecogeographic differences in body shape. As body mass varies with latitude and has a strong effect of postcranial robusticity, it is necessary to briefly investigate whether the body mass estimates used to standardize cross-sectional properties in this analysis are reasonably congruent with what would be predicted based on the original geographic location of the sample populations.

To fully explore this issue is beyond the scope of this study. However, to provide a rough estimate of body mass versus height, body mass values were divided by maximum femoral + tibial length. This ratio was then regressed on age using a quadratic equation (Body mass/(FEM+TIB) = 0.00011(Age) + 0.00014 (Age) + 0.03407, r^2 = 0.871; $P < 0.001$), and the residuals from this regression were used to evaluate population differences. Means, sample sizes, and confidence intervals for the body mass/leg length residuals are shown in Table 4.

TABLE 5. Mean crural indices by population

	N	Mean
Kulubnarti	91	0.8473
Dart	72	0.8429
Indian Knoll	89	0.8378
Cal Amerindian	69	0.8338
Mistihalj	44	0.8219
Luis Lopes	44	0.8115
Point Hope	49	0.7980

In general, the results of the analysis of body mass/leg length are congruent with what are expected based on crural indices, the only other measure of body proportions available for this analysis (Table 5), although the correspondence is not exact. While body mass relative to leg length is generally high in populations from temperate and cold environments (Luis Lopes, Mistihalj, and Point Hope) and low in populations with higher crural indices (Dart and Kulubnarti), the Native American populations are rather variable. The lack of precise correspondence between the two indicators of body proportions does not necessarily indicate that the body masses predicted here are not reasonably accurate at the population level, given that a more relevant independent skeletal estimate of body mass would have been bi-iliac breadth, had that measurement not been impossible to collect on unfused skeletal remains. Based on the general relationship between the predicted body masses and what was previously known about the body proportions of individuals in these samples, it seems that the regression formulae from Ruff (2007) are applicable to populations differing in body shape from the original test sample.

Statistical standardization. To remove the effect of body mass on humeral and femoral cross-sectional properties, logged cross-sectional properties were regressed on logged body mass (total and cortical area) or logged body mass × beam length^2 (polar second moment of area) using OLS regression. The use of body mass × beam length^2 to standardize the polar second moment of area is based on beam deflection theory, and is the correct factor to include in order to control for the same relative deflection of a beam under loading (Biewener, 1992; Ruff, personal communication). Standardized residuals, which are the raw residuals divided by the standard deviation of residuals, were then used in comparisons of population differences.

Sample comparisons

To determine if populations in the comparative sample differed during growth, nonparametric Kruskal-Wallis tests were used to evaluate population differences in body mass standardized residuals between birth and age eighteen, with Mann-Whitney U tests employed to determine what specific populations differed. To establish when these population differences emerged during development, the comparative sample was divided into four age categories and the patterns of population-level differences in postcranial strength were evaluated separately

TABLE 6. Results of Mann-Whiteney pair-wise comparisons of femoral and humeral properties (all ages)

		Cal Amerindian	Dart	Indian Knoll	Kulubnarti	Luis Lopes	Mistihalj	Point Hope
				Femoral cross-sectional properties				
Cal Amerindian	TA				0.000*		0.000*	0.000*
	CA				0.000*		0.000*	0.012
	J			0.001*	0.000*		0.000*	0.000*
Dart	TA				0.000*		0.000*	0.000*
	CA				0.000*		0.000*	0.031
	J			0.001*	0.000*		0.000*	0.000*
Indian Knoll	TA				0.000*		0.000*	0.000*
	CA				0.000*		0.000*	0.078
	J		0.019		0.000*	0.002*	0.000*	0.000*
Kulubnarti	TA	0.000*	0.000*	0.000*		0.000*	0.000*	0.000*
	CA	0.000*	0.000*	0.000*		0.000*	0.000*	0.000*
	J	0.000*	0.000*	0.000*		0.000*	0.000*	0.000*
Luis Lopes	TA				0.000*		0.000*	0.003*
	CA		0.026	0.014	0.000*		0.000*	0.032
	J				0.000*		0.000*	0.000*
Mistihalj	TA	0.000*	0.000*	0.000*	0.000*	0.000*		0.022
	CA	0.000*	0.000*	0.000*	0.000*	0.000*		0.000*
	J	0.000*	0.000*	0.000*	0.000*	0.000*		0.002*
Point Hope	TA	0.002*		0.003*	0.000*	0.060	0.005*	
	CA				0.000*		0.000*	
	J	0.004*		0.000*	0.000*	0.002*	0.002*	
				Humeral cross-sectional properties				

* Significant with multiple comparison corrections.

in each age sub-sample. When comparing the level of humeral and femoral robusticity in the fossil samples to that found in the comparative sample, it was generally possible to treat the temporally-divided Late Pleistocene sub-samples as small samples, and avoid evaluating each specimen as an individual datum point. However, in some analyses, the available fossil sample was simply too small for this to be statistically feasible. When this was the case, adjusted z-scores were calculated in order to evaluate the likelihood of a given fossil specimen being a member of the recent human population of age-appropriate subadults (Sokal and Rohlf, 1995).

Bonferroni corrections are frequently employed to reduce the probability of spurious positive results when multiple analyses are conducted. However, with these corrections comes a serious loss of statistical power, leading some researchers to question their widespread use and raise several issues with the procedure (Perneger, 1998; Moran, 2003; Nakagawa, 2004). Moran (2003) argues that while the possibility of finding one significant result due to chance is quite high, the likelihood of finding several is dramatically lower. In addition, it is difficult to decide how and when to apply Bonferroni corrections, as there are no well established standards. Lastly, the practical ramifications of the use of Bonferroni corrections may actually act to discourage complex, detailed analyses: the more samples and variables included in the analysis, the lower the probability of detection of significant results (Moran, 2003; Nakagawa, 2004). Because of the large number of comparative samples, initial alpha levels with multiple comparison corrections in this analysis are less than 0.002. Like Moran and others, I would argue that careful, logical evaluation of the results of these analyses is preferable to the widespread rejection of nonsignificant results out of hand, particularly when sample differences present clear and reasonable patterns. Therefore, while sequentially reductive Bonferroni adjustments (Holms, 1979; Rice, 1989) are made and reported in this study's statistical tables, priority is given to results that indicate plausible biological patterns in the discussion of these results.

RESULTS

Comparative sample

All ages. Kruskal-Wallis tests of population differences across all pooled ages were significant for all body mass standardized femoral and humeral properties ($P < 0.001$). Sample sizes and boxplots of medians for humeral and femoral standardized residuals for all ages are shown in Figure 1. The results of pair-wise Mann-Whitney comparisons for both elements are shown in Table 6. In both the upper and lower limb, significantly different pair-wise comparisons reflect very low values of diaphyseal strength in the Kulubnarti sample, and high values at Mistihalj and Point Hope.

Age birth to 0.9 years. All femoral properties under the age of 1 year show significant population differences (TA: $P = 0.048$; CA and J: $P < 0.001$), and all humeral properties except total area are significantly different at the population level (CA: $P < 0.001$; J: $P = 0.004$). Sample sizes and boxplots of medians for humeral and femoral standardized residuals between birth and 0.9 years are shown in Figure 2, and the results of the pair-wise comparisons for this age category are shown in Table 7. Kulubnarti and Luis Lopes possess relatively weak femora and humeri, whereas Mistihalj and Point Hope are already showing elevated levels of diaphyseal strength. Although the population medians for humeral diaphyseal strength are generally following the same trends as seen in the entire comparative sample, the results of the Mann-Whitney population comparisons only highlight relatively high values at Mistihalj. Both boxplots and the population comparisons, however, show population variation even at this early age.

