

# THE COEVOLUTION OF HUMAN HANDS AND FEET

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Received September 28, 2009

Accepted December 14, 2009

Human hands and feet have longer, more robust first digits, and shorter lateral digits compared to African apes. These similarities are often assumed to be independently evolved adaptations for manipulative activities and bipedalism, respectively. However, hands and feet are serially homologous structures that share virtually identical developmental blueprints, raising the possibility that digital proportions coevolved in human hands and feet because of underlying developmental linkages that increase phenotypic covariation between them. Here we show that phenotypic covariation between serially homologous fingers and toes in *Homo* and *Pan* is not only higher than expected, it also causes these digits to evolve along highly parallel trajectories under episodes of simulated directional selection, even when selection pressures push their means in divergent directions. Further, our estimates of the selection pressures required to produce human-like fingers and toes from an African ape-like ancestor indicate that selection on the toes was substantially stronger, and likely led to parallel phenotypic changes in the hands. Our data support the hypothesis that human hands and feet coevolved, and suggest that the evolution of long robust big toes and short lateral toes for bipedalism led to changes in hominin fingers that may have facilitated the emergence of stone tool technology.

**KEY WORDS:** Adaptation, coevolution, morphological evolution, pleiotropy, natural selection, variation.

Bipedalism and manipulative ability have long been recognized as important hallmarks of the hominin lineage, accounting for the uniquely derived hand and foot skeletons of humans relative to other primates, including African great apes. (Darwin 1871; Susman 1979; Lewis 1989; Harcourt-Smith and Aiello 2004). Genetic evidence indicates that humans and chimpanzees shared a last common ancestor (LCA) between 5 and 8 million years ago, to the exclusion of gorillas (Ruvolo 1997). In addition, African apes share many morphological similarities that are thought to be adaptations for vertical climbing, suspensory locomotion, and knuckle walking (Aiello and Dean 1990). Unless these similarities are the result of extensive homoplasy, they suggest the LCA of gorillas, chimpanzees, and humans were African ape-like (Pilbeam 1996). If true, then the most parsimonious interpretation of morphology in the chimpanzee–human LCA is that it was also somewhat

ape-like (Pilbeam 1996; Richmond and Strait 2000; Wrangham and Pilbeam 2001). In other words, human morphological evolution can be interpreted within the framework of an evolutionary transition from a partly arboreal, knuckle-walking ape, to a fully bipedal and dexterous hominin (Pilbeam 1996).

Within this framework, derived skeletal traits in the human hand and foot are usually treated as separate adaptations that evolved independently in response to selection for enhanced dexterity in the hand, and for bipedal locomotion in the foot (Harcourt-Smith and Aiello 2004; Tocheri et al. 2008). For example, in the human foot, derived tarsal morphology is thought to strengthen the unique plantar arches and facilitate the excursion of the tibia and fibula over the ankle (Bojsen-Moller 1979; Latimer et al. 1987; Harcourt-Smith and Aiello 2004). Similarly, the longer, more robust, and adducted hallux of humans is thought

to be adaptive for resisting bending forces associated with the distribution of body weight over medial aspects of the foot during stance (Susman 1983); whereas uniquely short lateral phalanges in *Homo* may have been selected in the context of reducing bending forces and digital muscular effort during the second half of stance in walking, but especially in running (Preuschoft 1969; Rolian et al. 2009). Likewise, in the human hand, carpal joint surfaces have been substantially remodeled, facilitating convergence of the tips of the fingers and thumb when flexed (Lewis 1977, 1989). Convergence and opposition of the fingertips—a functionally important aspect of precision grasping in humans—may also have been facilitated by derived manual phalangeal proportions, specifically a relatively longer thumb and shorter lateral digits (Napier 1962; Marzke 1997).

Did all the derived features of the human hand and foot evolve independently? One reason to question this assumption is the many apparent similarities between the manual and pedal phalanges. Compared to *Pan*, lateral digits in *Homo* are short and less curved in the sagittal plane, and both the thumb and big toe are relatively longer and more robust (Schultz 1963; Susman 1979). In addition, recent advances in evolutionary developmental biology have found that the genetic blueprints for vertebrate development comprise a limited number of pathways and processes that are used repeatedly at different times and locations during organismal development (Hall 1998; Carroll 2005). Hand and foot digits are no exception, as they are serially homologous. Serial homology occurs when a structure's underlying genetic program is partially or completely duplicated and expressed in a new place and time during development (Hall 1995). Because individual genes and/or developmental processes affect multiple phenotypic traits, the phenotypic variation that is available to selection in one trait is typically not independent of other traits. Accordingly, complex organisms tend to be composed of semiautonomous sets of phenotypic traits, modules, which evolve independently of each other (Cheverud 1996; Wagner 1996). By virtue of their serial homology (Shou et al. 2005), hand and foot digits in primates should show modular properties such as increased phenotypic covariation (Tuttle and Rogers 1966; Hallgrímsson et al. 2002; Le Minor and Rozak 2005; Young and Hallgrímsson 2005), making it reasonable to hypothesize that they coevolved in humans through a common genetic architecture that produced matching patterns of variation in the size and shape of homologous phalanges.

