



## Cross-sectional geometric analysis of a foot bone assemblage from Mangaia, Cook Islands

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### Abstract

This study describes a human foot bone assemblage from prehistoric Mangaia, Cook Islands in the context of diaphyseal cross-sectional strength measures. We use this sample to test the hypothesis that habitually unshod individuals who walk over rugged terrain will have stronger foot bones than a sample of habitually shod industrialized people. Specifically, we examine whether the Mangaian sample has a stronger size-adjusted metatarsal (MT) and phalangeal cross-sectional properties than the industrial sample, drawn from the Terry Collection. Contrary to expectations, residual analyses showed that most values of cross-sectional area (CA) and torsional resistance ( $J$ ) of MTs 1–4 and the hallucal proximal phalanx (HPP) of the Mangaians are among those in the lower range of the Terry Collection sample. However, the bending strength ratios ( $Z_y/Z_x$ ) of the Mangaian HPP are significantly greater than those of the Terry Collection. While characteristics such as forefoot shape variation between the sexes and among geographic populations cannot be ruled out as influential factors, cross-sectional properties of the hallucal proximal phalanges, but not the MTs, indicate terrain complexity in prehistoric populations.

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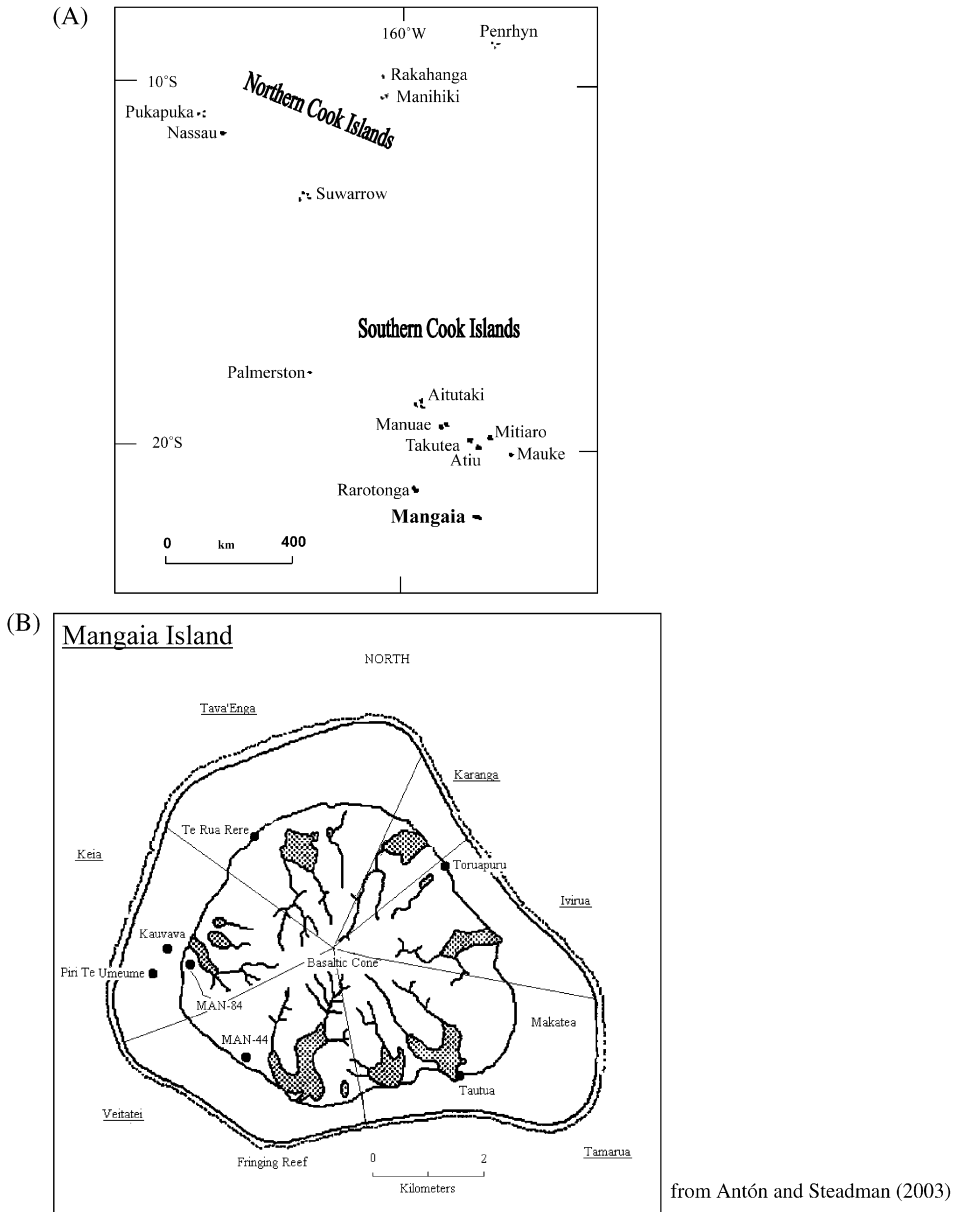
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## Introduction