Age 1.0–5.9 years. Sample sizes and boxplots of population medians (Fig. 3) and the results of Mann-Whitney

TABLE 7. Results of Mann-Whitney pair-wise comparisons femoral and humeral properties (<1 year)

		Cal Amerindian	Dart	Indian Knoll	Kulubnarti	Luis Lopes	Mistihalj	Point Hope
				Femoral cross-sectional properties				
Cal Amerindian	TA						0.039	
	CA				0.002*	0.031		
	J				0.002*		0.013	
Dart	TA							
	CA				0.000*	0.043		
	J				0.005		0.001*	
Indian Knoll	TA							
	CA				0.001*	0.032		
	J				0.023		0.000*	
Kulubnarti	TA						0.022	
	CA		0.010	0.002*			0.001*	0.003
	J						0.000*	0.016
Luis Lopes	TA						0.015	
	CA						0.008	0.028
	J						0.002*	
Mistihalj	TA							
	CA	0.007	0.008	0.032	0.001*			
	J	0.015	0.002*	0.017	0.000*			0.027
Point Hope	TA							
	CA				0.009			
	J				0.013			
				Humeral cross-sectional properties				

* Significant with multiple comparison corrections.

TABLE 8. Results of Mann-Whitney comparisons of femoral and humeral properties (1.0–5.9 years)

		Cal Amerindian	Dart	Indian Knoll	Kulubnarti	Luis Lopes	Mistihalj	Point Hope
				Femoral cross-sectional properties				
Cal Amerindian	TA				0.000*		0.000*	0.046
	CA				0.000*		0.000*	
	J				0.000*		0.000*	
Dart	TA				0.003*		0.000*	0.024
	CA				0.001*	0.023	0.000*	
	J				0.000*		0.000*	
Indian Knoll	TA				0.000*		0.000*	0.026
	CA				0.000*		0.000*	
	J				0.000*		0.000*	
Kulubnarti	TA	0.000*	0.000*	0.000*		0.000*	0.000*	0.000*
	CA	0.000*	0.000*	0.000*		0.000*	0.000*	0.000*
	J	0.000*	0.000*	0.000*		0.000*	0.000*	0.000*
Luis Lopes	TA				0.002*		0.000*	
	CA				0.000*		0.007	
	J				0.001*		0.001*	
Mistihalj	TA	0.003*	0.002*	0.000*	0.000*	0.003*		0.006
	CA	0.010	0.000*	0.000*	0.000*	0.033		0.000*
	J	0.024	0.028	0.001*	0.000*	0.018		0.002*
Point Hope	TA			0.030	0.000*	0.055		
	CA				0.000*			
	J				0.000*			
				Humeral cross-sectional properties				

* Significant with multiple comparison corrections.

comparisons (Table 8) for individuals in this age group generally show a strengthening of the pattern detected in the pooled-ages sample. All femoral and humeral properties show significant population differences between 1.0 and 5.9 years of age ($P < 0.001$). The pattern of humeral and femoral strength among populations is very similar. Significant differences in this age group highlight the very gracile diaphyses at Kulubnarti, in contrast to the strong femora and humeri at Mistihalj, with a few population differences between Point Hope and other groups.

Age 6.0–11.9 years. All femoral and humeral properties show significant population differences between 6.0 and 11.9 years of age ($P < 0.001$). Sample sizes and boxplots of population medians are shown in Figure 4, and the results of Mann-Whitney comparisons are displayed in Table 9. Again, the results are similar to the previous age group. Differences between Kulubnarti and Mistihalj are maintained in this age group, and Point Hope shows significantly higher humeral strength than several other samples.

Age 12.0–17.9 years. Finally, over the age of 12, Kruskal-Wallis comparisons indicate that all femoral and humeral properties display significant population-level differences ($P \leq 0.001$). Inspection of population medians indicate that, in general, the same trends that began in

TABLE 9. Results of Mann-Whitney comparisons for femoral and humeral properties (6.0–11.0 years)

		Cal Amerindian	Dart	Indian Knoll	Kulubnarti	Luis Lopes	Mistihalj	Point Hope
				Femoral cross-sectional properties				
Cal Amerindian	TA						0.000*	0.000*
	CA				0.000*		0.000*	0.010
	J				0.002*		0.000*	0.000*
Dart	TA						0.001*	0.019
	CA			0.039			0.000*	0.003*
	J						0.001*	0.001*
Indian Knoll	TA				0.014		0.000*	0.000*
	CA				0.000*		0.000*	0.018
	J				0.000*	0.024	0.000*	0.000*
Kulubnarti	TA	0.021	0.006	0.000*		0.003*	0.000*	0.000*
	CA	0.000*	0.002*	0.000*		0.003*	0.000*	0.000*
	J	0.000*	0.005	0.000*		0.000*	0.000*	0.000*
Luis Lopes	TA	0.014			0.000*		0.004	0.032
	CA				0.000*		0.002*	0.028
	J				0.000*		0.001*	0.001*
Mistihalj	TA	0.000*	0.027	0.000*	0.000*	0.007		
	CA	0.000*	0.001*	0.000*	0.000*	0.002*		0.041
	J	0.000*	0.012	0.000*	0.000*	0.001*		
Point Hope	TA	0.000*		0.000*	0.000*		0.025	
	CA		0.031		0.000*		0.011	
	J	0.000*		0.000*	0.000*	0.007	0.051	
				Humeral cross-sectional properties				

* Significant with multiple comparison corrections.

TABLE 10. Results of Mann-Whitney comparisons for femoral and humeral properties (>12 years)

		Cal Amerindian	Dart	Indian Knoll	Kulubnarti	Luis Lopes	Mistihalj	Point Hope
				Femoral cross-sectional properties				
Cal Amerindian	TA		0.002*					0.030
	CA		0.018		0.005			
	J			0.018	0.004			0.015
Dart	TA			0.000*	0.000*	0.027		
	CA			0.028	0.000*	0.027		0.037
	J			0.000*	0.000*			
Indian Knoll	TA							0.016
	CA				0.010			0.641
	J					0.013	0.017	0.000*
Kulbnarti	TA	0.004	0.000*	0.004		0.028	0.026	0.007
	CA	0.000*	0.000*	0.005			0.030	0.007
	J	0.001*	0.000*	0.010		0.002*	0.005	0.000*
Luis Lopes	TA	0.451			0.073			
	CA				0.429			
	J				0.051			0.045
Mistihalj	TA	0.351	0.378	0.470	0.007	0.183		
	CA	0.560	0.933	0.541	0.012	0.051		
	J	0.221	0.801	0.182	0.001*	0.131		
Point Hope	TA	0.658		0.866	0.001*		0.487	
	CA		0.003		0.227		0.045	
	J	0.626		0.446	0.000*	0.356	0.280	
				Humeral cross-sectional properties				

* Significant with multiple comparison corrections.

the first year of life and solidified between 1 and 6 years of age are apparent during adolescence: Kulubnarti has relatively weak diaphyses; Mistihalj and Point Hope have relatively strong femora and humeri, with the only anomaly being the exceptionally high levels of humeral strength in the Dart sample for this age group (Fig. 5 and Table 10). Patterns of population differences appear to be relatively stable across the entire developmental age range and are reasonably consistent between the upper and lower limb. Table 11 shows a relative ranking of the populations by the means of their standardized residuals for femoral and humeral polar moment of area across all age categories to illustrate the general consistency of this trend across ontogeny.