Here, we test the hypothesis of independent evolution in the digits of the human hand and foot by comparing patterns of phenotypic variation/covariation and evolvability in these structures in chimpanzees and humans. Specifically, a common developmental architecture in hands and feet (autopods) leads to three predictions regarding hand–foot covariation in humans and chimpanzees, and its effect on the capacity of human fingers and toes to evolve inde-

pendently. First, the strength of phenotypic covariation between homologous elements in the hand and foot should be higher than expected, reflecting their common developmental origin. Second, correlated patterns of variation in the size and shape of the fingers and toes should lead to correlated evolutionary responses to selection (Lande and Arnold 1983; Cheverud 1996). Third, if the evolution of fingers and toes in humans was correlated, then one expects that selection on the toes caused parallel changes in the fingers, or vice versa.

## Materials and Methods

### SAMPLE AND DATA

The sample comprises individuals from *Homo sapiens* (70 African–American females, 63 African–American males, 28 Caucasian females, 41 Caucasian males, total  $n = 202$ ) and wild-shot *Pan troglodytes troglodytes* (57 females, 32 males, total  $n = 89$ ) collected in the Cleveland Museum of Natural History, Powell–Cotton Museum, Harvard Museum of Comparative Zoology, and American Museum of Natural History. All specimens were adults of known sex and ethnicity with no visible skeletal pathologies. Proximal and middle phalanges of all hand and foot digits from a single side were placed ventrally in anatomical position on a flatbed scanner (Microtek i320 ScanMaker, Carson, CA) and scanned in TIFF format at 300 dpi (Rolian 2009). Distal phalanges were excluded, as they are rarely present in skeletal collections. The identity of the phalanges was determined by size and morphological differences, and when available by comparison with the articulated side of the skeleton.

Two-dimensional digital landmarks were placed on homologous features in both taxa (e.g., center of phalangeal base, intercondylar trough of phalangeal head, medial and lateral extents of the distal articular condyles) using TPSDig2 (Rohlf 2005). Landmarks were used to derive lengths of the phalanges and the width of the distal end of the proximal phalanx in the first, third, and fifth rays, using the scaling factor determined by the scanning resolution. These rays were chosen because they are easily distinguishable and avoid potential sex effects known to affect lengths of the second and fourth digital rays (2D:4D ratios; e.g., McFadden and Bracht 2005). To minimize redundancy, the lengths of the phalangeal elements were summed within a digit, providing a width and length variable for each digit (12 variables total).

### Estimation of covariance and correlation matrices

Phalangeal data were used to estimate phenotypic correlation and variance/covariance (VCV) matrices in each taxon. The quantitative evolutionary framework used in this study ideally requires knowledge of the additive genetic (co)variances among autopod

traits (Lande 1979; Hansen and Houle 2008). Genetic (co)variance matrices are difficult to obtain, however, so we used the phenotypic VCV matrices in lieu of their genetic counterparts. Several studies have shown that phenotypic and genetic VCV matrices are proportional, particularly when considering morphological traits with similar heritabilities, as is likely the case for phalangeal traits (Cheverud 1988; Kohn and Atchley 1988; Koots and Gibson 1996; Ackermann and Cheverud 2004). Prior to obtaining the matrices, both species were corrected for sex-related size dimorphism, and humans were corrected for size dimorphism related to ethnic origin, by adjusting each individual to the average of the subgroup means (Cheverud 1982). Although sex- and ethnicity-related size dimorphism in these species is modest (*Pan* mean dimorphism = 4%, range 0.5%–7.5%, *Homo* mean dimorphism, 7.2%, range 3.8%–9.3%), this procedure reduces the inflationary effect of sample heterogeneity on variances and covariances (Wagner 1990). All analyses were done on mean-standardized raw data (Hansen and Houle 2008). All analyses were performed with custom-written routines in Matlab version 7.4 (The MathWorks, Natick, MA).

