

Metacarpal Trabecular Architecture Variation in the Chimpanzee (*Pan troglodytes*): Evidence for Locomotion and Tool-Use?

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ABSTRACT Trabecular architecture was assessed by 3D micro-computed tomography from spherical volumes of interest located within the head and base of metacarpals (MC) 1, 2, and 5 from $n = 19$ adult common chimpanzees. Two subspecies, West African *Pan troglodytes verus* from the Tai Forest, Côte d'Ivoire ($n = 12$) and Central African *P. t. troglodytes* from Cameroon ($n = 7$), were studied. For the combined sample, the metacarpal head is distinguished by greater bone volume fraction across all metacarpals, though the MC 1 is distinctive in having thicker, more plate-like trabeculae. The architecture in the MC 2 and MC 5 can be related to strains associated with terrestrial knuckle-walking. In particular, the relatively robust MC 5 head

architecture may result from functional loading incurred during braking and use of a palm-in hand posture. Examining differences between samples, we found that the Cameroon chimpanzees possess a more robust architecture across all metacarpals in the form of greater bone volume fraction, higher connectivity, and somewhat more plate-like structure. These differences are not explicable in terms of population distinctions in body size or daily travel distance, but possibly reflect a combination of more terrestrial knuckle-walking in the Cameroon sample and more diverse hand postures and precision handling required of nut-cracking in West African chimpanzees. *Am J Phys Anthropol* 144:215–225, 2011. © 2010 Wiley-Liss, Inc.

Two functional enterprises dominate the use of the hominoid upper limb: locomotion and manipulation. The impact of locomotion on long bone morphology and cross-sectional geometry has been well-studied (Ruff and Runestad, 1992; Demes et al., 2001; Ruff, 2002; e.g., Carlson et al., 2006; Zihlman et al., 2008), while behavioral variation (e.g., tool use) has received less attention (e.g., Morbeck et al., 1994; Sarringhaus et al., 2005). To date, comparatively few studies have addressed the relationship between skeletal anatomy and primate locomotion through an examination of trabecular morphology, and fewer have ventured to consider the impact on trabecular bone of differences in manipulation (Zylstra, 2000; Lazenby et al., 2008c). This study investigates variation in trabecular mass and architecture in samples of first, second, and fifth metacarpals of Western (*Pan troglodytes verus*) and Central African (*Pan troglodytes troglodytes*) common chimpanzees, using noninvasive 3D microcomputed tomography (μ CT). Specifically, it assesses variation in trabecular structure within and between each metacarpal and tests hypotheses linking trabecular architecture to both locomotor repertoire and degree of manual manipulation, as well as testing for subspecific differences.

Trabecular bone is well suited to the study of functional adaptation (Ruff et al., 2006) as it is highly responsive to variation in its mechanical environment, particularly through the growth phase (Ducher et al.,

2006; Pontzer et al., 2006). As a tissue, trabecular bone has received considerable research within biomedicine and biomechanics, emphasizing the relation of properties of volume, mineral density, and structure to material properties such as strength, stiffness, and resistance to failure (Haddock et al., 2004; Renders et al., 2008). At the microstructural level, studies have demonstrated that the amount of trabecular bone (characterized as bone volume fraction) is a robust predictor of structural strength measured as Young's modulus (e.g., Beville et al., 2006). Moreover, specific architectural features such as trabecular number, thickness, orientation, and degree of "plate-ness" versus "rod-ness" have been shown

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to contribute to the ability of trabecular bone to withstand functional loads (Ruimerman et al., 2005a). Current research suggests that trabecular bone responds to large functional loads through an increase in trabecular number, thickness, and “plate-ness,” contributing to a larger bone volume fraction (Stauber and Müller, 2006; Stauber et al., 2006). Moreover, orientation of trabecular rods and plates correlates with load direction, such that loading diversity results in more isotropic trabecular volumes. Finally, axial loads tend to be borne preferentially by plate-like elements, which have a higher stiffness and resistance to failure (Stauber and Müller, 2006).

Given the now well-recognized variation in behavioral diversity among chimpanzees (Boesch and Tomasello, 1998; Whiten, 2007) and the sensitivity of trabecular bone to functional loading noted above, the possibility of discerning an osseous signal for locomotion and/or tool use at the microstructural level in forms such as *Pan* should be considered. In chimpanzee terrestrial or arboreal knuckle-walking, body weight, and momentum combine to generate significant biomechanical loads among digits, which are highest in the second and third rays and reduced by about 50% in rays four and five; the first metacarpal is effectively isolated (Wunderlich and Jungers, 2009). These loads have been estimated at about 20% body weight in terrestrial knuckle-walking, and up to twice body weight in one-handed suspension (Preuschoft, 2004).

We hypothesize that trabecular architecture will show a lateral to medial (II–V) gradient in declining strength within the palm, with the first metacarpal least robust. Within a biomechanical framework, we predict that elements most heavily loaded in locomotion will present with higher trabecular volume and an architecture favoring a preponderance of thick, well-connected, and anisotropic plates. Significant head versus base differences have been noted for the human second metacarpal (Lazenby et al., 2008a), largely explicable by the greater degrees of freedom and subsequent loading diversity experienced by the distal epiphysis. Thus, a second hypothesis is that the distal and proximal epiphyses will also differ as a consequence of variation in loading pattern (independent of magnitude) associated with joint structure.

While locomotion contributes most to functional loading in the chimpanzee forelimb, the well-recognized cultural repertoire expressed by *Pan* implies that variation in manipulative roles may produce unique biomechanical signals mediating trabecular bone morphology. The most striking behavioral distinction among the various common chimpanzee populations in western, central, and eastern Africa is the propensity for western chimpanzees (*Pan troglodytes verus*) to use large wood or stone hammers to crack nuts as a typical subsistence strategy (Boesch et al., 1994; McGrew et al., 1997). The energy involved in nut-cracking with regard to time spent, weight of hammer employed, and frequency of act can be substantial (Boesch and Boesch-Achermann, 2000), suggesting not only that it is adaptive but that it also imparts nontrivial mechanical loads. Boesch and Boesch (1993) documented a variety of grips and hand postures used in positioning nuts on anvils, or holding nuts for subsequent processing. The thumb is directly involved in the majority of these grips and postures in both unimanual (arboreal nut processing with smaller hammers) or bimanual (terrestrial activity with hammers as large as 20 kg; (see Boesch and Boesch, 1993; their Figs. 5, 7,

and 8). As such we hypothesize that the first metacarpal, isolated from locomotory activity (see below) but frequently recruited in manipulation, will possess a trabecular architecture reflecting such behaviors. We predict that *P. t. verus* MC 1 architecture will be characterized by greater isotropy and a bone volume fraction composed of more numerous rod-like trabeculae compared to that found in *P. t. troglodytes*.

MATERIALS AND METHODS

Seventy-nine first, second, and fifth left and right metacarpals were selected from 17 adult and 2 late adolescent chimpanzees. Of these, 12 are West African *P. t. verus* from the Tai National Park, Côte d’Ivoire, (curated at the Max Planck Institute for Evolutionary Anthropology, Leipzig), and 7 specimens from southern Cameroon housed at the Museum für Naturkunde (Berlin). The latter typically date to the early 20th c., and are likely *P. t. troglodytes* (surmised from geographic references noted by the collector, e.g., “Akonolinga, Afrika” or “Sangmelima, Kamerun”). The Tai sample comprises a number of known individuals, many of which have been the subject of long-term ethological study including research concerning handedness and tool-using behavior (Boesch, 1991; Boesch and Boesch-Achermann, 2000). Of the 19 individuals in the combined sample, 10 were identified as female and 8 male; one of the Cameroonian specimens was catalogued as “unknown sex,” though standard osteometric measures (data not reported) lead us to conclude that this individual is female. Seven individuals contributed complete sets of paired metacarpals, with the remainder supplying one or two pairs. Unpaired data were collected for some metacarpals from five animals due to absence or postmortem damage to the contralateral element. With the exception of one adult female from the Tai sample, all forelimbs were free of manifest pathology. This individual exhibited a moderate degree of myositis ossificans of the volar surface on the left second metacarpal just distal to midshaft. However, one-sample *t* tests (not reported) failed to demonstrate significant differences from the nonpathological sample for any trabecular variable; consequently, we have included these data in subsequent analyses.