Fossil samples

Among the fossil samples, none of the femoral properties show significant differences among groups, both within the Late Pleistocene sample and between the Late Pleistocene groups and the comparative sample (TA: $P = 0.260$; CA: $P = 0.084$; J: $P = 0.290$). For the right humerus, however, there are significant differences in cortical area (CA: $P = 0.010$). Figure 6 contains scat-

TABLE 11. Relative ranking of the population means of standardized residuals for femoral and humeral polar moment of area across all age categories

Relative Ranking of Samples			
Under age 1	Age: 1–6 years	Age: 6–12 years	Age: 12–18 years
Femoral second polar moment of area			
1. Mistihalj	1. Mistihalj	1. Mistihalj	1. Point Hope
2. Cal Amerindian	2. Point Hope	2. Point Hope	2. Mistihalj
3. Point Hope	3. Cal Amerindian	3. Luis Lopes	3. Dart
4. Dart	4. Luis Lopes	4. Cal Amerindian	4. Luis Lopes
5. Indian Knoll	5. Dart	5. Dart	5. Cal Amerindian
6. Luis Lopes	6. Indian Knoll	6. Indian Knoll	6. Indian Knoll
7. Kulubnarti	7. Kulubnarti	7. Kulubnarti	7. Kulubnarti
Humeral second polar moment of area			
1. Mistihalj	1. Mistihalj	1. Mistihalj	1. Mistihalj
2. Point Hope	2. Point Hope	2. Point Hope	2. Dart
3. Luis Lopes	3. Dart	3. Luis Lopes	3. Cal Amerindian
4. Indian Knoll	4. Cal Amerindian	4. Dart	4. Point Hope
5. Cal Amerindian	5. Luis Lopes	5. Indian Knoll	5. Indian Knoll
6. Dart	6. Indian Knoll	6. Cal Amerindian	6. Luis Lopes
7. Kulubnarti	7. Kulubnarti	7. Kulubnarti	7. Kulubnarti

terplots of the standardized residuals from both Late Pleistocene and comparative samples. Mann-Whitney comparisons indicate that both Neandertals and Late Upper Paleolithic individuals have relatively larger cortical areas than the comparative sample (Neandertal-Comparative: $P = 0.048$; Late Upper Paleolithic-Comparative: $P = 0.018$) (see Fig. 7). When the fossil samples are divided into broad age groups to determine when these trends begin (greater than and less than 10 years of age), differences between the fossil and comparative sample are nonsignificant.

DISCUSSION

Possible limitations of study

To maximize both Late Pleistocene and Holocene sample size, several levels of estimation were employed, and it is necessary to evaluate how these manipulations of the data may have affected the results of this analysis. While ages for most of the sample were determined from crown and root development, lack of association between postcranial and dental remains occasionally necessitated prediction of developmental age from long bone length. Within the fossil samples, it is debatable whether modern human standards are appropriate for establishing age in immature Neandertals, and, in this analysis, a correction factor of six months was added to predicted Neandertal ages to make them congruent with known dental ages in other Neandertal individuals. At first inspection, it may seem that the level of error introduced into this study through the aging of both fossil and recent specimens could heavily bias the results.

However, this is unlikely to be the case. The primary units of analysis used in this study are standardized residuals from the regression of cross-sectional properties on body mass and/or body mass multiplied by beam length^2. Therefore, the ages estimated in this study only serve to place individuals into relatively large age categories, but are not utilized in the actual construction or evaluation of the data. For example, in the analysis of the femoral geometric properties in the fossil samples as a whole, where the residuals of the all the Late Pleistocene samples are compared to the residuals of the Holocene samples without age categories, the actual developmental ages, however estimated, are not actually used. The fossil analysis is almost "age free."

The only way the aging errors could affect the results is if individual specimens on the border of age categories are misclassified and placed in inappropriate age categories. However, even this is not great cause for concern because the population patterns detected in this analysis are consistent over the course of growth and between age categories. Since populations that display high or low levels of postcranial strength in the first age category tend to remain that way throughout development, placing a few individuals in the incorrect age category is unlikely to influence the actual results.

Population differences

Although comparisons of cross-sectional properties in more than one immature sample have been previously undertaken (Cowgill and Hager, 2007; Robbins, 2007), this represents the first time the developmental acquisition of long bone strength has been evaluated in such a large sample of immature individuals from diverse genetic, temporal and geographic backgrounds. The results of this analysis indicate that differences in diaphyseal strength are present during growth, and that they develop very early in ontogeny, likely before the age of one year. In addition, these differences appear to be systemic; patterns of population-level variation are consistent between the upper and lower limb.

However, there are few differences that exist between immature Late Pleistocene individuals and more recent groups. The relative paucity of significant differences within the fossil samples is not surprising, given that few exist in adults, particularly in the lower limb. Once controlled for body mass, relative levels of lower limb robusticity remained relatively constant during the Late Pleistocene (Trinkaus, 1997; Trinkaus and Ruff, 1999; Holliday, 2002), although diaphyseal shape does vary (Trinkaus, 1997; Holt, 1999, 2003; Churchill et al., 2000). Adult humeral diaphyseal robusticity follows a bimodal distribution through the Late Pleistocene, exhibiting a gradual decline from Middle Paleolithic Neandertals to Middle Upper Paleolithic humans, followed by an increase in robusticity during the Late Upper Paleolithic

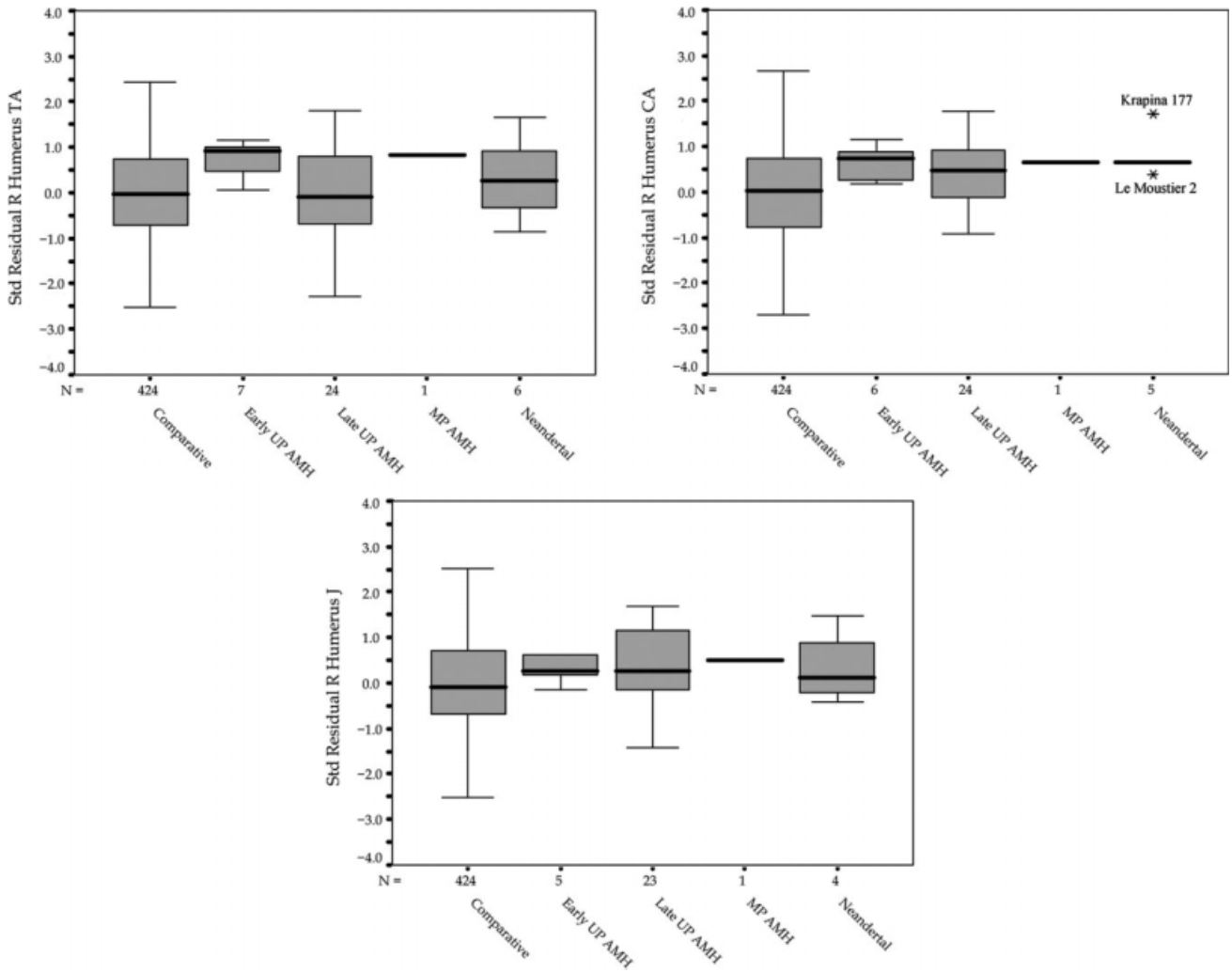

Fig. 7. Sample sizes and boxplots of fossil subsample residual medians for right humeral properties (all ages).