Mangaia Island (21.5°S, 157.9°W) (Fig. 1), the most southerly of the Cook Islands, consists of an inner basalt cone surrounded by a 70-m raised limestone reef (*makatea*). Ethnohistorical and archeological evidence indicate that before European contact Mंगाians regularly traveled over the *makatea* from the inland crop fields to the coast in order to fish, forage, and conduct religious ceremonies (Kirch, 1996; Antón and Steadman, 1998; Steadman et al., 2000). This living pattern changed under Christian missionary influence when Mंगाians were encouraged to inhabit coastal villages (Gill, 1894; Buck, 1934). Here, we infer pre-contact Mंगाians went unshod, for even today inhabitants frequently go barefoot, often over severe terrain. The internal structure of cortical bone is known to respond to mechanical demand (e.g. Currey, 2002 and references therein); therefore we hypothesize that differences in loading levels between activity regimes will be captured in the cross-sectional geometry of the forefoot skeleton.

Reconstructing activity levels and subsistence patterns of prehistoric populations from skeletal material often includes the study of long bone cortical geometry using computed tomography (CT) (Larsen, 2002). Although it has been infrequently employed as a means of differentiating human groups based on levels of terrestrial mobility (Stock and Pfeiffer, 2001), the function of the forefoot makes it an appropriate area to test whether cross-sectional geometry can discriminate among populations traversing different types of terrain. As opposed to the hind and mid-foot, the flexible design of the forefoot enables it to become a lever at push-off and affords it the ability to adjust to uneven terrain (Donatelli, 1990; Sammarco and Hockenbury, 2001).

Foot pressure research demonstrates how the magnitudes and distribution of forces change with variation in the ground's topography. For example, *in vivo* studies indicate that with the transition from level walking to climbing upstairs, plantar pressure increases in both magnitude and duration (Lundeen et al., 1994). With the increase in the steepness of an incline, peak pressures in the forefoot increase, especially in the first ray and in both the second and third metatarsals (MTs) (Grampp et al., 2000). Sideslope walking also produces a difference in plantar pressure distribution. In contrast to pressures measured during level walking, pressures in the medial fore-region are greater when one foot occupies the downslope position during locomotion. When the same foot occupies the upslope position during gait, pressures in the lateral region of the forefoot are greater than those measured during level walking (Urry, 2002). Substrate conformity also affects pressure distribution in the forefoot. Both forefoot pressure and pressure time integral (a measure of pressure and contact duration) significantly increase with the transition from a compliant surface such as either grass or carpet to a harder substrate like concrete. In addition, barefoot individuals walking over concrete experienced greater forefoot pressures and pressure time integrals than those walking with shoes (Mohamed et al., 2005). Overall, data show that forefoot pressure changes with terrain grade and compliancy and also use of footwear, with the greatest forefoot pressure occurring when barefoot individuals locomote over the



**Fig. 1.** Belonging to the Southern Cook Islands group (A), Mangaia Island (B) is composed of a basaltic cone surrounded by a 70-m tall limestone reef (makatea). The adult foot bone assemblage included in this study comes from rockshelter site, MAN-84.

steepest and least compliant terrain. Here, we present a comparison of cortical bone structure in the forefoot from populations of the known substrates and footwear use.