Heads and bases were scanned using a SkyScan (Aartselaar, Belgium) 1172 Desktop μ CT Scanner (parameters: 100 kV, 0.094 mA, 0.5-mm aluminum filter, 0.5-rotation step, 360° of rotation, two frame averaging). Raw projections were converted into TIFF image stacks using NRecon[®] (parameters: ring artifact correction = 5; beam hardening = 50%). Pixel dimensions and slice spacing of the resultant images was ~14 microns (μ m). Trabecular mass and architecture was characterized from 4.5-mm diameter spherical volumes of interest (VOI; Fig. 1) using CTAn[®] and a global thresholding algorithm (Lazenby et al., 2008b). The VOI was located centrally within the proximal and distal epiphyses¹ with the mid-slice positioned such that all slices in the stack included only trabecular bone. The specific global threshold value demarcating the bone–nonbone interface varied for each VOI, and was determined with reference to the gray-level histogram generated over all of the slices in the stack. In each case the

¹The 1st metacarpal does not have an epiphysis per se (i.e., occurring as a separate center of ossification). We use the term here as a convenient reference to anatomical location of the proximal and distal subarticular masses.

threshold was determined as the minimum inter-peak value from the histogram, with all voxels below this value specified as background and those above as bone.

The variables analyzed include measures of relative bone mass, strength, and structure (Table 1). As we found no evidence for significant directional asymmetry or sexual dimorphism for trabecular morphology in this sample, side, and sex were combined in the present study. The absence of sexual dimorphism is consistent with previous research suggesting a lack of body size dependence for features of trabecular size such as thickness (Swartz et al., 1998), though parameters such as connectivity and number did vary when viewed over several orders of magnitude size change. Thus, scaling of trabecular skeletal parameters to standardize for body size, typically performed for analysis of diaphyseal cortical bone structure (Ruff, 2000), was not deemed necessary for the present study given the relatively small size range sampled. General patterns of variation between epiphyses and elements for the entire sample (*P. t. verus* and *P. t. troglodytes* combined) were examined using a nested analysis of variance (epiphysis nested within element); post-hoc pairwise comparisons for

significant ANOVA results were assessed by the Scheffé test. Comparison of the *Pan t. verus* and *Pan t. troglodytes* samples, in which we explore the impact of behavioral differences, was undertaken using a Kruskal-Wallis nonparametric ANOVA given the attendant reduction in sample size. All analyses were carried out using Systat 11.0 and $\alpha = 0.05$. In the following Results and Discussions sections we first present findings for the combined sample, followed by the between-population analyses.

RESULTS

General patterns of variation

Descriptive statistics for the combined Tai and Cameroon samples are given in Table 2. Nested ANOVA (Table 3) reveal differences in trabecular architecture between head and base for all variables, and the significant inter-element differences (BV/TV, Tb.Th, Tb.N, Tb.Sp, and DA) are consequential to epiphyseal differences. An example is the distinction in BV/TV for the MC 1 head compared to its base (16.50% vs. 12.69%). The pollical distal VOI has a significantly larger bone volume fraction, due to greater trabecular thickness (Tb.Th) rather than number (Tb.N), than any of the other heads or bases with the exception of the MC 5 head (Table 4). Among elements, the 2nd metacarpal head has significantly lower BV/TV. It is notable that across all three of the metacarpals, the distal VOI invariably has a greater bone volume fraction than its corresponding base (see Fig. 2).

Figure 3 summarizes the pattern of variation among epiphyses and elements. The MC 1 presents clear distinctions with the head having significantly higher connectivity than the base (Scheffé post-hoc $P = 0.01$; 147 df) and a greater proportion of plate-like trabeculae relative to the base (Scheffé post-hoc $P = 0.04$; 147 df). Indeed, the average connectivity for the MC 1 head is the lowest among all VOIs at 0.32 ± 0.44 . These variations in structure are clearly evident in comparing 3D surface models of the epiphyseal VOIs for MC 1 versus MC 2 (see Fig. 4). A consequence of these architectural differences in Tb.Pf and SMI is the illusion that the distal MC 1 has a lower bone volume fraction, but as noted

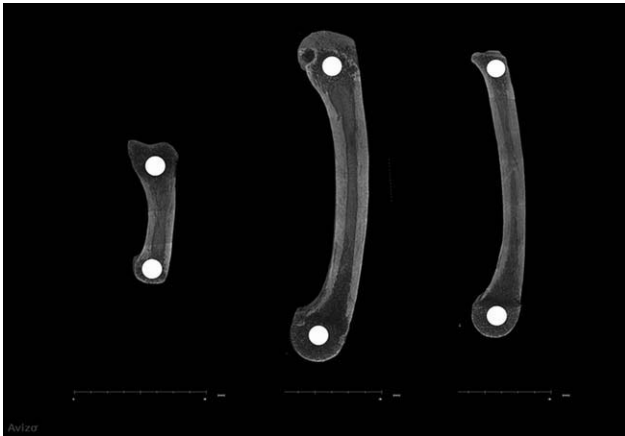


Fig. 1. First, second, and fifth metacarpals (left to right, head inferior) showing the placement of the volume of interest (VOI).

TABLE 1. Trabecular variables selected for analysis

Variable	Symbol (unit)	Definition
Bone volume fraction	BV/TV (%)	The proportion of the total volume of the VOI occupied by trabeculae.
Trabecular bone pattern factor	Tb.Pf (mm^{-1})	A proxy measure trabecular connectivity within a VOI. Higher Tb.Pf values indicate greater fragmentation and the presence of isolated struts; lower values reflect structural integrity and greater connectivity.
Structure model index	SMI	SMI is a dimensionless measure of the relative proportion of plate-like versus rod-like structures in the VOI. Values range from 0 (idealized plates) to 3 (idealized rods).
Trabecular thickness	Tb.Th (mm)	The mean minimum thickness of trabeculae in a VOI summed over all local voxels (3D pixel elements) based on the diameters of a series of spheres fully contained within the structure.
Trabecular number	Tb.N (mm^{-1})	The ratio of bone volume fraction to trabecular thickness.
Trabecular separation	Tb.Sp (mm)	The average width of the spaces between adjacent trabeculae in a VOI.
Degree of anisotropy	DA	DA describes trabecular orientation. Anisotropic structures have a preferred orientation while isotropic structures demonstrate symmetry of orientation in 3D space. CTAn employs the mean intercept length (MIL) algorithm for calculating DA. Anisotropy values are reported as a dimensionless value ranging from 0 (fully isotropic) to 1 (fully anisotropic).

Full descriptions and calculation protocols are available from <http://www.skyscan.be/next/CTAn03.pdf>.

TABLE 2. Means and standard deviations for the complete sample, by element and epiphysis

	BVTV	TBPF	SMI	TBTH	TBN	TBSP	DA
MC I head (n = 20)	16.50 (2.58)	0.05 (1.30)	0.32 (0.44)	0.21 (0.03)	0.80 (0.11)	0.80 (0.06)	0.35 (0.05)
MC I base (n = 23)	12.69 (2.57)	1.75 (1.70)	0.71 (0.35)	0.15 (0.02)	0.86 (0.12)	0.75 (0.03)	0.40 (0.11)
MC II head (n = 29)	13.23 (2.57)	1.59 (1.59)	0.66 (0.42)	0.16 (0.03)	0.83 (0.11)	0.76 (0.04)	0.37 (0.06)
MC II base (n = 27)	12.04 (2.17)	1.03 (1.55)	0.57 (0.39)	0.17 (0.02)	0.70 (0.11)	0.86 (0.10)	0.36 (0.06)
MC V head (n = 27)	14.62 (2.70)	1.27 (1.22)	0.62 (0.31)	0.17 (0.04)	0.86 (0.10)	0.76 (0.04)	0.38 (0.06)
MC V base (n = 29)	13.91 (1.41)	1.17 (0.99)	0.61 (0.27)	0.19 (0.02)	0.75 (0.09)	0.79 (0.05)	0.41 (0.09)