(Trinkaus, 1997; Churchill et al., 2000). The sample of immature Middle Paleolithic modern humans may be too small to detect the relatively weak humeri that have been documented in Middle Paleolithic adults (Trinkaus, 1997; Trinkaus and Churchill, 1999). Immature Late Upper Paleolithic humans consistently show elevated values of cortical area in the right humerus, which is at least roughly consistent with the patterns documented in adults from this time period (Churchill et al., 2000; Holt, 2003).

The lack of many significant differences between immature Late Pleistocene samples and recent humans is perhaps more surprising based on previous research in adults. Previous research comparing long bone strength in adults has detected a steady decline in average femoral robusticity from early *Homo* into the Holocene (Ruff et al., 1993). However, the range of variation in recent human femoral robusticity completely subsumes the range of variation in Late Pleistocene Neandertal and early modern human femoral strength (Ruff et al., 1993). Recently, Shackelford (2005) has suggested that the decrease in long bone strength during the Holocene may not be universal, as individual samples, such as the Jomon Japanese and Anadaman Islanders, show highly elevated levels of postcranial robusticity. Therefore, it remains possible that in studies of diverse samples restricted to more narrow time ranges, the degree of overlap between Holocene and Late Pleistocene samples may be large enough to prevent significant statistical differences from being found.

In general, however, the results reported here are not incompatible with previous analyses of single immature Late Pleistocene individuals. While comparisons of the femoral cortical area of La Ferrassie 6 and Teshik-Tash 1 show a slight increase in postcranial robusticity relative to immature recent humans (Ruff et al., 1994), other studies of immature Late Pleistocene individuals have detected few differences between fossil and recent specimens. The femur of Legar Velho 1 displays relatively thin cortical bone and was found to be only slightly above average in femoral robusticity when compared to the Denver Growth Sample (Trinkaus et al., 2002a). The early modern human, Yamashita-cho 1, falls near the limits but within the range of recent human variation in measures of cross-sectional shape, cortical area, and polar moment of area (Trinkaus and Ruff, 1996). Geometric properties of the femur of Dederiyeh 1 are generally above the means, but within the range of values seen in recent children between the ages of one and two; however, the femur of Dederiyeh 2 is less robust than simi-

larly aged recent remains (Kondo and Dodo, 2002a,b). Odwak (2000) found that the humeral and tibial cortical and medullary areas of Amud 7 were indistinguishable from modern children, and the tibia of the recently discovered Shanidar 10 infant also displays a level of robusticity close to that recent humans of similar developmental age (Cowgill et al., 2007). Given this, it is possible that the slightly elevated levels of long bone strength detected in adult populations may take most of the growth period to develop, despite the very early differences in postcranial strength found among some samples here (see below).

Activity patterns and long bone strength during growth

The evidence that bone functionally adapts to its mechanical environment is overwhelming (see Ruff et al., 2006 for a review), and the results of the analyses of Holocene samples conform loosely to what would be expected based on what is known about their activity patterns (see Apendix). In general, individuals from Point Hope and Mistihalj show elevated levels of postcranial robusticity, whereas individuals from Kulubnarti display very low levels of postcranial strength. Individuals from Point Hope were likely to be participating in a highly active hunting and gathering economy, primarily focused on caribou hunting, and later, whaling (Larsen and Rainey, 1948). Although the sample from Mistihalj is derived of pastoralists, two additional factors may be contributing to the very high values of long bone strength detected in this analysis. First, this population was seasonally migratory and likely to be highly mobile. Second, terrain may have an influence on the elevated lower limb strength found in this sample. Individuals from Mistihalj were spending summers in the highland pastures and winters in the warmer coastal valleys, necessitating movement over hilly or mountainous landscapes (Alexeeva et al., 2003). Previous analyses of adults have found that terrain has a strong effect on levels of postcranial robusticity, with individuals from mountainous regions possessing relatively stronger lower limbs than those from coastal environs (Ruff, 2000b).

However, it is difficult for arguments based solely on mechanical loading to explain all the differences detected in this analysis. While children in active populations were likely participating in similarly physically demanding lifestyles, it is hard to argue the case that this alone could be responsible for producing population differences before the age of one.

Genetic propensities and long bone strength during growth

Genetic factors may play a part in the very early developmental differences detected in this study. Previous research documenting different levels of mechanosensitivity in mice hints at the possibility that this could be a factor in human populations, particularly human populations separated by large spans of time and space (Akhter et al., 1998; Kodama et al., 2000; Robling and Turner, 2002). Akhter et al. (1998) used a four-point bending device to apply in vivo loads to the tibia in C57BL/6J and C3H/HeJ mice, and found that after loading, medullary area, total area, and cross-sectional moment of inertia were significantly larger in C57BL/6J mice than in C3H/HeJ mice. In addition, under similar levels of loading, different breeds of mice appear to possess different genetic adaptations for obtaining increased bone strength (Akhter et al., 2000; Turner et al., 2001). If genetic differences between groups could alter the magnitude of bone response to mechanical loading, it is possible that even the relatively low level of mechanical stimuli due to muscle contractions experienced by the fetus in utero could have an effect on neonatal limb strength. While genetic evidence suggests a possible explanation for the very early differences detected here, further research is necessary to determine if the differences in mechanosensitivity between laboratory-bred animal strains are applicable to natural populations.

Nutrition and long bone strength during growth

The Kulubnarti sample, consistently on the low end of the robusticity continuum, may be a reflection of another combination of factors known to effect cortical bone growth, particularly nutrition and maternal environment. Previous studies of the Kulubnarti sample have concluded that individuals from this site were experiencing severe and persistent nutritional stress and that their diets included almost no protein component (Van Gerven et al., 1995). In this context, the extremely low levels of postcranial robusticity found in this group are probably a reflection of a lifetime of nutritional difficulties.

However, this need not be an example of a direct nutritional effect on bone growth per se, but an illustration of the complex relationship between long bone strength and body mass. While several studies have documented reduced bone mass and mineral in nutritionally deprived animals (Dickerson and McCance, 1961; Jha et al., 1968; Adams, 1969; Salomon and Volpin, 1972), many of these studies failed to account for the dramatically reduced body masses of their nutritionally deprived cohort. Given that the strong relationship between bone strength and body mass during growth is well-documented (van der Meulen et al., 1996; Moro et al., 1996; Ruff, 2003b), it remains possible that the differences between well-nourished and nutritionally stressed individuals could be a result of the reduction in body mass in starving individuals.

Two recent studies provide support for this interpretation. When Lambert et al. (2005) compared tibial strength properties of well-fed growing rats to those of calorically deprived controls, tibial length, mass, area, and cross-sectional moment of inertia were indeed reduced in deprived animals. However, when the reduced structural properties were scaled to the reduced body mass of the deprived sample, this pattern disappeared. Similar arguments can be made for reduced bone mass in humans. Galusca et al. (2008) compared cross-sectional properties of the radius and tibia in anorexics to those of very thin women with a BMI range of 12.0–16.5 kg/m^2, but normal fat mass percentages, menstrual cycles, hormonal levels, and energy metabolism. Cortical thickness, total area, and second moments of area of bone in the radius and the tibia were decreased in both very thin women and long-standing anorexics, leading the authors to suggest that the primary determinant of reduced skeletal mass in these subjects is not nutritional deficit or hormonal changes associated with amenorrhea, but insufficient skeletal load.