Coupling the knowledge of how the forefoot is loaded during gait (Preuschoft, 1969, 1970; Stokes et al., 1979; Ferris et al., 1995; Sharkey et al., 1995; Donahue and Sharkey, 1999) with evidence that long bone diaphyseal dimensions respond to applied mechanical loading (Currey, 2002), we hypothesize that habitually unshod people walking over rugged terrain will have stronger forefoot bones than habitually shod people from modern, industrialized societies. Specifically, we test the hypothesis that individuals from the Manganian Collection, representing a population that went habitually barefoot on complex terrain, have relatively stronger MT diaphyses at midlength than those from the Terry Collection who mainly led more sedentary lifestyles, not encountering rugged terrain on a regular basis. Even on such occasions, it is most likely the latter would have worn protective footwear. Based on Trinkaus' (2005) study which found habitually unshod individuals to have greater standardized measures of torsional resistance (i.e., external diaphyseal measurements) for the hallucal proximal phalanx (HPP) than shod peoples, we predict that a lifestyle of habitually walking unshod over uneven terrain would have contributed to greater size-adjusted MT and phalangeal cross-sectional geometric property measures [e.g., cross-sectional area (CA) and torsional resistance ( $J$ )] for Manganians compared to the industrial human sample. Furthermore, in their study Trinkaus and Hilton (1996) determined that for the external measurement ratio of midlength mediolateral breadth to midlength dorsoplantar height, Neandertal hallucal phalanges were found within the upper range of modern humans. Trinkaus and Hilton (1996) used this difference, as well as wider lateral proximal phalanges, as support for the proposal that the Neandertal lower limb was adapted to a higher level and/or greater frequency of mediolateral bending, possibly as a result of unshod locomotion over uneven terrain. To test this hypothesis, we compare the ratios of bending strength in the mediolateral and dorsoplantar planes ( $Z_y/Z_x$ ) between Manganian and Terry Collection hallucal phalanges with the expectation that the former will have greater ratios. Corresponding external diaphyseal measures need not be considered here because when a long bone is modeled as a simple beam, the cross-sectional geometry provides more accurate measures of axial and bending strengths (Larsen, 2002).

## Materials and methods

The sample from Mangaia Island has been recovered from the site MAN-84 and within the stratigraphic layers radiocarbon dated to ca. AD 1400–1450, and therefore, represents a pre-contact population. The entire assemblage consists of skeletal remains ranging in age from fetal to adult, and many bones are burned and fragmented, suggesting non-traditional burial (Antón and Steadman, 2003). The adult foot bones selected for study cannot be differentiated by exact age or sex. For an archeological assemblage, foot remains are slightly overrepresented as 17% rather

than 13.6% (Steadman et al., 2000) and many exhibit signs of arthritis in the form of marginal lipping as well as undulations on articular surfaces. Only the MTs ( $n = 15$ ) and hallucal phalanges ( $n = 10$ ) were used in this study because lateral proximal phalanges could not be confidently identified to the corresponding rays. Due to the incompleteness of one of the first MTs and one HPP as well as signs of a healed fracture of the only fifth MT in the assemblage, these three bones from the Manganian assemblage were not included in the analysis.

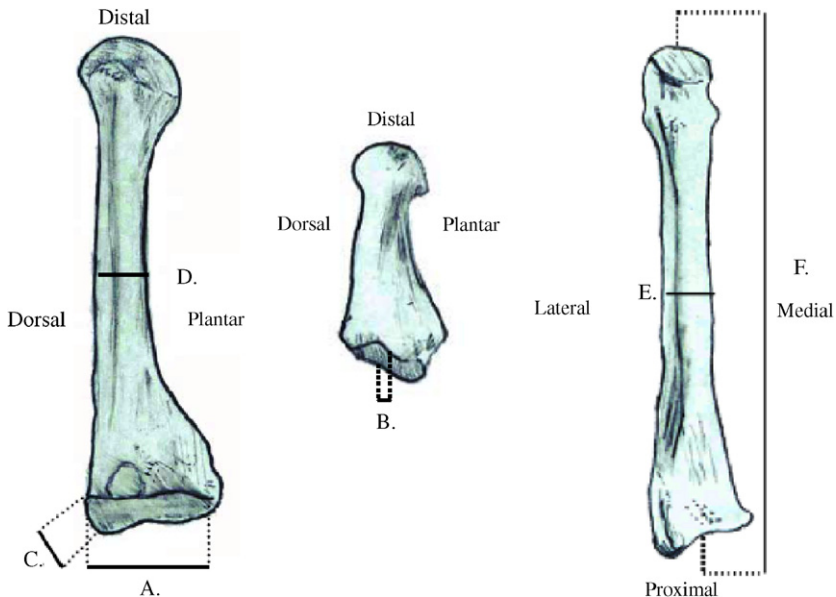
A comparative sample is drawn from the Robert J. Terry Collection and is equally represented by males and females of African and European American descent ( $n = 40$ ). The sample is described in further detail in a previous study (Griffin and Richmond, 2005). Age at death is known for each individual; the mean age of this sample is 26.2 years, with a range between 20 and 38 years.

MTs (1–4) and HPPs were scanned at midlength using a Siemens Somatom AR.SP scanner (for more details see Griffin and Richmond, 2005). Four HPPs from the Terry Collection were not included in the analysis because in each case, cortical bone could not be differentiated from the medullary cavity without introducing an error. Cross-sectional geometric properties were obtained using a Scion Image macro based on established geometric computations (Sumner et al., 1985); the macro was provided courtesy of Drs. Christopher Ruff and Valerie Burke DeLeon.