TABLE 3. Results of nested ANOVA, epiphyses within elements

Contrast	BV/TV		Tb.Pf		SMI		Tb.Th		Tb.N		Tb.Sp		DA	
	F	P	F	P	F	P	F	P	F	P	F	P	F	P
Element	10.30	0.000	1.05	0.35	1.14	0.32	3.22	0.04	4.71	0.01	6.57	0.00	3.23	0.04
Epiphysis	10.55	0.000	5.76	0.00	4.24	0.01	18.73	0.00	13.94	0.00	16.23	0.00	2.92	0.04

TABLE 4. Scheffé post-hoc probabilities by epiphysis for BV/TV

	MC 1 B	MC 1 H	MC 2 B	MC 2 H	MC 5 B	MC 5 H
MC 1 B						
MC 1 H	0.00					
MC 2 B	0.97	0.00				
MC 2 H	0.99	0.00	0.62			
MC 5 B	0.66	0.02	0.12	0.94		
MC 5 H	0.17	0.21	0.01	0.43	0.93	

Significant differences are in bold.

above, BV/TV is actually greater at this site than elsewhere as the more plate-like trabeculae are much thicker.

While the 2nd and 5th metacarpals are similar in many respects, the MC 2 head and base have thinner and fewer trabeculae per unit volume, contributing to greater trabecular spacing and lower BV/TV. In the metacarpal heads, values for DA range from 0.35 to 0.38 moving from 1st to 5th metacarpals; that is, the 5th metacarpal distal epiphysis has more preferentially oriented trabeculae, though the differences are not statistically significant. Among bases, the proximal MC 2 (DA = 0.36) is more isotropic than either the MC 1 or MC 5 (significantly more so in the case of the latter). The greater trabecular isotropy in the MC 2 base may be due to its more complex carpometacarpal arthroses and the multiplanar facet morphology of the proximal epiphysis (Tocheri et al., 2005). This would favor a trabecular structure able to accommodate loading from multiple directions.

Interpopulation variation

Values for the Tai and Cameroon samples are reported in Tables 5 and 6 while Tables 7 and 8 provide results of the Kruskal-Wallis ANOVA. Across VOIs the Cameroon sample has a significantly greater bone volume fraction (BV/TV), with the exception of the MC 2 and MC 5 bases, though the former approaches significance ($\chi^2 = 3.43$; $P = 0.06$). This difference is especially marked for the MC 2 and MC 5 heads, and the MC 1 base. The primary contributors here are SMI and Tb.Th. The Central African chimpanzees have a greater proportion of thick, plate-like trabeculae, which add to a higher degree of connectivity and bone volume fraction. While the Cameroon chimpanzee metacarpals tend to have more trabeculae in both head and base, the differences are not that pronounced (as shown by Tb.Sp). There are also insub-

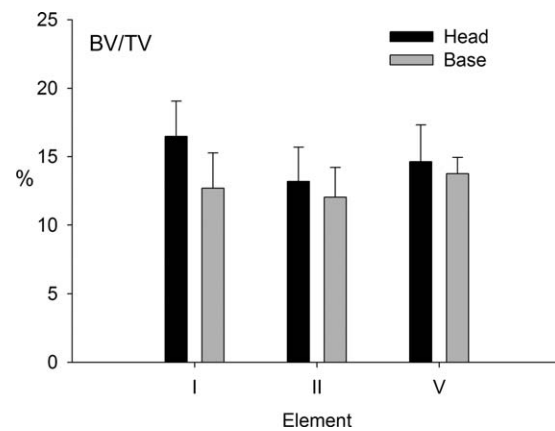


Fig. 2. Inter-element differences in BV/TV (mean + sd). The head is consistently greater than its corresponding base; that of the MC 1 is significantly larger than all other instances with the exception of the MC 5 head (see Table 4).

stantial differences in the degree of anisotropy among the volumes of interest between the two populations. Regardless of structural variation (i.e., plates or rods), the samples do not deviate markedly in terms of preferred trabecular orientation.

Examining the populations separately clarifies the general patterns of variation noted above. For example, the distal VOI invariably having greater BV/TV than its corresponding base can be ascribed to the influence of the Cameroon sample, as this distinction does not occur for the MC 2 and MC 5 among Tai chimpanzees. If fact, in the Tai sample, the MC 5 base has a larger (albeit nonsignificant; $t = 1.26$; $P = 0.22$) bone volume fraction than in the head. Similarly, while both populations possess greater trabecular connectivity (Tb.Pf) and a more plate-like structure (SMI) in the MC 1 head relative to its base (contrary to our prediction), these distinctions are more pronounced for the Cameroon sample. Indeed, with a SMI value of 0.01 ± 0.44 for the MC 1 head VOI, *P. t. troglodytes* approaches the value for idealized plates.

DISCUSSION

General patterns of variation

Trabecular architecture in *Pan troglodytes* varies in mass and structure between head and base across meta-

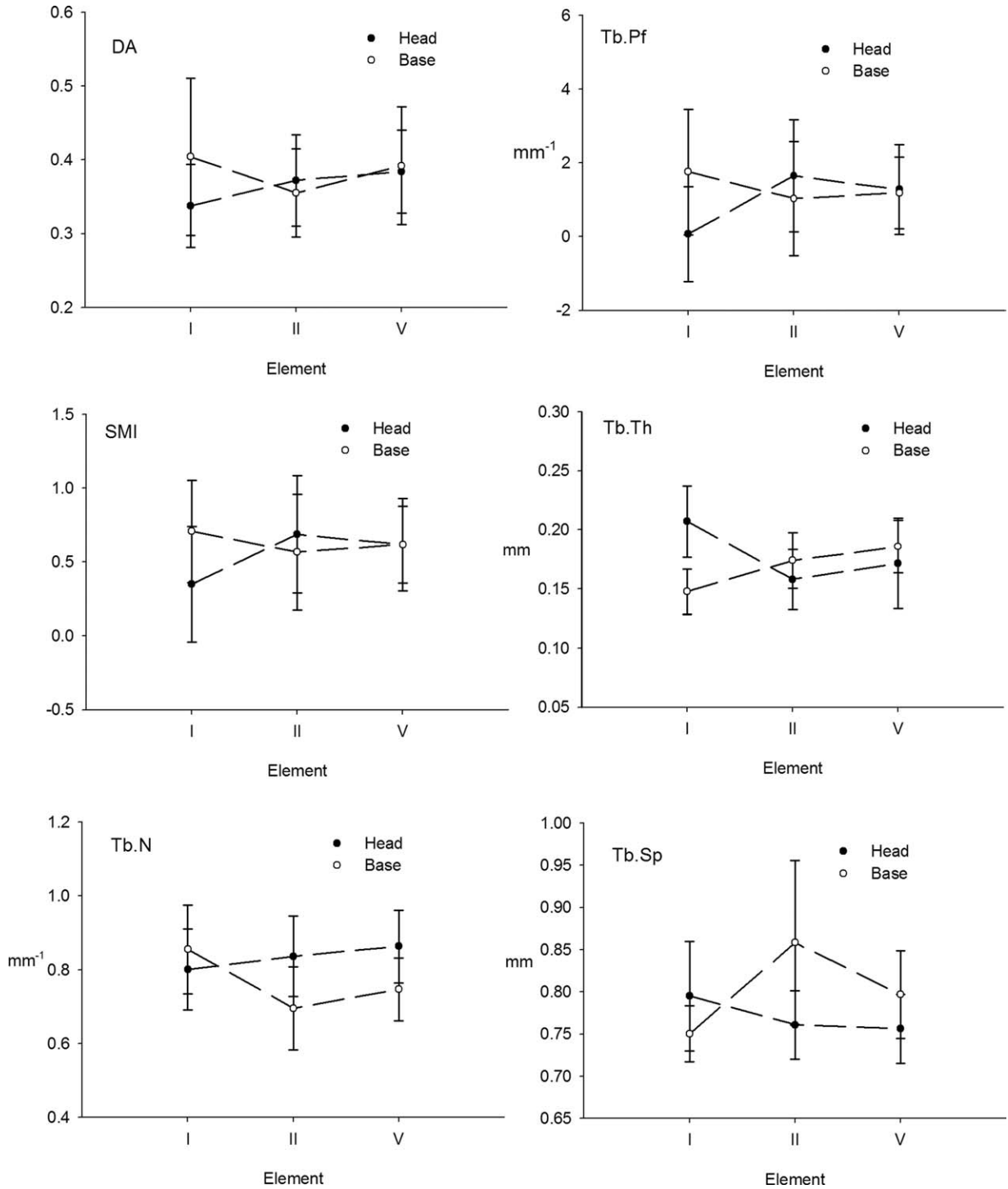


Fig. 3. Plots for architectural variables by “epiphysis” and element (mean ± sd). The pattern of MC 1 head and base differences is clearly distinct from that of the 2nd and 5th metacarpals.