## ANALYSES

### Strength of covariation

Average Pearson's cross-product correlations were used to evaluate the strength of the association among autopods as a whole and within specific regions (e.g., within the hand/foot, between homologous traits, between nonhomologous traits). As correlations are not normally distributed, correlations were transformed using Fisher's *Z* before obtaining average correlations. Raw data were bootstrapped (1000 times) to assess the effect of sampling error on the estimation of the mean correlations. The analysis was then repeated using Fisher's *Z*-transformed partial correlations, which measure the strength of the association between two variables while holding the effects of all other variables constant. When computed from raw datasets, the remaining "fixed" variables for a given pair can be construed as an estimate of body size (Magwene 2001 p. 1743). The significance of any difference in the strength of correlations between individual autopod regions and the overall magnitude of correlation was determined using a resampling technique (Manly 1991). Specifically, 1000 average correlations based on samples of a given size (e.g., sample size of two for correlations among homologous traits in individual rays) were obtained by resampling, with replacement, from the *Z*-transformed off-diagonal correlation matrix elements. If the observed average correlation exceeds 95% of the resampled correlations, the observed correlation was deemed significantly greater than expected given the overall magnitude of correlation in the original correlation matrices (Hallgrímsson et al. 2002). *Z*-transformed Pearson's and partial correlation data are given for *Homo* in Table S1 and for *Pan* in Table S2.

### Evolvability of the hand and foot phalanges

In evolutionary quantitative genetics theory, the evolutionary response of a population's phenotypic multivariate mean to selection is given by the following equation:

$$\Delta z = \mathbf{G}\beta, \quad (1)$$

where  $\Delta z$  is the evolutionary response, a column vector of change in the population's phenotypic multivariate mean between generations,  $\mathbf{G}$  is the additive genetic VCV matrix (substituted here with its phenotypic counterpart  $\mathbf{P}$ , see above), and  $\beta$  is a column vector of directional selection gradients (Lande 1979; Lande and Arnold 1983). The evolutionary potential of a population can be assessed by subjecting its VCV matrix to selection gradients ( $\beta$ ) representing different selective scenarios, and comparing the evolutionary response vectors ( $\Delta z$ ) to these selective scenarios (Hansen and Houle 2008; Rolian 2009).

We wished to determine the extent to which the hand and foot phalanges respond to selection in a correlated manner. Because the set of measured variables in the hand and foot is homologous, each 12-element response vector ( $\Delta z$ ) was divided into two homologous six-element hand and foot response vectors,  $\Delta z_{\text{hand}}$  and  $\Delta z_{\text{foot}}$ , respectively. These vectors were normalized and correlated using dot products. The resulting dot product is the cosine of the angle between the normalized hand and foot response vectors in a multivariate space comprising six dimensions. This dot product is thus a measure of the collinearity of hand and foot evolutionary responses, or how much the covariation between hands and feet biases their ability to evolve in different directions in multivariate space.

The mean dot product between normalized  $\Delta z_{\text{hand}}$  and  $\Delta z_{\text{foot}}$  was obtained for three different selection regimes. First, VCV matrices were subjected to a set of 1000 symmetrically distributed random selection gradients with coefficients between  $-1$  and  $1$ , normalized to a length of  $1$ . Vector correlations among the hand and foot portions of these selection gradients are normally distributed with a mean of  $0$ , with a little over half the correlations being negative. Next, this process was repeated with two additional sets of 1000 random selection gradients where the selection gradient portions acting on the foot and hand were set to zero, respectively. These selection regimes were used to evaluate the collinearity of the evolutionary responses when selection acted only on one of the two autopods. These regimes model relaxed selection on one of the autopods, that is, a situation in which variation in the phenotype of that autopod has no effect on individual fitness (Lande 1979).

In all selection regimes, the statistical significance of the mean dot product was evaluated against a null hypothesis of no collinearity between hand and foot response vectors, by comparing it against the distribution of dot products among 10,000 pairs

of random six-element vectors (Cheverud and Marroig 2007). If the computed dot product exceeds 95% of these random dot products, there is significantly more common orientation among the selection and response vectors than expected by chance alone. For six-element vectors, 95% of the dot products are 0.67 or less.

**Reconstructing evolutionary history of hand and foot digits**

To reconstruct the historical patterns of selection required to produce observed differences between two population means, equation 1 can be rewritten as follows:

$$\beta = G_n^{-1}[z_m - z_n], \tag{2}$$

where  $\beta$  is the differential selection gradient summed over generations,  $[z_m - z_n]$  is the difference in population means between species  $m$  and  $n$ , and  $G_n^{-1}$  is the inverse of the additive genetic VCV matrix of the ancestral population, substituted here with its phenotypic counterpart (Lande 1979; Ackermann and Cheverud 2004). We wished to estimate the patterns and strength of selection required to produce human-like phalanges given an LCA with chimpanzee-like hands and feet. Thus, we used the chimpanzee phenotypic VCV matrix as a model of the LCA covariation structure, and calculated the vector of standardized mean differences between humans and chimpanzees. The advantage of this method is that it can be used to determine the relative strength of selection among different phenotypic traits.