Before comparisons could be made between the cross-sectional properties of the Manganian and the Terry Collection samples, these values needed to be adjusted for the body size or an estimate thereof. This presents a challenge because the Manganian foot assemblage is represented by isolated finds and each bone was assumed to belong to a separate individual. With this limitation, it is necessary to establish a measure of overall size for every type of foot bone in this analysis, HPP and MTs 1–4. Here, we use the geometric mean [ $GM = \sqrt[n]{(a_1 * a_2 * \dots * a_n)}$ , where ‘ $a$ ’ is a measurement variable and ‘ $n$ ’ is the number of variables] of certain foot bone variables (Fig. 2) as bone size, because GMs have been proved to be useful measures of overall size (Mosimann, 1970; Jungers et al., 1995). Measurements were not taken at the distal epiphysis because this region of the MT was missing in several of the Manganian specimens. All measurements were taken with digital calipers.

Empirical studies testing the relationship between cross-sectional properties and body size and shape of other weight-bearing bones, such as the femur and tibia (Ruff, 2000), provide a basis for MT and phalanx scaling predictions. Using only the Terry sample, we generated least-squares regressions of  $\log CA$  and  $\log J$  against  $\log GM$  and  $\log GM * BL$ , respectively, to test for isometry. Although it is assumed that cross-sectional values of the Manganian foot bones will scale isometrically with  $GM$  or  $GM * BL$  as do the Terry individuals, the hypothesis predicts that the Manganians will have significantly higher cross-sectional properties relative to size.

Lastly, the ratio of  $Z_y/Z_x$ , or the bending strength in the mediolateral plane relative to bending strength in the dorsoplantar plane, was compared between the samples with the expectation that a lifetime of barefoot walking on uneven terrain would result in relatively higher mediolateral bending in the proximal hallucal phalanx (Trinkaus and Hilton, 1996). Firstly, both cross-sectional properties,  $\log$  values of  $Z_x$  and  $Z_y$  for the HPP belonging to the Terry sample, were independently



**Fig. 2.** (A) HPP and MTs 1–4 proximal articular height: measured distance from the dorsal edge of the proximal articular surface edge at midpoint to the plantar articular surface edge at midpoint. (B) HPP and MT 1 proximal articular breadth: measured distance from the medial edge of the proximal articular surface at midpoint to the lateral articular surface at midpoint. (C) MTs 2–4 proximal articular breadth: measured distance from the dorsal edge of the medial point of the proximal articular surface to the dorsal edge of the lateral point. (D) HPP and MTs 1–4 midlength height: measured distance from the dorsal point of the bone at midlength to the plantar point at midlength. (E) HPP and MTs 1–4 midlength breadth: measured distance from the medial point of the bone at midlength to the lateral point at midlength. (F) HPP and MTs 1–4 bone length: measured distance from the midpoint of the proximal articular surface to the midpoint of the distal articular surface.

regressed against the log size ( $GM*BL$ ). Then residuals for the Terry and Manganian sample from the Terry regressions were generated for each comparison to understand how the samples differed in both  $Z_x$  and  $Z_y$  at the same size. To test if the ratio between the two samples differed significantly, specifically if Manganian bones have a higher  $Z_y/Z_x$  ratio, Mann–Whitney  $U$ -tests were run for residuals of both collections from the regressions of the Terry Collection, individually and then the  $Z_y/Z_x$  ratio (using raw values).

## Results

Summary statistics can be found in Table 1. In the Terry sample,  $GM$  and  $GM*BL$  scale isometrically with  $CA$  and  $J$ , respectively (Table 2). Also,  $GM*BL$  scales isometrically with both  $Z_x$  and  $Z_y$  in all cases with the exception of HPP and