carpals 1, 2, and 5. These differences are most marked in the MC 1 and most apparent with respect to BV/TV and its contributing architectural features (e.g., SMI and Tb.Th for MC 1 and Tb.Sp and Tb.N for MC 2 and MC 5). Lazenby et al. (2008a) reported a similar head versus base dichotomy for the human second metacarpal, again principally expressed in terms of bone volume fraction, reduced spacing, and increased trabecular number. They attributed that pattern to a more dynamic and diverse

loading history experienced by the less anatomically constrained head. A similar argument applies in the present case for *Pan*, in particular for MC 2 and MC 5, in which the carpometacarpal arthroses limit range of motion and enhance stability during knuckle-walking (Marzke and Shackley, 1986; Tocheri et al., 2003). Preuschoft (1973) emphasized this point in considering the metacarpals and carpals as a unified functional unit. The present study also found that the *Pan* pollical metacarpal stands

out in having trabecular architecture in the head which is quantitatively and qualitatively distinct from that found in the MC 1 base or in the palmar elements, notably having much thicker, more plate-like trabeculae. Both of these principal findings speak to variation in robusticity and strength of these elements in relation to their primary modes of functional loading (locomotion versus manipulation).

Why is MC 5 more robust than MC 2?

We had hypothesized that the MC 2 would have a more robust architecture than the MC 5 given its greater loading in knuckle-walking progression. However, the fifth metacarpal has greater bone volume fraction than the second, in both head and base, primarily a consequence of higher values for Tb.N and Tb.Th (see Figs. 2 and 3), parameters that have been shown through finite element analysis to reflect increased functional loading (Ruimerman et al., 2005a). This may be explicable in light of particular characteristics of the

locomotor dynamics of chimpanzees. *Pan* locomotor and postural repertoires can best be described as complex and diverse (Hunt et al., 1996). Carlson et al. (2006) documented four primary locomotor modes for *P. troglodytes*: quadrupedal walk, quadrupedal climb, quadrupedal scramble, and suspension, the last three arboreal activities. Climbing, scrambling, and suspensory activity typically involves a “hook-grip” involving digits two to five (Marzke and Wullstein, 1996). As noted by Preuscheft (2004), arboreal locomotion, particularly suspension, subjects palmar metacarpals to a net compressive force which may result in greater strain magnitudes than that experienced in terrestrial knuckle-walking. Although locomotion constitutes only a small portion of chimpanzee activity schedules [less than 16% of observed activities involved locomotion for either males or females, and about 85% of these behaviors were recorded as terrestrial knuckle-walking (Carlson et al., 2006)], the MC 5 will be under some (at present unknown) level of functional loading in vertical climbing and/or suspension.

Recent qualitative and quantitative kinetic and/or kinematic studies in *Pan* and *Gorilla* have identified a number of important distinctions relevant to understanding metacarpal trabecular structure, both functionally in terms of hand posture and peak force distribution among digits (Wunderlich and Jungers, 2009), as well as ontogenetically, particularly regarding the variable recruitment of the fifth ray in knuckle-walking in subadult (Inouye, 1994) and adult (Tuttle, 1969) chimpanzees. Matarazzo (2008, 2009) demonstrated that the 3rd digit experiences the highest compressive pressures during knuckle-walking in chimpanzees and gorillas, regardless of how many other digits contact the substrate. Chimpanzees also evinced greater variability in hand posture in locomotion. Wunderlich and Jungers (2009) reported peak pressures and contact sequence data in knuckle-walking for digits two to five for a small ($n = 2$) chimpanzee sample. They found that peak pressures varied by forelimb placement (inside or outside of the advancing “overstriding” hindlimb) as well as hand posture. Hand posture contrasted a “palm-in” (semi-pronated) versus “palm-back” (fully pronated) orientation. Both postures are used regularly, though palm-in was more commonly employed when walking on the ground.

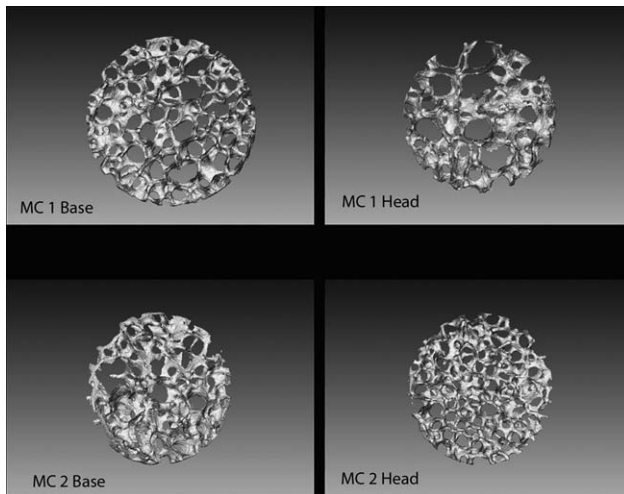


Fig. 4. The 3D renders of head and base VOIs for the 1st and 2nd metacarpals from an adult female chimpanzee. The 5th MC generally mimics the structural pattern of the 2nd MC.

TABLE 5. Tai forest sample means and standard deviations

	BTVT	TBPF	SMI	TBTH	TBN	TBSP	DA
MC I head ($n = 12$)	15.47 (2.64)	0.60 (1.23)	0.52 (0.31)	0.20 (0.02)	0.77 (0.10)	0.80 (0.05)	0.34 (0.05)
MC I base ($n = 11$)	10.92 (1.92)	2.87 (1.43)	0.93 (0.23)	0.14 (0.01)	0.80 (0.10)	0.76 (0.03)	0.49 (0.09)
MC II head ($n = 18$)	11.70 (1.04)	2.58 (0.84)	0.91 (0.17)	0.15 (0.01)	0.81 (0.08)	0.76 (0.04)	0.38 (0.05)
MC II base ($n = 18$)	11.44 (1.88)	1.55 (1.4)	0.71 (0.32)	0.17 (0.01)	0.68 (0.08)	0.85 (0.05)	0.35 (0.07)
MC V head ($n = 15$)	12.97 (1.87)	1.90 (1.07)	0.75 (0.26)	0.15 (0.02)	0.88 (0.10)	0.75 (0.04)	0.38 (0.05)
MC V base ($n = 18$)	13.58 (1.00)	1.37 (0.85)	0.64 (0.27)	0.19 (0.02)	0.74 (0.07)	0.79 (0.04)	0.41 (0.05)

Sex and side combined; see Table 1 for units of measurement.

TABLE 6. Cameroon sample means and standard deviations

	BTVT	TBPF	SMI	TBTH	TBN	TBSP	DA
MC I head ($n = 8$)	18.04 (1.63)	-0.76 (0.98)	0.01 (0.44)	0.22 (0.04)	0.85 (0.11)	0.79 (0.08)	0.36 (0.06)
MC I base ($n = 10$)	14.65 (1.58)	0.53 (1.00)	0.46 (0.28)	0.16 (0.02)	0.92 (0.12)	0.74 (0.04)	0.39 (0.13)
MC II head ($n = 11$)	15.72 (2.37)	-0.04 (1.09)	0.27 (0.40)	0.18 (0.03)	0.88 (0.13)	0.77 (0.05)	0.37 (0.08)
MC II base ($n = 9$)	13.23 (2.33)	0.01 (1.38)	0.28 (0.38)	0.19 (0.04)	0.73 (0.16)	0.88 (0.16)	0.36 (0.02)
MC V head ($n = 12$)	16.69 (2.11)	0.49 (0.92)	0.45 (0.29)	0.20 (0.04)	0.85 (0.10)	0.77 (0.04)	0.39 (0.07)
MC V base ($n = 11$)	14.43 (1.83)	0.84 (1.15)	0.54 (0.28)	0.19 (0.03)	0.78 (0.11)	0.80 (0.08)	0.42 (0.12)

Sex and side combined; see Table 1 for units of measurement.