Based on this, it is entirely possible that the body mass estimates used here, which were generated from

data collected on healthy, well-nourished children, are overestimating the body masses of individuals from Kulubnarti. This entails the assumption that cross-sectional properties are more sensitive to rapid declines in body mass than articulations, which may be constrained by the need to maintain congruent joint surfaces. The differing sensitivity of these two variables to sudden drops in body mass could result in very low values of body mass standardized postcranial strength. This, in combination with potential maternal affects of malnourished mothers giving birth to small infants and generally lower activity levels among the nutritionally stressed, could potentially create the pattern of low postcranial strength across the entire developmental range. In such a scenario, it might be possible to detect starvation not through conventional nutritional analyses, but via methodological approaches that are biomechanical in their perspective and theoretical foundation (Cowgill, 2008).

CONCLUSIONS

This research raises new possibilities for avenues of future research and some interesting questions about the interpretation of patterns of postcranial strength in adult populations. The "signal" being detected in the analysis of cross-sectional properties in adults may indeed have much to do with mechanical loading. But it is also a signal rich in ontogenetic information, a partial recording of a lifetime of loading experienced by an individual. Furthermore, the translation of mechanical stimuli into new bone deposition, and the various factors that influence and affect this transmission of biomechanical information, is not yet fully understood. Additional research on both mature and immature individuals is necessary to further elucidate the complex underpinnings of these processes, and to tease out and separate how the factors affecting long bone strength act in isolation and in concert to produce variation in postcranial morphology.

ACKNOWLEDGMENTS

I thank E. Trinkaus, C.B. Ruff, G. Conroy, C. Hildebolt, H. Pontzer, R. Smith, and J. Adams for their assistance and advice throughout the course of this project. In addition, I would like to thank E. Tyler and C. Kinsinger for help with data collection. I also appreciate the anonymous reviewers who made many helpful comments on this manuscript. Lastly, I am truly grateful to many individuals across the globe who entrusted me with access to the skeletal and fossil samples in their care. This project would not have been possible without them.

APPENDIX: IMMATURE HOLOCENE SAMPLES USED IN THE STUDY

Point Hope Inuits

The site of Point Hope, Alaska is situated on a peninsula in the Chuckchi Sea, ~200 km north of the Arctic Circle (Larsen and Rainey, 1948). Excavations at Point Hope by Larson, Rainey, Shapiro and Giddings between 1939 and 1941 recovered a large skeletal sample of precontact Inuit foragers, including multiple immature skeletons from several archaeological horizons, consisting of the Norton, Ipiutak, Birnirk, and Tigara cultural periods. The best represented of the cultural groupings from Point Hope are the Ipiutak (2100–1500 BP) and the Tigara (800–300 BP), which, despite having occupied different temporal periods of the same site, show archaeological evidence of having utilized different subsistence strategies and consumed different diets. While the earlier Norton and Ipuitak periods do show evidence of seasonal hunting of fish and seals, these periods are characterized by a greater reliance on caribou hunting and the absence of archaeological evidence of whaling (Larsen and Rainey, 1948). The artifacts associated with the later Birnirk and Tigara periods indicate a more extensive dependence on the exploitation of maritime resources such as walruses, seals, and whales (Larsen and Rainey, 1948; Rainey, 1971). For this analysis, immature skeletal remains from the multiple cultural periods excavated at Point Hope were combined into a single sample. While this compromise may result in behavioral heterogeneity within the sample of immature individuals, this designation is supported by previous analyses of Point Hope adults that found little biomechanical difference between the early and late periods at this site (Shackelford, 2005). This sample is currently located at the American Museum of Natural History.

Californian Amerindians

The California Amerindian sample used in this analysis is derived from 28 sites in the Alameda, Sacramento, and San Joaquin counties of north-central California, primarily clustered along the San Francisco Bay and the Sacramento and San Joaquin River valleys. While some of these locations are occupation and burial sites (such as the King Brown and Brazil sites in Sacramento County), many of the human remains used in this sample were excavated from the large shell mounds that typify this region (such as the Emeryville and West Berkeley shell mounds in Alameda County). Of the 28 sites sampled here, 46% have associated radiocarbon dates, ranging in age from 500 to 4,600 BP (Schulz, 1981; Moratto, 1984). Despite the range in ages and geography, the California Amerindians of this area are best characterized as precontact semi-sedentary foraging populations. California Amerindians in the Sacramento and San Joaquin river valleys subsisted by hunting for deer, elk, and antelope, fishing (particularly for Chinook salmon), and extensive exploitation of acorns. Their counterparts near the San Francisco Bay relied on similar resources supplemented with shellfish collection (Moratto, 1984). This sample is currently located at the Phoebe Hearst Museum at the University of California, Berkeley.

Indian Knoll Native Americans

Indian Knoll is an Archaic Period shell-midden site located on the Green River in Kentucky. Excavations by Moore (1916) and Webb (1946) recovered over 1,000 burials. Radiocarbon dates from this site suggest that Indian Knoll was occupied from 6,415 to 4,143 BP, with the majority of the burials from Indian Knoll attributed to the middle or late Archaic period. Individuals from Indian Knoll were likely semi-sedentary with prolonged residences at seasonally occupied sites with relatively high population densities. They participated in a sophisticated hunting and gathering subsistence economy that relied heavily on a narrow spectrum of essential resources, such as deer, turkey, mussels, nuts and a variety of

locally collected plant materials (Winters, 1974). The Indian Knoll sample is currently located University of Kentucky, Lexington.

Kulubnarti Sudanese Nubians

The site of Kulubnarti is located in Upper Nubia in the Batn el Hajar region, ~130 kilometers south of Wadi Halfa. Two medieval Christian cemeteries containing 406 burials were excavated at Kulubnarti in 1979 (van Gerven et al., 1995). While population levels have varied through time, this region has been historically characterized by low population densities due to the relative lack of resources in this rocky and inhospitable environment. With marginal subsistence levels, individuals have traditionally lived in small villages and participated in small-scale agriculture. In addition, individuals at medieval Kulubnarti likely suffered from chronic nutritional difficulty combined with bouts of infectious disease during growth. Incidence of iron deficiency and nonspecific developmental stress are extremely high among immature individuals at this site, with 82–94% of all immature crania exhibiting signs of cribra obritalia, and all individuals having at least one enamel hypoplasia (Van Gerven et al., 1990). This sample is currently located at the University of Colorado, Boulder.

Mistihalj Central Europeans

Excavated in 1967 and 1968 by the Joint Stanford-Yugoslav archaeological expedition, Mistihalj is a medieval burial site located in former Yugoslavia, currently on the border between Bosnia-Herzegovina and Montenegro. Analysis of cemetery monuments, coins, and grave goods indicates that the Mistihalj cemetery was used primarily in the middle of the 15th century, between 1400 and 1475. The remains at Mistihalj are culturally associated with the Vlakhs, an indigenous ethnic group that still persists in the Balkan region today in small numbers. Historically, Vlakhs have been nomadic pastoralists, primarily engaged in breeding sheep, horses, mules, and cattle. Vlakhs migrated seasonally over varied terrain, spending summers in the highland pastures and winters in the warmer costal valleys (Alexeeva et al., 2003). The Mistihalj collection is currently located at the Peabody Museum at Harvard University.

Dart collection Sub-Saharan Africans

The Dart Collection is an ethnically mixed, native African cadaver sample derived from hospitals in the Transvaal region in South Africa. This collection was started by Raymond Dart in 1924 and continued by Phillip V. Tobias for most of the 20th century, resulting in a collection that now totals over 3,000 skeletons. The skeletal catalog includes a variety of details, including ethnic group or tribe, reported age, hospital source, date of acquisition, and cause of death (Sanuders and Devito, 1991). The immature individuals in this sub-sample of the collection died between 1927 and 1980, with 74% of all individuals having died before 1950, and ~92% of the individuals within this sample are South African Blacks. In light of the relatively wide geographic area from which these individuals are derived and the fifty-year time span of their collection, it remains difficult to conclusively categorize them as exclusively urban or rural. This collection is located at the School of Medicine, University of Witwatersrand, Johannesburg, South Africa.