**Table 1.** Statistical summary of properties across the forefoot

Foot bone	Terry Collection females			Mangaian Collection			Terry Collection males		
	<i>N</i>	Mean	Std. dev.	<i>N</i>	Mean	Std. dev.	<i>N</i>	Mean	Std. dev.
<b>HPP</b>									
PAH	17	17.2	0.8	10	17.7	1.3	19	19.4	1.5
PAB	17	13.4	1.1	10	14.7	1.4	19	15.1	1.5
MH	17	11.5	1.2	10	12.2	1.2	19	12.9	1.2
MB	17	8.7	1.0	10	8.9	0.7	19	10.2	1.1
CA	17	40.8	7.1	10	41.2	7.9	19	51.4	9.0
<i>I<sub>x</sub></i>	17	328.8	101.8	10	365.5	128.3	19	549.0	211.6
<i>I<sub>y</sub></i>	17	490.5	154.1	10	599.0	192.9	19	823.6	294.4
<i>J</i> *	17	819.2	248.2	10	964.5	314.2	19	1372.6	491.4
<i>Z<sub>x</sub></i>	17	90.0	42.3	10	73.5	18.4	19	118.0	53.9
<i>Z<sub>y</sub></i>	17	103.1	51.1	10	93.0	22.5	19	142.5	71.7
BL	17	27.7	2.1	10	27.6	2.1	19	29.4	3.2
<b>MT 1</b>									
PAH	20	12.8	2.0	3	12.0	1.1	20	13.4	1.6
PAB	20	27.5	1.4	3	26.3	0.4	20	30.2	1.6
MH	20	13.2	1.3	3	11.7	1.1	20	14.1	1.8
MB	20	13.3	1.3	3	12.0	0.9	20	14.2	1.4
CA	20	63.0	9.1	3	49.1	5.1	20	81.8	15.9
<i>I<sub>x</sub></i>	20	962.9	212.0	3	721.7	204.4	20	1673.4	611.8
<i>I<sub>y</sub></i>	20	1020.8	248.9	3	714.1	200.5	20	1709.2	701.7
<i>J</i> *	20	1983.7	444.1	3	1435.8	402.3	20	3431.6	1233.6
<i>Z<sub>x</sub></i>	20	146.9	31.6	3	111.6	28.3	20	213.6	75.0
<i>Z<sub>y</sub></i>	20	147.1	27.6	3	108.7	24.7	20	215.5	71.4
BL	20	60.2	4.0	3	56.7	2.4	20	63.7	3.9
<b>MT 2</b>									
PAH	20	14.3	1.9	4	13.2	0.9	20	14.8	1.6
PAB	20	18.8	1.2	4	18.8	1.5	20	20.7	1.5
MH	20	7.3	0.7	4	7.8	0.5	20	7.8	0.7
MB	20	8.5	0.9	4	8.6	0.6	20	9.1	1.1
CA	20	35.3	4.6	4	38.7	5.2	20	42.6	9.2
<i>I<sub>x</sub></i>	20	192.7	51.3	4	219.9	55.0	20	276.7	118.0
<i>I<sub>y</sub></i>	20	153.7	39.5	4	194.2	37.6	20	234.6	96.0
<i>J</i> *	20	346.4	83.1	4	410.8	91.7	20	511.3	204.0
<i>Z<sub>x</sub></i>	20	41.5	9.3	4	48.6	8.4	20	56.6	21.3
<i>Z<sub>y</sub></i>	20	37.6	7.4	4	44.6	6.3	20	52.7	19.1
BL	20	72.3	4.6	4	73.8	2.8	20	76.0	5.8
<b>MT 3</b>									
PAH	20	12.2	0.9	6	13.2	1.0	20	14.0	1.3
PAB	20	18.5	1.5	6	19.5	1.4	20	21.1	1.6
MH	20	6.5	0.8	6	7.3	1.3	20	6.9	0.9
MB	20	8.6	0.9	6	8.6	0.8	20	9.1	1.0
CA	20	30.9	5.5	6	33.4	7.2	20	39.9	8.9

**Table 1.** (continued)

Foot bone	Terry Collection females			Mangaian Collection			Terry Collection males		
	<i>N</i>	Mean	Std. dev.	<i>N</i>	Mean	Std. dev.	<i>N</i>	Mean	Std. dev.
$I_x$	20	168.3	64.4	6	212.6	89.5	20	266.9	114.6
$I_y$	20	125.5	47.8	6	153.2	52.4	20	222.5	96.8
$J^*$	20	293.8	108.9	6	351.1	124.7	20	489.5	202.8
$Z_x$	20	46.0	26.9	6	43.3	11.3	20	60.4	20.6
$Z_y$	20	41.3	26.7	6	37.0	8.4	20	53.6	17.9
BL	20	68.8	5.1	6	71.4	2.5	20	72.7	5.8
<b>MT 4</b>									
PAH	20	10.3	1.4	2	10.8	0.3	20	11.5	1.5
PAB	20	16.5	1.2	2	17.9	0.5	20	18.2	1.2
MH	20	6.6	1.1	2	7.2	0.9	20	7.4	0.8
MB	20	9.0	1.3	2	9.8	1.2	20	10.1	1.3
CA	20	33.2	6.8	2	33.3	1.8	20	42.9	10.8
$I_x$	20	171.1	79.1	2	282.3	68.5	20	295.4	164.3
$I_y$	20	212.7	99.7	2	153.5	54.9	20	352.2	159.0
$J^*$	20	383.9	169.2	2	432.5	128.1	20	647.6	301.6
$Z_x$	20	44.6	17.4	2	53.0	9.7	20	67.3	25.5
$Z_y$	20	41.1	12.8	2	37.8	10.3	20	62.4	28.2
BL	20	67.4	5.1	2	65.4	4.8	20	71.4	5.5

HPP = hallual proximal phalanx; MT = metatarsal; PAH = proximal articular height; PAB = proximal articular breadth; MH = midlength height; MB = midlength breadth; CA = cross-sectional area;  $I_x$  = bending rigidity about the  $y$ -axis;  $I_y$  = bending rigidity about the  $x$ -axis;  $J^* = I_{\min} + I_{\max}$ ;  $Z_x$  = bending strength about the  $y$ -axis;  $Z_y$  = bending strength about the  $x$ -axis; BL = bone length.