TABLE 7. Kruskal-Wallis ANOVA for population differences in the metacarpal head

	BV/TV	TBPF	SMI	TBTH	TBN	TBSP	DA
First metacarpal							
χ^2	5.72	6.48	7.92	0.60	3.43	1.72	1.52
$P =$	0.02	0.01	0.01	0.44	0.06	0.19	0.22
Second metacarpal							
χ^2	16.00	17.47	16.36	9.90	2.62	0.20	0.05
$P =$	0.00	0.00	0.00	0.00	0.11	0.65	0.82
Fifth metacarpal							
χ^2	13.75	9.15	6.94	15.62	0.86	2.14	0.12
$P =$	0.00	0.00	0.01	0.00	0.35	0.14	0.73

Significant differences are in bold.

In this posture, initial contact with the substrate is made with the 5th digit, though the second and third rays experience significantly higher peak pressures as the hand rolls over to complete the loading cycle and the animal's center of mass (COM) moves over the extended forelimb. In the palm-back posture, peak pressures are distributed across digits two to four, and digit five again experiences significantly lower loading. However, Wunderlich and Jungers (2009) note that the animal's age modified the pattern of loading—at a younger age, the subject animals had higher peak pressures for digits three and four, though when older, the highest loading (for both postures) occurred for digit two, closely followed by digit three; loading of digit five was about 25–33% that of digit two (e.g., 20 N cm⁻² vs. 60–80 N cm⁻², their Fig. 8b). Importantly, Doran (1997) has noted that adult locomotor behaviors in *Pan* are established during the transition from infancy to juvenile life stages, some 6–8 years before completion of skeletal growth.

A further consideration for the present study is disparity in forelimb and hindlimb force and weight support when braking during locomotion. Demes et al. (1994) reported greater braking force for the forelimb than the hindlimb in walking and galloping. While more of body mass is accommodated by the hindlimb in chimpanzees during locomotion (Demes et al., 1994; Raichlen et al., 2009), dynamic loading associated with deceleration is born primarily by the forelimb. This suggests the hypothesis that the difference in braking force may account for the relatively high trabecular robusticity in the head of MC 5 seen in the present study. This could occur because bone modeling is sensitive not only to strain magnitude, but even more so to strain rate (Martin et al., 1998; Ruimerman et al., 2005b). The braking hypothesis would be particularly relevant in the case of palm-in postures in which initial substrate contact is borne by the head of the MC 5. Wunderlich and Jungers (2009) found that the highest peak pressures for the 5th digit occurred for the palm-in posture during the initial contact sequence (i.e., the “braking” phase) with the substrate. This argument would also account for our finding that the *base* of MC 5 has the highest degree of trabecular anisotropy among all epiphyses. The fact that the forelimb in general provides comparatively little propulsive force (Demes et al., 1994) and the 5th digit none at all (Wunderlich and Jungers, 2009) suggests that metacarpal trabecular architecture of this ray may be strongly influenced by dynamic, high strain-rate loading associated with braking, particularly when employing a semi-pronated palm-in posture. However, factors which would need to be incorporated into a robust test of this hypothesis include the quantitative and qualitative aspects of loading on the ulnar side of the hand in arboreal climbing/scrambling.

TABLE 8. Results of Kruskal-Wallis ANOVA for population differences in the metacarpal base

	BV/TV	TBPF	SMI	TBTH	TBN	TBSP	DA
First metacarpal							
χ^2	10.95	9.17	10.04	10.04	4.17	1.79	0.50
$P =$	0.00	0.00	0.00	0.00	0.04	0.18	0.48
Second metacarpal							
χ^2	3.43	5.36	6.61	2.23	2.38	0.52	0.10
$P =$	0.06	0.02	0.01	0.14	0.12	0.47	0.76
Fifth metacarpal							
χ^2	1.37	2.77	0.89	0.20	1.94	1.47	0.16
$P =$	0.24	0.10	0.35	0.65	0.16	0.23	0.69

Significant differences are in bold.

Why is the MC 1 head as robust as it is?

The trabecular architecture of the chimpanzee MC 1 head is distinctive compared to all other sampled VOIs (including the MC 1 base), with significantly larger bone volume fraction (Table 4; Fig. 2) as a consequence of thick, well-connected, plate-like trabeculae. These features suggest that chimpanzees have a comparatively robust pollical morphology adapted to relatively high levels of functional loading (Ruimerman et al., 2005b; Bevill et al., 2006), a conclusion which seems paradoxical in that the thumb in *Pan* does not participate in terrestrial locomotor activity. Although less is known regarding the use of the thumb in arboreal contexts (e.g., climbing and suspension), the relative infrequency of arboreal locomotion more generally among chimpanzees (Doran, 1993; Carlson et al., 2006) argues against such activity as a source of consistent elevated functional loading in the MC 1. In their analysis of femoral and humeral cross-sectional geometry in wild chimpanzees, Carlson et al. (2006) argued that arboreal locomotion, which may involve thumb abduction or opposition on sufficiently large supports (Marzke and Wullstein, 1996; see their Table 1), generated more varied loading patterns with relatively high strain magnitudes. However, chimpanzees also have reduced dorsiflexion capability at the radiocarpal joint compared to other terrestrial catarrhines (including gorillas) to provide structural rigidity to the wrist and forelimb in knuckle-walking (Patel and Carlson, 2007). Such restriction may act to limit mechanical loading diversity within the hand, though in the absence of empirical data this should be considered a testable hypothesis. It seems reasonable to posit, nonetheless, that arboreal locomotion is likely to contribute only a limited degree of functional loading.

Given that the MC 1 plays a relatively minor role in locomotion, the alternative explanation for a relatively robust MC 1 head trabecular architecture rests in manipulative behavior. In the wild, chimpanzees are known to fashion and use a variety of tools, for display, comfort, therapeutic, or resource extractive purposes, from both organic and lithic raw materials (Boesch and Boesch, 1990; Biro et al., 2007). Such behaviors are expressed with considerable diversity among chimpanzee populations from East to West Africa, and geographic “gaps” in their presence raises interesting questions regarding cultural invention versus extinction (Wrangham, 2006). Many of these activities (e.g., branch dragging, throwing, and nut-cracking) have the potential to impart significant forces to the forelimb, while others (e.g., ant-

dipping, termite, or leaf folding) involve dextrous and often precise object manipulation. Chimpanzees have been reported to have relatively weak precision grips, an absence of dextrous unimanual precision handling, relatively weak diagonal power grips, and deficient thumb/index distal pad-to-pad opposition (Marzke and Wullstein, 1996; Marzke, 1997). Studies of hand musculature have shown that, compared to humans, *Pan* has relatively weak thumb muscle development (Marzke et al., 1999; Ogiwara et al., 2005). Moreover, the extrinsic *flexor pollicis longus* muscle, a major force generator when recruited in power grips in human tool use and manufacture (Hamrick et al., 1998), is frequently reduced or absent in *Pan*.

Nonetheless, the thumb is involved in the majority of grips used by chimpanzees in manipulating objects either unimanually or bimanually (Marzke, 1997). Recently, Crast et al. (2009) expanded our appreciation of the manipulative capacity of *Pan troglodytes*. These authors recorded “in-hand” movements for juvenile and adult chimpanzees in which individual animals were presented with the task of passing objects of differing geometric shape through matched cutouts in a plexiglas sheet. Various movements were recorded, including thumb push, roll, rotation, thumb abduction/adduction, and turnover; in the majority of situations the thumb was integral to these behaviors. Crast et al. (2009) noted that adults were more adept at unimanual in-hand movements and consequently more successful in task completion; however, both young and older animals used digit combinations of “one to two” or “one to two to three” for over 90% of all in-hand movements.