Luis Lopes Western Europeans

The Luis Lopes skeletal collection consists of 20th century Portuguese from several cemeteries in Lisbon. The vast majority of immature individuals in this sample died between 1900 and 1960, and their remains were collected after 1980 when they were exhumed and scheduled to be placed in communal burials. Because coffin plates and cemetery registries are available to identify all individuals, reasonably reliable ages, addresses, causes of death, and parental occupation are accessible for many of these remains (Cardoso, 2005). In general, the sample is best categorized as an urban population of low to middle socioeconomic status. Previous analyses of paternal occupation show that the heads of most of these households earned their livings in skilled manual occupations, such as tailor or locksmith, although parental employment in partially skilled or unskilled labor occupations is not uncommon in the sample (Cardoso, 2005). The sample is located at the Bocage Museum (National Museum of Natural History) in Lisbon, Portugal.

LITERATURE CITED

Adams P. 1968. The effect of experimental malnutrition on the development of long bones. Nutritional aspects of the development of bone and connective tissue. In: Symposium of the Group of European Nutritionist, Cambridge. 13:69–73.

Akhter MP, Cullen DM, Pedersen EA, Kimmel DB, Recker RR. 1998. Bone response to in vivo mechanical loading in two breeds of mice. Calcif Tissue Int 63:442–449.

Akhter MP, Iwaniec UT, Covey MA, Cullen DM, Kimmel DB, Recker RR. 2000. Genetic variation in bone density, histormorphology, and strength in mice. Calcif Tiss Int 67:337–344.

Alexeeva TI, Bogatenkov DV, Lebedinskaya GV. 2003. Anthropology of medieval Vlakhs in comparative study: on date of Mistikhaly burial site. Moskva: Scientific World (in Russia, summery in English).

Bass S, Pearce G, Bradney M, Hendrich E, Delmas PD, Harding A, Seeman E. 1998. Exercise before puberty may confer residual benefits in bone density in adulthood: studies in active prepubertal and retired female gymnasts. J Bone Miner Res 13:500–507.

Bass SL, Saxon L, Daly RM, Turner CH, Robling AG, Seeman E, Stuckey S. 2002. The effect of mechanical loading on the size and shape of bone in pre-, peri-, and postpubertal girls: a study in tennis players. J Bone Miner Res 17:2274–2280.

Biewener AA, Bertram JEA. 1994. Structural response of growing bone to exercise and disuse. J Appl Physiol 76:946–955.

Biewener AA, Swartz SM, Bertram JEA. 1986. Bone modeling during growth: dynamic strain equilibrium in the chick tibiotarsus. Calcif Tissue Int 39:390–395.

Biewener AA. 1992. Overview of structural mechanics. In: Biewener AA, editor. Biomechanics—structures and systems: a practical approach. Oxford: Oxford University Press. p 1–20.

Bradney M, Pearce G, Naughton G, Sullivan C, Bass S, Beck T, Carlson J, Seeman E. 1998. Moderate exercise during growth in perubertal boys: changes in bone mass, size, volumetric density, and bone strength: a controlled prospective study. J Bone Miner Res 13:1814–1821.

Cardoso HFV. 2005. Patterns of growth and development of the human skeleton and dentition in relation to environmental quality: a biocultural analysis of a sample of 20th century Portuguese subadult documented skeletons. Ph.D. thesis. McMasters University.

Carter DR, Beaupré GS. 2001. Skeletal function and form: mechanobiology of skeletal development, aging and regeneration. Cambridge: Cambridge University Press.

Carter DR, Orr TE, Fyhrie DP, Schurman DJ. 1987. Influences of mechanical stress on prenatal and postnatal skeletal development. Clin Orthop Relat Res 219:237–250.

Carter DR, Wong M. 1988. Mechanical stress and endochondral ossification in the chondroepiphysis. J Orthop Res 6:148–154.

Churchill SE. 1994. Human upper body evolution in the Eurasian Late Pleistocene. Ph.D. dissertation. University of New Mexico, Albuquerque.

Churchill SE, Formicola V, Holliday TW, Holt B, Schumann BA. 2000. The Upper Paleolithic population in Europe in an evolutionary perspective. In: Roebroeks W, Mussi M, Svoboda J, Fennema K, editors. Hunters of the Golden Age. Leiden: University of Leiden.

Conroy BP, Kraemer WJ, Maresh CM, Fleck SJ, Stone MH, Fry AC, Miller PD, Dalsky GP. 1993. Bone mineral density in elite junior Olympic weightlifters. Med Sci Sports Exerc 25:1103–1109.

Cowgill LW. 2008. The ontogeny of recent and late pleistocene human postcranial robusticity. Ph.D. dissertation. Washington University, St. Louis.

Cowgill LW, Hager LD. 2007. Variation in the development of postcranial robusticity: an example from Çatalhöyük, Turkey. Int J Osteoarchael 17:235–252.

Cowgill LW, Trinkaus E, Zeder MA. 2007. Shanidar 10: a Middle Paleolithic immature distal lower limb from Shanidar Cave, Iraqi Kurdistan. J Hum Evol 53:213–223.

Dickerson JWT, McCance RA. 1961. Severe undernutrition in growing and adult animals: the dimensions and chemistry of the long bones. Brit J Nutr 15:567–576.

Eschman PN. 1992. SLCOMM Version 1.6. Eschman Archaeological Services, Albuquerque, NM.

Fazekas IG, Kósa F. 1978. Forensic fetal osteology. Budapest: Akadémiai Kiadó.

Ferembach D, Dastugue J, Poitrat-Targowla M-J. 1962. La Nécropole Épipaléolithique de Taforalt: etude des squelettes humains. Paris: Centre National de la Recherche Scientifique.

Formicola V, Giannecchini M. 1999. Evolutionary trends in stature in Upper Paleolithic and Mesolithic Europe. J Hum Evol 36:319–333.

Galusca B, Zouch M, Germain N, Bossu C, Frere D, Lang F, Lafage-Proust M-H, Thomas T, Vico L, Estour B. 2008. Constitutional thinness: unusual human phenotype of low bone quality. J Clin Endocrinol Metab 93:110–117.

Grimston SK, Willows ND, Hanley DA. 1993. Mechanical loading regime and its relationship to bone mineral density in children. Med Sci Sports Exerc 25:1203–1210.

Guatelli-Steinberg D, Reid DJ, Bishop TA, Larsen CS. 2005. Anterior tooth growth periods in Neandertals we comparable to those of modern humans. Proc Natl Acad Sci USA 102:14197–14202.

Hall BK. 1972. Immobilization and cartilage transformation into bone in the embryonic chick. Anat Rec 173:391–404.

Haapasalo H. 1998. Physical activity and growing bone: development of peak bone mass with special reference to the effects of unilateral physical activity. Ann Chir Gynaecol 87: 250–252.

Haapasalo H, Kannus P, Sievänen H, Pasanen M, Uusi-Rasi K, Heinonen A, Oja P, Vouri I. 1998. Effect of long-term unilateral activity on bone mineral density of female junior tennis players. J Bone Miner Res 13:310–319.

Henderson JH, Carter DR. 2002. Mechanical induction in limb morphogenesis: the role of growth-generated strains and pressures. Bone 31:645–653.

Holliday TW. 1999. Body proportions in Late Pleistocene Europe and modern human origins. J Hum Evol 32:423–447.

Holliday TW. 2002. Body size and postcranial robusticity of European Upper Paleolithic hominins. J Hum Evol 43:513–528.

Holms S. 1979. A simple sequentially reductive multiple test procedure. Scand J Stat 6:65–70.

Holt BM. 1999. Biomechanical evidence of decreased mobility in upper Paleolithic and Mesolithic Europe. Ph.D. thesis. University of Missouri, Columbia.