**Table 2.** Least-squared regressions of size vs. CA and  $J$ 

Element	log GM vs. log CA	log GM*BL vs. log $J$
HPP	0.76 (0.43)	0.77 (0.38)
MT 1	0.99 (0.42)	1.17 (0.61)
MT 2	0.82 (0.33)	0.98 (0.44)
MT 3	1.09 (0.63)	1.27 (0.71)
MT 4	0.98 (0.51)	1.21 (0.55)

Slopes with coefficients of determination in parentheses.

Only Terry Collection values used.

No scaling relationships deviate significantly from isometry.

$Z_x$  of MT 4 (Table 3). Although trend lines do not significantly differ from isometry, they do not have slopes of 1.0. Residuals for both samples have been calculated in two ways to take into account two possibilities: (1) that the observed regression slope is the actual relationship and (2) that the actual relationship is isometric. First, residuals have been generated from the observed slope line using Terry Collection



**Table 3.** Least-squared regressions of size and moment arm vs.  $Z$

Element	Variable	log GM*BL vs. log $Z_x$	log GM*BL vs. log $Z_y$
HPP	Slope	<b>0.05 (0.001)</b>	<b>0.048 (0.001)</b>
MT 1	Slope	1.15 (0.42)	1.08 (0.48)
MT 2	Slope	1.14 (0.45)	1.01 (0.36)
MT 3	Slope	0.99 (0.27)	1.07 (0.29)
MT 4	Slope	<b>1.54 (0.76)</b>	1.23 (0.62)

Slopes with coefficients of determination in parentheses.  
 Only Terry Collection values used.  
 Bold indicates significant deviation from isometry.

**Table 4.** Terry Collection and Manganian sample comparisons of cross-sectional residuals: Mann–Whitney  $U$ ,  $p$ -values

Element	Observed regression		Isometric scaling	
	log GM vs. log CA	log GM*BL vs. log $J$	log GM vs. log CA	log GM*BL vs. log $J$
HPP	-0.13	-0.76	-0.27	-0.93
MT 1	-0.014	-0.54	-0.04	-0.18
MT 2	0.49	0.52	0.37	0.49
MT 3	-0.13	-0.76	-0.28	-0.38
MT 4	-0.23	0.71	0.26	-0.79

$p < 0.005$  significance after Bonferroni multiple comparison correction. (–) indicates Manganian values are smaller.

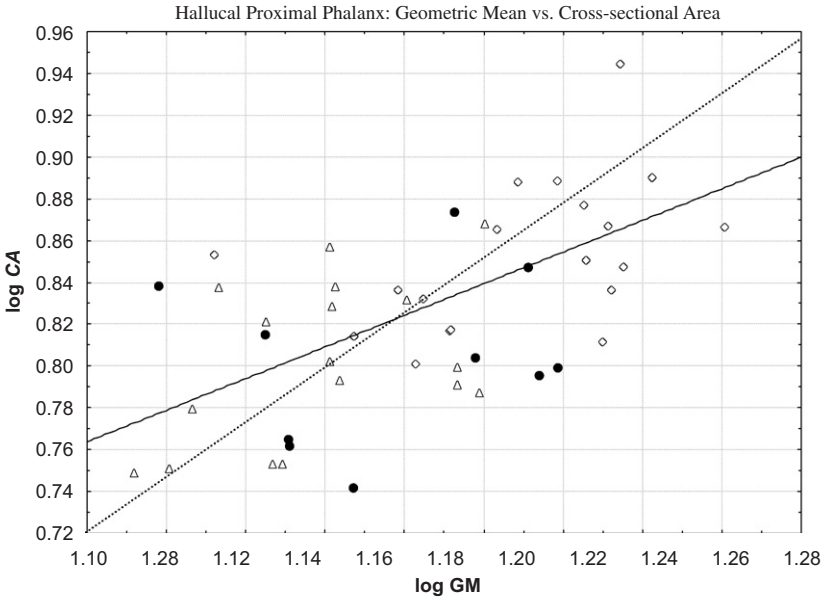
values only, and then another set of residuals has been generated from an isometric line that passes through the  $x$  and  $y$  means of the Terry Collection data.