The question remains whether even rigorous manipulative activity could produce the robust architecture seen in the MC 1 distal VOI. However, it is not possible to validate this argument in the absence of corroborating experimental data, such as EMG analysis of thumb musculature cf. Susman and Stern (1980), or finite element modeling of the trabecular mesh in the VOI (e.g., Stauber et al., 2006).

Why does *P. t. troglodytes* have a more robust architecture than *P. t. verus*?

Although our analysis of between-population variation resulted in reduced sample sizes, clear distinctions between the Cameroon and Tai Forest groups emerged. These can best be described as *P. t. verus* having a less robust trabecular structure across all three metacarpals (e.g., lower bone volume fraction; fewer, thinner, and more rod-like trabeculae). Several contributing factors which might distinguish these populations are considered, including differences in body size/mass, patterns of locomotor behavior (e.g., degree of arboreality), daily traveling distance, and nut-cracking behavior. Unfortunately, there is little direct comparative data available for Central African chimpanzee populations; thus in the following discussion we rely on observations principally derived from East African study sites.

Body size. While the Tai chimpanzee tends to be somewhat larger than East African populations, body mass estimates for 10 animals (six Tai, four Mahale) reported in Carlson et al. (2006; sexes combined) are not significantly different. Pearson's correlation coefficients were calculated for BV/TV and maximum bone length as a proxy for body size; in only two instances (Tai MC 5 base, $r = 0.72$ and MC I head, $r = 0.71$) did the correla-

tion exceed 0.30. As such, it is unlikely that the slightly larger body size of *P. t. verus* would account for the observed differences.

Differences in arboreality. Carlson et al. (2006) found that Tai chimpanzees were more arboreal than those from Mahale (in this case, *P. t. schweinfurthii*); the time spent in terrestrial quadrupedal knuckle-walking was thus greater in the latter (91.49% vs. 85.63% for females and 93.85% vs. 86.61% for males, though these data are based on only seven animals). It is perhaps understandable then that the Cameroon chimpanzees have a more robust trabecular architecture; however, the difference in time spent in terrestrial locomotion is perhaps less important than the above figures might suggest, as both populations typically spend less than 20% of their time moving across all modalities, terrestrial and arboreal. Although both the Tai and Cameroon chimpanzee metacarpals can best be described as “plate-like,” with values less than 1.0 (idealized rods have values of 3.0), trabecular structure in the Cameroon *Pan* sample is considerably more plate-like. With the exception of the MC 5 base, the proportion of rods versus plates in the remaining VOIs varies from 40 to 98% greater in the Tai sample (Tables 7 and 8). Biomechanically, plates have been argued to be more adapted to withstand axial loading (Stauber et al., 2006; Liu et al., 2009). Moreover, Beville et al. (2006) report that, after bone volume fraction, SMI was the single best predictor of bone strength, though values of yield stress leading to deformation failure in human trabecular bone occurred for SMI values in the range of that reported for the Tai chimpanzees. Thus, the somewhat more plate-like architecture and larger BV/TV in the Cameroon sample may be more adaptive as the frequency of terrestrial knuckle-walking increases.

Distance traveled per day. Over 85% of chimpanzee locomotor activity is terrestrial (Doran, 1993; Carlson et al., 2006), the majority of which is slow quadrupedal knuckle-walking. A further possibility accounting for population variation in trabeculae morphology is the distance traveled each day by members of these groups. Few comparative data exist for different chimpanzee day ranges. Herlinger et al. (2001) provided minimum average estimates for daily travel for the three Tai populations (North, Middle, South) of between 2 and 4 km, with a range of <0.5–9 km. Kibale chimpanzees averaged 2.4 km day⁻¹ (males) to 2.0 km day⁻¹ (females), considerably less than reported for Gombe (4.6 and 3.2 km day⁻¹ for males and females, respectively; Pontzer and Wrangham, 2004; their Table 1). The inter-site comparability and variation in day range across sites suggests that this variable would not be decisive in establishing the pattern of trabecular differences seen in our analysis.

The role of nut-cracking. Nut-cracking presents a relevant cultural behavior to explore with respect to population differences in trabecular bone morphology. Among wild chimpanzees this activity has been considered unique to *P. t. verus* in West Africa (Boesch and Boesch, 1990; Wrangham et al., 1994; Boesch and Tomasello, 1998; Whiten et al., 1999; Whiten, 2007). It has been asserted recently that the subspecies *P. t. ellioti* in the Ebo forest of western Cameroon uses stone hammers to crack nuts (Morgan and Abwe, 2006), though this contention derives from perceived sounds of nut-cracking and associated debris rather than through direct observation. Nuts, such as Coula and Panda, are invariably

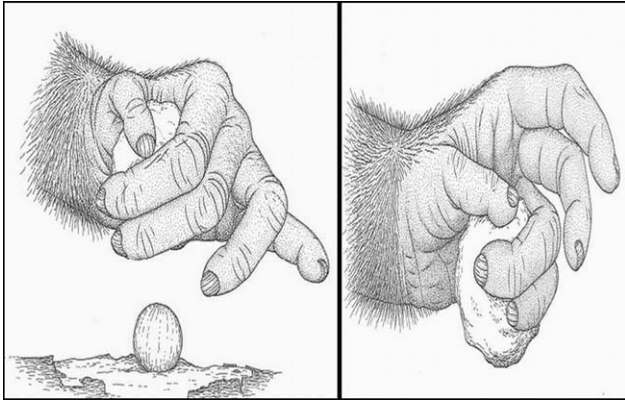


Fig. 5. Tai chimpanzees use a variety of grips in unimanual nut-cracking, two of which are illustrated here. Note involvement of all three digits examined in the present study, in particular the relative position of the hammer adjacent to the metacarpal heads. From Figure 5 in Boesch C, Boesch H. 1993. Different hand postures for pounding nuts with natural hammers by wild chimpanzees. In: Preuschoft H, Chivers D, editors. *Hands of Primates*. Wein: Springer-Verlag. p 31–43. Reproduced by permission of the author.

cracked on anvils on the ground using stone hammers (Boesch and Boesch, 1984; Boesch and Boesch-Acher-mann, 2000). Boesch et al. (1994) have argued that the irregular geographic distribution of this technology within West Africa is analogous to the variable distribution of cultural traits within human societies. Such geographic discontinuities are well known for chimpanzee behavioral and technological accomplishments, though explanation remains elusive (Wrangham, 2006).

The relevance of nut-cracking toward understanding variation in trabecular structure lies in several observations. First, it is acquired by males and females as subadults during skeletal and trabecular maturation. Second, nuts provide a high rate of return for both energy (up to 18,000 kJ day⁻¹) and protein (64 g), (Boesch and Boesch, 1993). As such, the behavior presents a significant cost-benefit adaptive strategy, estimated at a ratio of 1:9 in energetic terms (Günther and Boesch, 1993). This advantage could be expected to reinforce the behavior once acquired. Third, nut-cracking is often unimanual when involving hammers (wood or stone) of small sizes, shapes, and weights. However, it is a bimanual activity when hammers weigh more than 4–5 kg, with some reaching weights up to 20 kg and diameters of about 20 cm (Boesch et al., 1994). Fourth, nut-cracking requires application of a significant amount of force, and may be practiced for as much as 270 min over the course of a day during the “nut season.” Boesch and Boesch (1993) estimated that the hardest of the five varieties of nut exploited, *Panda oleosa*, requires a force equivalent to a 10 kg stone dropped from a height of about 1.2 m. Finally, and perhaps most importantly, this activity invokes a wide diversity of hand postures in manipulating differently-sized hammers, orienting nuts, and positioning anvils. Boesch and Boesch (1993) documented six different grips used in holding hammers weighing between 300 and 600 g (see Fig. 5), and when cracking directly in the *Coula* trees, five different hand postures used in positioning nuts on anvils, or holding hammers for subsequent processing.