Holt BM. 2003. Mobility in Upper Paleolithic and Mesolithic Europe: evidence from the lower limb. Am J Phys Anthropol 122:200–215.

Jha GJ, Deo MG, Ramalingaswami V. 1968. Bone growth in protein deficiency: a study in Rhesus monkeys. Am J Pathol 53: 1111–1123.

Kannus P, Haapasalo H, Sankelo M, Sievänen H, Pasanen M, Heinonen A, Oja P, Vouri I. 1995. Effect of starting age of physical activity on bone mass in the dominant arm of tennis and squash players. Ann Intern Med 123:27–31.

Karlsson MK, Johnell O, Obrant KJ. 1995. Is bone mineral density advantage maintained long-term in previous weight lifters? Calcif Tissue Int 57:325–328.

Khan KM, Bennell KL, Hopper JL, Flicker L, Nowson CA, Sherwin AJ, Crichton KJ, Harcourt PR, Wark JD. 1998. Self-reported ballet classes undertaken at age 10-12 years and hip bone mineral density in later life. Osteoporos Int 8:165–173.

Kimura T, Takahashi H. 1982. Mechanical properties of cross section of lower limb long bones in Jomon Man. J Anthrop Soc Nippon 90(Suppl):105–118.

Kodama Y, Umemura Y, Nagasawa S, Beamer WG, Donahue LR, Rosen CR, Baylink DJ, Farley JR. 2000. Exercise and mechanical loading increase periosteal bone formation and whole bone strength in C57BL/6J mice but not in C3H/Hej mice. Calcif Tissue Int 66:298–306.

Kondo O, Dodo Y. 2002a. Postcranial bones of the Neanderthal child of the burial No. 1. In: Akazawa T, Muhesen S, editors. Neanderthal Burials. Excavations of the Dederiyeh Cave, Afin, Syria. Kyoto: International Research Center for Japanese Studies. p 139–201.

Kondo O, Dodo Y. 2002b. Postcranial bones of the Neanderthal child of the burial No. 2. In: Akazawa T, Muhesen S, editors. Neanderthal Burials. Excavations of the Dederiyeh Cave, Afin, Syria. Kyoto: International Research Center for Japanese Studies. p 299–313.

Kontulainen S, Sievanen H, Kannus P, Pasanen M, Vouri I. 2003. Effect of long-term impact-loading on mass, size, and estimated strength of humerus and radius of female racquet-sports players: a peripheral quantitative computed tomography study between young and old starters and controls. J Bone Miner Res 18:352–359.

Kriska AM, Sandler RB, Cauley JA, LaPorte RE, Hom DL, Pambianco G. 1988. The assessment of historical phycial activity and its relation to adult bone parameters. Am J Epidemiol 127:1053–1061.

Lambert J, Lamothe JM, Zernicke RF, Auer RN, Reimer RA. 2005. Dietary restriction does not adversely affect bone geometry and mechanical in rapidly growing male Wistar rats. Pediatr Res 57:227–231.

Larsen H, Rainey F. 1948. Ipiutak and the Arctic while hunting culture. Anthrop Pap Am Mus Nat Hist 42:1–276.

Lieberman DE, Devlin MJ, Pearson OM. 2001. Articular area responses to mechanical loading: effects of exercise, age, and skeletal location. Am J Phys Anthropol 116:266–277.

Liversidge HM, Molleson T. 2004. Variation in crown and root formation and eruption of human deciduous teeth. Am J Phys Anthropol 123:172–180.

Lovejoy OC, Meindl RS, Ohman JC, Heiple KG, White TD. 2002. The Maka femur and its bearing on the antiquity of human walking: applying contemporary concepts of mophogenesis to the human fossil record. Am J Phys Anthropol 119: 97–133.

Lovejoy OC, McCollum MA, Reno PL, Rosenman BA. 2003. Developmental biology and human evolution. Annu Rev Anthropol 32:85–109.

Macchiarelli R, Bondiolo L, Debénath A, Mazurier A, Tournepiche J-F, Birch W, Dean C. 2006. How Neandertal molar teeth grew. Nature 444:748–751.

McCulloch RG, Bailey DA, Whalen RL, Houson CS, Faulkner RA, Craven BR. 1992. Bone density and bone mineral content of adolescent soccer athletes and competitive swimmers. Pediatr Exerc Sci 4:319–330.

McKay HA, Petit MA, Schutz RW, Prior JC, Barr SI, Khan KM. 2000. Augmented trochanteric bone mineral density after modified physical education classes. J Pediatr 136:156–162.

Micklesfield L, Rosenberg L, Cooper D, Hoffman M, Kalla A, Stander I, Lambert E. 2003. Bone mineral density and life-