Mann–Whitney  $U$ -tests comparing the residuals from the regressions of cross-sectional properties to GM as well as sample residuals generated from an isometric scaling line, both show that Manganians do not significantly differ from the Terry sample for either CA or  $J$  (Table 4, Fig. 3). Furthermore, the Manganian sample does not significantly differ in  $Z_y$  residuals, whether generated from the Terry Collection trend line or from an isometric scaling line ( $Z_y$ ,  $p$ -values = 0.18 and 0.55, respectively). However, the difference in  $Z_x$  between the Manganian sample and Terry sample approaches significance ( $Z_x$ ,  $p$ -values = 0.02 and 0.11, relative to least squares and isometric lines, respectively). For the HPP  $Z_y/Z_x$  ratio, Manganians are significantly larger ( $p$ -value = 0.006) than the Terry Collection (Fig. 4).

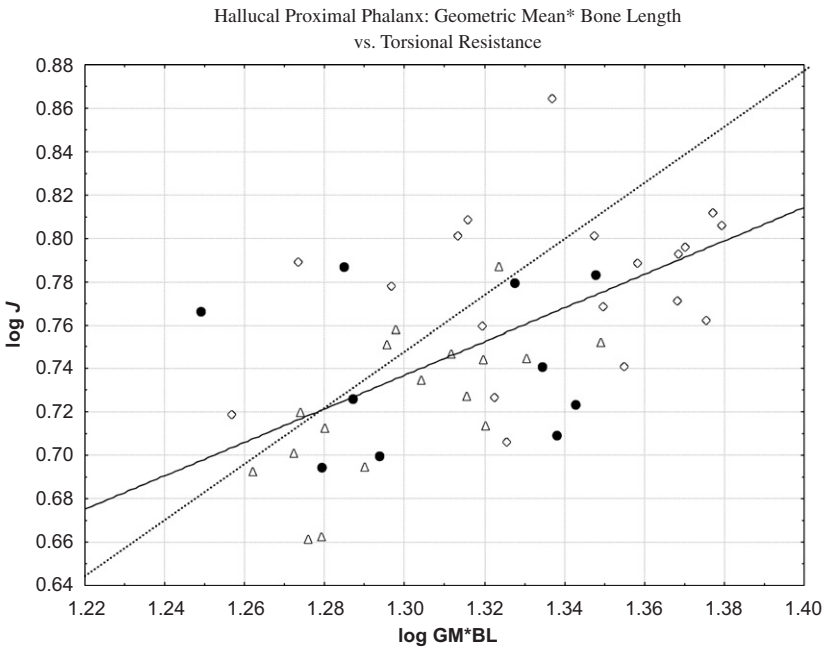
## Discussion

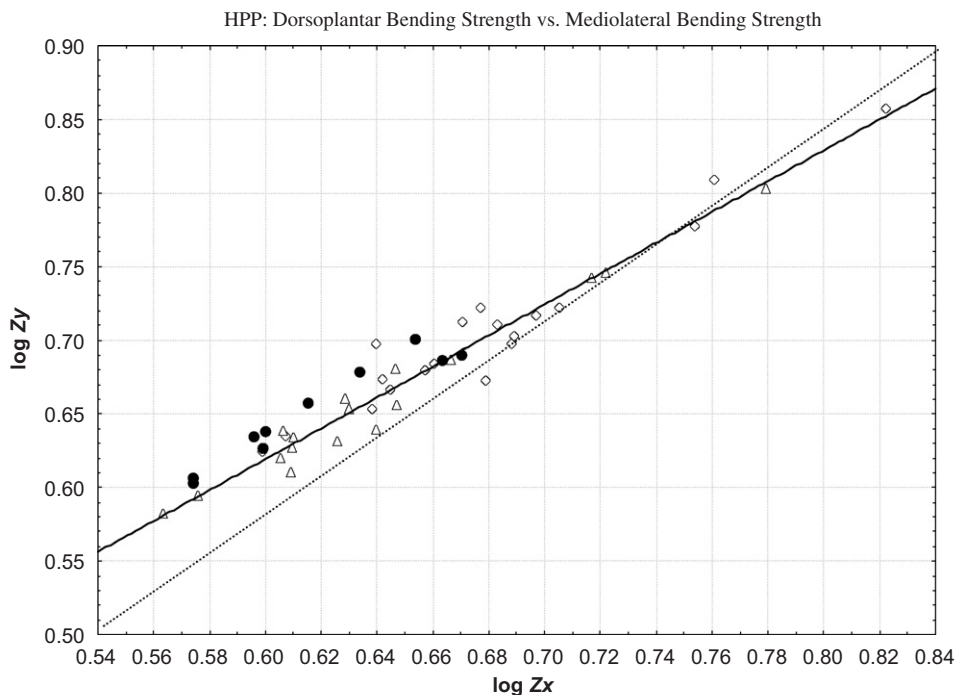
The results of this study provide no support for the hypothesis that the Manganian sample has greater relative forefoot CA or torsional resistance than the sample from