Nut-cracking behavior distinguishes our samples of *P. t. verus* and *P. t. troglodytes* with respect to the biomechanical environment of the forelimb. More specifically, we sug-

gest that the diverse grips and hand postures employed in coordinated use of hammers during nut-cracking activity offers the most parsimonious explanation for the clear distinctions observed in metacarpal trabecular bone mass and architecture between these species. As noted above, Tai chimpanzees begin to practice nut-cracking at age two. However, on average, chimpanzees do not become “proficient” at knuckle-walking until several months later (Doran, 1997), although they are active in locomotion by 6 months of age (primarily vertical climbing or palmi-grade quadrupedalism). Thus, in nut-cracking chimpanzees there are two significant osteogenic signals present in the hand early in development, one locomotory and one manipulative, and the latter may act to constrain transition to the plate-dominated architecture seen in the non-nut-cracking chimpanzees from Cameroon.

Limitations

There are two limitations which must be considered when interpreting the results of this study. First, the sample size is small, especially regarding the inter-population comparison. Clearly, adding to the size of the sample (and extending it to other taxa, e.g., *Pan paniscus*) should be a goal of future research. Moreover, while we did not find differences between the male and females in the combined sample, the Tai sample is predominately female. Given the fact that female Tai chimpanzees are the more adept nut-crackers, it would be useful to test for sex differences within this population, as we would predict that differences in nut-cracking proficiency may appear in trabeculae structure.

A second limitation pertains to the different developmental history of the MC 1 head. While the heads of metacarpals 2–5 form from “typical” secondary centers of ossification, and that of the MC 1 does not. Rather, in humans for whom some observations have been made (though generally on poor samples), the distal trabecular mass in the thumb appears to develop as a pseudoepiphysis (Haines, 1974), emerging from the marrow of the shaft about age 3–4 years. This pseudoepiphysis coalesces as a distinct trabecular mass though remaining attached to the shaft, thereby permitting no independent growth between the two. We are aware of no similar literature for *Pan*. To our knowledge, studies which would shed light on the relation of this mode of growth on trabecular development have not been carried out. In any case, the current study was undertaken of adult animals in which all “epiphyses” were fused. While it is not possible to suggest that the different development of the head of MC 1 would not have an effect on the form of trabeculae within it, we have no reason to believe that trabecular structure at that site would respond differently to loading once growth has ceased, compared to digits 2–5.

SUMMARY AND CONCLUSIONS

In this study we sought to provide baseline data for trabecular architectural variation in the head and base of metacarpals 1, 2, and 5 of two populations of the common chimpanzee. We also assessed whether trabecular architecture might vary with respect to behavioral disparities recognized for each population. Significant differences in mass and structure were observed, between head and base within elements, but also among elements. The MC 1 distal VOI is notable for having a significantly greater bone volume fraction related to a higher proportion of

well-connected, plate-like trabeculae, particularly evident in *P. t. troglodytes*. The MC 5 is more robust than anticipated, perhaps related to loading during braking, particularly when the animal employs a palm-in hand posture. Interestingly, there were no major differences in trabecular orientation (DA) among the VOIs, with the exception of the significantly more isotropic MC 2 base.

We also found significant differences between populations, primarily in the metacarpal head VOIs. Comparatively large BV/TV values for the distal MC 1 VOI, for example, are present in the Cameroon *P. t. troglodytes* sample. The most apparent behavioral distinction between the two populations lies in the degree of nut-cracking behavior practiced by the Tai Forest chimpanzee. For the hands, this means large, repetitive dynamic strains, which we argue could account for the different metacarpal trabecular architecture observed for *P. t. verus* and *P. t. troglodytes*. In conclusion, micro-CT analysis of trabecular architecture in the hand skeleton provides important insight into both qualitative and quantitative aspects of species-specific modes of functional loading (e.g., locomotion, hand postures, and grips) as well as population-specific behavioral variation.

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LITERATURE CITED

- Bevill G, Eswaran SK, Gupta A, Papadopoulos P, Keaveny TM. 2006. Influence of bone volume fraction and architecture on computed large-deformation failure mechanisms in human trabecular bone. *Bone* 39:1218–1225.
- Biro D, Sousa C, Matsuzawa T. 2007. Ontogeny and cultural propagation of tool use by wild chimpanzees at Boussou, Guinea: Case studies in nut cracking and leaf folding. In: Matsuzawa T, Tomonaga M, Tanaka M, editors. *Cognitive development in chimpanzees*. Tokyo: Springer. p 476–508.
- Boesch C. 1991. Handedness in wild chimpanzees. *Int J Primatol* 12:541–558.
- Boesch C, Boesch-Achermann H. 1984. Possible causes of sex differences in the use of natural hammers by wild chimpanzees. *J Hum Evol* 13:415–440.
- Boesch C, Boesch-Achermann H. 1990. Tool use and tool making in wild chimpanzees. *Folia Primatol* 54:86–99.
- Boesch C, Boesch-Achermann H. 1993. Different hand postures for pounding nuts with natural hammers by wild chimpanzees. In: Preuschoft H, Chivers D, editors. *Hands of primates*. Wein: Springer-Verlag. p 31–43.
- Boesch C, Boesch-Achermann H. 2000. *The chimpanzees of the Tai Forest. Behavioural ecology and evolution*. Oxford: Oxford University Press.
- Boesch C, Marchesi P, Marchesi N, Fruth B, Joulain F. 1994. Is nut-cracking in wild chimpanzees a cultural behavior? *J Hum Evol* 26:325–338.
- Boesch C, Tomasello M. 1998. Chimpanzee and human cultures. *Curr Anthropol* 39:591–614.
- Carlson KJ, Doran-Sheehy DM, Hunt KD, Nishida T, Yamanaka A, Boesch C. 2006. Locomotor behavior and long bone morphology in individual free-ranging chimpanzees. *J Hum Evol* 50:394–404.
- Crast J, Fragaszy D, Hayashi M, Matsuzawa T. 2009. Dynamic in-hand movements in adult and young juvenile chimpanzees (*Pan troglodytes*). *Am J Phys Anthropol* 138:274–285.
- Demes B, Larson S, Stern J Jr, Jungers W, Biknevicius A, Schmitt D. 1994. The kinetics of primate quadrupedalism: “hindlimb drive” reconsidered. *J Hum Evol* 26:353–374.
- Demes B, Qin Y-X, Stern J, Larson S, Rubin CT. 2001. Patterns of strain in the macaque tibia during functional activity. *Am J Phys Anthropol* 116:257–265.
- Doran D. 1993. Sex differences in adult chimpanzee positional behavior: the influence of body size on locomotion and posture. *Am J Phys Anthropol* 91:99–115.
- Doran D. 1997. Ontogeny of locomotion in mountain gorillas and chimpanzees. *J Hum Evol* 32:323–344.
- Ducher G, Tournaire N, Meddahi-Pelle A, Benhamou C-L, Courteix D. 2006. Short-term and long-term site-specific effects of tennis playing on trabecular and cortical bone at the distal radius. *J Bone Miner Metab* 24:484–490.
- Günther M, Boesch C. 1993. Energetic cost of nut-cracking behaviour in wild chimpanzees. In: Preuschoft H, Chivers D, editors. *Hands of primates*. Wein: Springer-Verlag. p 109–129.
- Haddock SM, Yeh OC, Mummaneni PV, Rosenberg WS, Keaveny TM. 2004. Similarity in the fatigue behavior of trabecular bone across site and species. *J Biomech* 37:181–187.
- Haines R. 1974. The pseudoepiphysis of the first metacarpal of man. *J Anat* 117:145–158.
- Hamrick M, Churchill S, Schmitt D, Hylander WL. 1998. EMG of the human flexor pollicis longus muscle: implications for the evolution of hominid tool use. *J Hum Evol* 34:123–136.
- Herbinger I, Boesch C, Rothe H. 2001. Territory characteristics among three neighbouring chimpanzee communities in the Tai National Park, Côte d'Ivoire. *Int J Primatol* 22:143–167.
- Hunt KD, Cant JGH, Gebo DL, Rose MD, Walker SE, Youlatos D. 1996. Standardized descriptions of primate locomotor and postural modes. *Primates* 37:363–387.
- Inouye S. 1994. Ontogeny of knuckle-walking hand postures in African apes. *J Hum Evol* 26:459–485.
- Lazenby R, Angus S, Cooper D, Hallgrímsson B. 2008a. A three-dimensional microcomputed tomographic study of site-specific variation in trabecular microarchitecture in the human second metacarpal. *J Anat* 213:698–705.
- Lazenby R, Cooper D, Angus S, Hallgrímsson B. 2008b. Articular constraint, handedness, and directional asymmetry in the human second metacarpal. *J Hum Evol* 54:875–885.
- Lazenby R, Skinner M, Hublin J-J, Cooper D, Hallgrímsson B. 2008c. A comparative 3D micro-CT study of trabecular architecture in the second metacarpal of *Homo* and *Pan*. *Am J Phys Anthropol Supp* 46:138.
- Liu XS, Bevill G, Keaveny TM, Sajda P, Guo XE. 2009. Micro-mechanical analyses of vertebral trabecular bone based on individual trabeculae segmentation of plates and rods. *J Biomech* 42:249–256.
- Martin RB, Burr DB, Sharkey NA. 1998. *Skeletal tissue mechanics*. New York: Springer.
- Marzke M. 1997. Precision grips, hand morphology, and tools. *Am J Phys Anthropol* 102:91–110.
- Marzke M, Marzke R, Linsheid R, Smutz P, Steinberg B, Reece S, An K. 1999. Chimpanzee thumb muscle cross sections, moment arms and potential torques, and comparisons with humans. *Am J Phys Anthropol* 110:163–178.
- Marzke MW, Shackley MS. 1986. Hominid hand use in the pliocene and pleistocene: evidence from experimental archaeology and comparative morphology. *J Hum Evol* 15:439–460.
- Marzke MW, Wullstein KL. 1996. Chimpanzee and human grips: a new classification with a focus on evolutionary morphology. *Int J Primatol* 17:117–139.