time physical activity in South African Women. Calcif Tissue Int 73:463–469.
Moore CB. 1916 Some aboriginal sites on the Green River, Kentucky. J Phila Acad Nat Sci 16:431–487.
Moran MD. 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. Oikos 100:403–405.
Moratto MJ. 1984. California archaeology. Orlando: Academic Press.
Moro M, Van der Meulen MCH, Kiratli BJ, Marcus R, Bachrach LK, Carter DR. 1996. Body mass is the primary determinant of midfemoral bone acquisition during adolescent growth. Bone 19:519–526.
Mosley JR, March BM, Lynch J, Lanyon LE. 1997. Strain magnitude related changes in whole bone architecture in growing rats. Bone 20:191–198.
Nagurka ML, Hayes WC. 1980. An interactive graphics package for calculating cross sectional properties of complex shapes. J Biomech 13:59–64.
Nakagawa S. 2004. A farewell to Bonferroni: the problems of low statistical power and publication bias. Behav Ecol 15: 1044–1045.
Nelson AJ, Thompson JL. 2000. Adolescent postcranial growth in Homo neanderthalensis. In: Minugh-Purvis N, McNarmara KJ, editors. Human evolution through developmental change. Baltimore: John Hopkins University Press. p 442–463.
Nordström P, Pettersson U, Lorentzon R. 1998. Type of physical activity, muscle strength, and pubertal stage as determinants of bone mineral density and bone area in adolescent boys. J Bone Miner Res 13:1141–1148.
Odwak H. 2000. Long bone robusticity and claviculo-humeral proportions of the Amud baby. Am J Phys Anthropol 111: 241.
O'Neill MC, Ruff CB. 2004. Estimating human long bone cross-sectional geometric properties: a comparison of noninvasive methods. J Hum Evol 47:221–235.
Pearson OM, Lieberman DE. 2004. The aging of Wolff's "law": ontogeny and responses to mechanical loading in cortical bone. Yrbk Phys Anthropol 47:63–99.
Perneger TV. 1998. What's wrong with Bonferroni adjustments. Brit Med J 316:1236–1238.
Pettersson U, Alfredson H, Nordström P, Henriksson-Larsén K, Lorentzon R. 2000a. Bone mass in female cross-country skiers: relationship between muscle strength and different BMD sites. Calcif Tissue Int 67:199–206.
Pettersson U, Nordström P, Alfredson H, Henriksson-Larsén K, Lorentzon R. 2000b. Effect of high impact activity on bone mass and size in adolescent females: a comparative study between two different types of sports. Calcif Tissue Int 67: 207–214.
Raab DM, Smith EL, Crenshaw TD, Thomas DP. 1990. Bone mechanical properties after exercise training in young and old rats. J Appl Physiol 68:130–134.
Rainey F. 1971. The Ipiutak culture: excavations at point hope. Alaska: Addison-Wesley Modular Publications in Anthropology8:1–32.
Ramirez Rozzi FV, Bermudez de Castro JM. 2004. Surprisingly rapid growth in Neandertals. Nature 936–939.
Ramsay HL, Weaver DS, Seidler H. 2005. Bone histology in the Le Moustier Neandertal child. In: Ullrich H, editor. The Neandertal adolescent Le Moustier 1: new aspects, new results. Berlin: Staatliche Museen zu Berlin -Preussischer Kulturbesitz. p. 282–290.
Rice WR. 1989. Analyzing tables of statistical tests. Evolution 43:223–225.
Robbins G. 2007. Population dynamics, growth and development in Chalcolithic sites of the Deccan Peninsula, India. Ph.D. dissertation, University of Oregon, Eugene.
Robling AG, Turner CH. 2002. Mechanotransduction in bone: genetic effects on mechanosensitivity in mice. Bone 31:562–569.
Rodriguez JI, Garcia-Alix A, Palacios J, Paniagua R. 1988b. Changes in the long bones due to fetal immobility caused by neuromuscular disease. J Bone Joint Surg 70:1052–1060.
Ruff CB. 2000a. Body size, body shape and long bone strength in modern humans. J Hum Evol 38:269–290.
Ruff CB. 2000b. Biomechanical analyses of archaeological human skeletons. In: Katzenberg MA, Saunders SR, editors. Biological anthropology of the human skeleton. Wiley-Liss. p 71–102.
Ruff CB. 2003a. Ontogenetic adaptation to bipedalism: age changes in femoral to humeral length and strength proportions in humans, with a comparison to baboons. J Hum Evol 45:317–349.
Ruff CB. 2003b. Growth in bone strength, body size, and muscle size in a juvenile longitudinal sample. Bone 33:317–329.
Ruff CB. 2007. Body size prediction from juvenile skeletal remains. Am J Phys Anthropol 133:698–716.
Ruff CB, Trinkaus E, Walker A, Larsen CS. 1993. Postcranial robusticity in Homo. I. Temporal trends and mechanical interpretations. Am J Phys Anthropol 91:21–53.
Ruff CB, Walker A, Trinkaus E. 1994. Postcranial robusticity in Homo. III. Ontogeny. Am J Phys Anthropol 35–54.
Ruff CB, Holt B, Trinkaus E. 2006. Who's afraid of the Big Bad Wolff? "Wolff's Law"and bone functional adaptation. Am J Phys Anthropol 129:484–498.
Sakaue K. 1998. Bilateral asymmetry of the humerus in Jomon people and modern Japanese. Anthropol Sci 105:231–246.
Salomon CD, Volpin G. 1972. The effects of calcium-deficient diet on breaking strength and other physical parameters of rat bones. Clin Orthop Relat Res 82:207–213.
Saunders SR, DeVito C. 1991. Subadult skeletons in the Raymond Dart anatomical collection: research potential. Hum Evol 6:421–434.
Schönau E. 1998. The development of the skeletal system in children and the influence of muscular strength. Hom Res 49: 27–31.
Schulz PD. 1981 Osteoarchaeology and subsistence change in prehistoric Central California. Ph.D. dissertation. Department of Anthropology, University of California, Davis.
Sciulli PW, Blatt SH. 2008. Evaluation of juvenile stature and body mass prediction. Am J Phys Anthropol 136:387–393.
Shackelford LL. 2005. Regional variation in the postcranial robusticity of Late Upper Paleolithic humans. Ph.D. dissertation. Washington University, St. Louis.
Slemenda CW, Johnston CC. 1993. High intensity activities in young women: site specific bone mass effects among female figure skaters. Bone Miner 20:125–132.
Smith BH. 1991. Standards of human tooth formation and dental age assessment. In: Kelley MA and Larsen CS, editors. Advances in dental anthropology. New York: Wiley-Liss. p 143–168.
Smith TM, Toussaint M, Reid DJ, Olejniczak AJ, Hublin J-J. 2007. Rapid dental development in a Middle Paleolithic Belgian Neandertal. Proc Natl Acad Sci USA 104:20220–20225.
Söderman K, Bergström E, Lorentzon R, Alfredson H. 2000. Bone mass and muscle strength in young female soccer players. Calcif Tissue Int 67:297–303.
Sokal RR, Rohlf FJ. 1995. Biometry: the principles and practice of statistics in biological research, 3rd ed. New York: WH Freeman and company.
Steinberg ME, Trueta J. 1981. Effects of activity on bone growth and development of the rat. Clin Orthop Relat Res 156:52–60.
Sumner DR, Andriacchi TP. 1996. Adaptation to differential loading: comparison of growth related changes in cross-sectional properties of the human femur and humerus. Bone 19: 121–126.
Teegarden D, Proulx WR, Kern M, Sedlock D, Weaver CM, Johnston CC, Lyle RM. 1996. Previous physical activity relates to bone mineral measures in young women. Med Sci Sports Exerc 28:105–113.
Thompson JL, Nelson AJ. 2005. The postcranial skeleton of Le Moustier 1. In: Ullrich H, editor. The Neandertal adolescent Le Moustier 1: new aspects, new results. Berlin: Staatliche Museen zu Berlin-Preussischer Kulturbesitz. p 265–281.
Trinkaus E. 1997. Appendicular robusticity and the paleobiology of modern human emergence. Proc Natl Acad Sci USA 94: 13367–13373.

Trinkaus E, Churchill S. 1999. Diaphyseal cross-sectional geometry of the near eastern Middle Paleolithic humans: the humerus. J Archaeol Sci 26:173–184.

Trinkaus E, Ruff CB. 1999. Diaphyseal cross-sectional geometry of Near Eastern Middle Paleolithic humans: the femur. J Archaeol Sci 26:409–424.

Trinkaus E, Ruff CB. 1996. Early modern human remains from eastern Asia: the Yamashita-cho 1 immature postcrania. J Hum Evol 30:299–314.

Trinkaus E, Ruff CB, Esteves F, Coelho JMS, Silva M, Mendova M. 2002a. The lower limb remains. In: Zilhão J, Trinkaus E, editors. Portrait of the artist as a child. Lisbon: Intituto Portuguõs de Arqueologia. p 435–465.

Trinkaus E, Ruff CB, Esteves F, Coelho JMS, Silva M, Mendova M. 2002b. The upper limb remains. In: Zilhão J, Trinkaus E, editors. Portrait of the artist as a child. Lisbon: Intituto Portuguõs de Arqueologia. p 466–488.

Trinkaus E, Smith FH, Stockton TC, Shackelford LL. 2006. The human postcranial remains from Mladec. In: Teschler-Nicola M, editor. Early modern humans at the Moravian gate: the Mladec Caves and their remains. New York: SpringerWien. p 385–446.

Turner CH, Hsieh Y-F, Müller R, Bouxsein ML, Rosen CJ, McCrann ME, Donahue LR, Beamer WG. 2001. Variation in bone biomechanical properties, microstructure, and density in BXH recombinant inbred mice. J Bone Miner Res 16:206–213.

Van Gerven DP, Hummert JR, Burr DB. 1985. Cortical bone maintenance and geometry of the tibia in Prehistoric children from Nubia's Batn et Hajar. Am J Phys Anthropol 66:275–280.

Van Gerven DP, Beck R, Hummert JR. 1990. Patterns of enamel hypoplasia in two medieval populations from Nubia's Batn el Hajar. Am J Phys Anthropol 82:413–420.

van Gerven DP, Sheridan SG; Adams WY. 1995. The Health and nutrition of a medieval nubian population: the impact of political and economic change. Am Anthropol 97:468–480.

Van der Meulen MC, Ashford MWJ, Kiratli BJ, Backrach LK, Carter DR. 1996. Determinates of femoral geometry and structure during adolescent growth. J Orthop Res 14:22–29.

Webb WS. 1946. Indian Knoll, Site Oh 2, Ohio County, Kentucky: the University of Kentucky Reports in anthropology and archaeology. Lexington: Department of Anthropology. p 111–365.

Winters HD. 1974. Introduction to the new edition. In: Webb WS, editor. Indian knoll. Knoxville: University the Tennessee Press.

Woo SL-Y, Kuei SC, Amiel D, Gomez MA, Hayes WC, White FC, Akeson WH. 1981. The effect of prolonged physical training on the properties of long bone. J Bone Joint Surg 63:780–787.