A



B





**Fig. 4.** For the relationship between  $Zx$  (sagittal bending strength in the dorsoplantar plane) and  $Zy$  (transverse bending strength in the mediolateral plane) of the HPP, most Mogaiaans fall above the slope (solid line) generated using only the Terry Collection values. For the  $Zy/Zx$  ratio, Mogaiaans are significantly larger ( $p = 0.006$ ). This is the same case when residuals of the two samples are generated from an isometric scaling line. Mogaiaans are represented by the filled circles, Terry Collection females are triangles, and Terry Collection males are diamonds. The isometric line is dotted.

the Terry Collection. In most cases, members of the Mogaian sample have smaller cross-sectional values. Several factors may be responsible for producing this result. First, foot size and shape may vary between populations. A previous study using the same Terry Collection sample found higher values for African American than European American feet and that, in general, males had higher values than females (Griffin and Richmond, 2005), suggesting that ethnicity and sex play a role in cortical bone distribution. The genetic difference between samples and the inability

**Fig. 3.** Representative of most of the forefoot bones studied, when either (A) CA or (B)  $J$  of the HPP is scaled against the appropriate GM variable using exclusively Terry individuals, the residuals generated from the Terry trendline (solid line) for the Mogaiaans do not significantly differ from the Terry sample. This is also true when residuals for both samples are generated from an isometric scaling line. Mogaiaans are represented by the filled circles, Terry Collection females are triangles, and Terry Collection males are diamonds. The isometric line is dotted.

to determine sex of the foot elements in the Mangaian assemblage may thus influence our results. It may be the case that the two samples differ in foot length relative to body mass, making it difficult to control for the effect of mass. Ashizawa et al. (1997) found that for either sex, East Javanese have longer feet than Japanese of the same body size (stature and body weight). Whether this is due to ancestry, the use of footwear, or a combination of these factors requires further investigation. The low cross-sectional strength values of the Mangaians could potentially be a product of relatively long feet in the Mangaians compared to European Americans and African Americans. For example, if the Mangaians had larger feet relative to body mass, then their cross-sectional values would appear low when adjusted against measures of the bone size. Further research is needed to assess foot and size proportions across geographic populations.

Sex variation in foot strength may also play a role in the Mangaian results. It is notable that Mangaian external measurement values are most comparable to the females in the Terry Collection (Table 1). In general, females have a smaller foot length relative to body size variables (Ashizawa et al., 1997; Fessler et al., 2005) and smaller size-adjusted cross-sectional values (Griffin and Richmond, 2005) than males from the same population. It is possible, although unlikely, based on size discrepancies, that the Mangaian foot sample is composed mostly of females. Nevertheless, these data warn against the assumption that pedal and body proportions scale similarly in all populations and between the sexes.

It is also necessary to consider how other foot variables relate to forefoot cross-sectional geometry. Anthropometric data comparing industrial populations found that Asian (Japanese and Korean) males and Caucasoid males of similar statures vary in aspects of forefoot shape (Hawes et al., 1994). Differences in forefoot shape are likely to lead to measurable differences in pressure distributions. This, in turn, could affect how mechanical activity influences cross-sectional structure across the forefoot. A difference in general forefoot shape between the Mangaians and the Terry Collection may, therefore, obscure a substrate or footwear use signal in the MTs.

Despite these complicating factors, the results show relatively high mediolateral bending strength (high  $Z_y/Z_x$ ) in the hallux. These results support the hypothesis that a locomotor repertoire consisting of habitually traversing rugged terrain without footwear will result in relative greater mediolateral bending strength in the proximal phalanges. Overall, while Mangaians appear to have a weak MT cross-sectional structure, their HPP is relatively stronger in the mediolateral direction.

## Conclusion

Although relationships between cross-sectional properties and element size in the forefoot are influenced by several factors unknown in this case, the available data do not support a relationship between more rugged terrain, larger cross-sectional area, and torsional resistance in the metatarsals of the Mangaians compared to industrial populations. However, this study supports previous results that the relative bending

strength is greater in proximal pedal phalanges of unshod individuals who habitually traversed more rugged terrain than those who went shod over relatively flat substrate (Trinkaus and Hilton, 1996).

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