- Matarazzo S. 2008. Knuckle walking signal in the manual digits of *Pan* and *Gorilla*. *Am J Phys Anthropol* 135:27–33.
- Matarazzo S. 2009. Examination of pressure distribution across the manus of knuckle-walking apes. *Am J Phys Anthropol* 138:S186.
- McGrew W, Ham R, White L, Tutin C, Fernandez M. 1997. Why don't chimpanzees in Gabon crack nuts? *Int J Primatol* 18:353–374.
- Morbeck M, Galloway A, Mowbray K, Zihlman A. 1994. Skeletal asymmetry and hand preference during termite fishing by Gombe chimpanzees. *Primates* 35:99–103.
- Morgan B, Abwe, EE. 2006. Chimpanzees use stone hammers in Cameroon. *Curr Biol* 16:R632–R633.
- Ogihara N, Kunai T, Nakatsukasa M. 2005. Muscle dimensions in the chimpanzee hand. *Primates* 46:275–280.
- Patel B, Carlson K. 2007. Bone density spatial patterns in the distal radius reflect habitual hand postures adopted by quadrupedal primates. *J Hum Evol* 52:130–141.
- Pontzer H, Lieberman D, Momin E, Devlin M, Polk J, Hallgrímsson B, Cooper D. 2006. Trabecular bone in the bird knee responds with high sensitivity to changes in load orientation. *J Exp Biol* 209:57–65.
- Pontzer H, Wrangham R. 2004. Climbing and the daily energy cost of locomotion in wild chimpanzees: implications for hominoid locomotor evolution. *J Hum Evol* 46:317–335.
- Preuschoft H. 1973. Functional anatomy of the upper extremity. In: Bourne G, editor. *The chimpanzee*, Vol. 6. Baltimore: University Park Press. p 34–120.
- Preuschoft H. 2004. Mechanisms for the acquisition of habitual bipedality: are there biomechanical reasons for the acquisition of upright bipedal posture? *J Anat* 204:363–384.
- Raichlen D, Pontzer H, Shapiro L, Sockol M. 2009. Understanding hind limb weight support in chimpanzees with implications for the evolution of primate locomotion. *Am J Phys Anthropol* 138:395–402.
- Renders GAP, Mulder L, Langenbach GEJ, van Ruijven LJ, van Eijden TMGJ. 2008. Biomechanical effect of mineral heterogeneity in trabecular bone. *J Biomech* 41:2793–2798.
- Ruff CB. 2000. Body size, body shape, and long bone strength in modern humans. *J Hum Evol* 38:269–290.
- Ruff CB. 2002. Long bone articular and diaphyseal structure in Old World monkeys and Apes. I: locomotor effects. *Am J Phys Anthropol* 119:305–342.
- 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.
- Ruff CB, Runestad JA. 1992. Primate limb bone structural adaptations. *Ann Rev Anthropol* 21:407–433.
- Ruimerman R, Hilbers P, van Rietbergen B, Huiskes R. 2005a. A theoretical framework for strain-related trabecular bone maintenance and adaptation. *J Biomech* 38:931–941.
- Ruimerman R, van Rietbergen B, Hilbers P, Huiskes R. 2005b. The effects of trabecular-bone loading variables on the surface signaling potential for bone remodeling and adaptation. *Ann Biomed Eng* 33:71–78.
- Sarringhaus LA, Stock JT, Marchant LF, McGrew WC. 2005. Bilateral asymmetry in the limb bones of the chimpanzee (*Pan troglodytes*). *Am J Phys Anthropol* 128:840–845.
- Stauber M, Müller R. 2006. Volumetric spatial decomposition of trabecular bone into rods and plates—a new method for local bone morphometry. *Bone* 38:475–484.
- Stauber M, Rapillard L, van Lenthe G, Zysset P, Müller R. 2006. Importance of individual rods and plates in the assessment of bone quality and their contribution to bone stiffness. *J Bone Miner Res* 21:586–595.
- Susman R, Stern J Jr. 1980. EMG of the interosseous and lumbrical muscles in the chimpanzee (*Pan troglodytes*) hand during locomotion. *Am J Anat* 157:389–397.
- Swartz SM, Parker A, Huo C. 1998. Theoretical and empirical scaling patterns and topological homology in bone trabeculae. *J Exp Biol* 201:573–590.
- Tocheri MW, Marzke MW, Liu D, Bae M, Jones GP, Williams RC, Razdan A. 2003. Functional capabilities of modern and fossil hominid hands: 3D analysis of trapezia. *Am J Phys Anthropol* 122:101–112.
- Tocheri MW, Razdan A, Williams R, Marzke M. 2005. A 3D quantitative comparison of trapezium and trapezoid relative articular and nonarticular facet areas in modern humans and great apes. *J Hum Evol* 49:570–586.
- Tuttle R. 1969. Quantitative and functional studies on the hands of anthropoidea: I. The Hominoidea. *J Morphol* 128:309–363.
- Whiten A. 2007. Pan African culture: memes and genes in wild chimpanzees. *Proc Natl Acad Sci USA* 104:17559–17560.
- Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW, Boesch C. 1999. Cultures in chimpanzees. *Nature* 399:682–685.
- Wrangham R. 2006. Chimpanzees: The culture-zone concept becomes untidy. *Curr Biol* 16:R634–R635.
- Wrangham R, McGrew W, de Waal F, Heltne P, editors. 1994. *Chimpanzee cultures*. Cambridge: Harvard University Press.
- Wunderlich R, Jungers W. 2009. Manual digital pressures during knuckle-walking in chimpanzees (*Pan troglodytes*). *Am J Phys Anthropol* 139:394–403.
- Zihlman A, Stahl D, Boesch C. 2008. Morphological variation in adult chimpanzees (*Pan troglodytes verus*) of the Tai National Park, Côte d'Ivoire. *Am J Phys Anthropol* 135:34–41.
- Zylstra M. 2000. Trabecular architecture of metacarpal heads in catarrhines: a preliminary report (abstract). *Am J Phys Anthropol Supp* 30:331.