According to equation 1, the observed change in a trait mean is the cumulative result of direct selection acting on that trait plus the effects of indirect selection acting on all other traits with which it covaries (Lande and Arnold 1983):

$$\Delta z_j = G_{jj}\beta_j + G_{1j}\beta_1 + \dots + G_{ij}\beta_{ij}, \tag{3}$$

where  $\Delta z_j$  is the mean difference in the  $j^{\text{th}}$  trait before and after selection,  $G_{jj}$  is the variance of the  $j^{\text{th}}$  trait,  $\beta_j$  is the selection differential acting on the  $j^{\text{th}}$  trait,  $G_{1j} - G_{ij}$  are the covariances of the  $j^{\text{th}}$  trait with all other traits in the dataset, and  $\beta_1 - \beta_j$  are the selection differentials acting on these other traits. The term  $G_{jj}\beta_j$  is the direct effect of selection in changing the mean of the  $j^{\text{th}}$  trait, and all other terms represent the indirect effects of selection acting on all other traits with which the  $j^{\text{th}}$  trait is correlated. Equation 2 was used to determine the selection gradient vector  $\beta$  required to produce *Homo*-like autopods from a *Pan*-like LCA, and equation 3 was then used to break down  $\Delta z$  for a given trait into contributions from itself and from other traits or sets of traits. We partitioned  $\Delta z$  into its direct component, the indirect effect of selection acting on the serially homologous trait, and the sums of all other indirect effects acting within the same autopod and the other autopod, respectively.

**Results**

**PATTERNS AND MAGNITUDES OF PHENOTYPIC COVARIATION**

Average Fisher’s Z transformed Pearson’s correlations and partial correlations were computed among phalangeal lengths and widths in the autopods of humans and chimpanzees, first for the entire phalangeal dataset, and then partitioned into different regions of the autopods (Table 1). Virtually all Pearson’s correlations are significantly greater than zero (Tables S1 and S2). More importantly, as predicted, Pearson’s correlations show substantially stronger covariation (20%–50%) among serially homologous traits than in the background level of covariation observed across the entire dataset, although the difference in humans is not statistically significant (*Homo*  $P = 0.12$ , *Pan*  $P < 0.01$ ). In several cases,

**Table 1.** Average Z-transformed Pearson’s and partial correlations in *Pan* and *Homo* autopods. Average correlations are given for the whole autopod dataset, among serially homologous traits, among nonhomologous autopod traits, within the hand or foot, and among homologous traits in individual rays. All average Pearson’s correlations significantly greater than zero. Standard deviations of the mean are based on bootstrapping. Correlations in bold are significantly greater than the average level of correlation in the matrices at  $P < 0.05$ , italicized correlations are significant at the  $P < 0.10$  level, based on resampling the data.

	Pearson’s Correlations		Partial Correlations	
	<i>Homo</i>	<i>Pan</i>	<i>Homo</i>	<i>Pan</i>
Overall	0.60±0.04	0.62±0.05	0.09±0.006	0.09±0.01
Homologues	0.73±0.05	<b>0.94±0.06</b>	<i>0.20±0.04</i>	<b>0.39±0.06</b>
Nonhomologues	0.54±0.04	0.57±0.05	0.007±0.009	0.03±0.02
Within hand	<b>0.76±0.05</b>	0.56±0.06	<i>0.16±0.008</i>	0.07±0.02
Within foot	0.53±0.04	0.63±0.06	0.13±0.01	0.11±0.02
First rays	0.85±0.06	0.85±0.09	<i>0.33±0.06</i>	<b>0.44±0.09</b>
Third rays	0.72±0.06	<i>0.96±0.11</i>	0.14±0.06	<b>0.37±0.1</b>
Fifth rays	0.62±0.06	<b>1.02±0.09</b>	0.14±0.06	<b>0.37±0.11</b>

especially in *Pan*, covariation between serially homologous traits is substantially higher than the average covariation evident within each autopod. Furthermore, the partial correlations show that the correlations among serially homologous traits remain strong even after removing the effects of covariation with other traits within and between the autopods. In partial correlations analyses based on morphological traits, the traits that are controlled for (the covariates) often reflect body size-related covariation (Magwene 2001). Hence, our partial correlations data indicate that the increased covariation observed among serially homologous phalangeal traits is substantially above the level expected with variation in body size.

Phenotypic covariation among homologous traits is stronger in chimpanzees than in humans. If one substitutes the covariation patterns in *P. troglodytes* for the covariation structure in the *Pan-Homo* LCA and its immediate hominin descendants, then the correlations data (Table 1) suggest that the evolution of hands and feet in early hominins was characterized by increased variational constraints relative to later species. Note, however, that although absolute magnitudes of covariation among homologues remain high in *H. sapiens*, they are lower in magnitude compared to *P. troglodytes* because of weaker covariation among lateral digits, especially among phalangeal width variables (Fig. 1, Table S1). Covariation between the first rays is strong in both species, suggesting the thumb and big toe may be prone to relatively stronger variational constraints than the lateral digits. These constraints

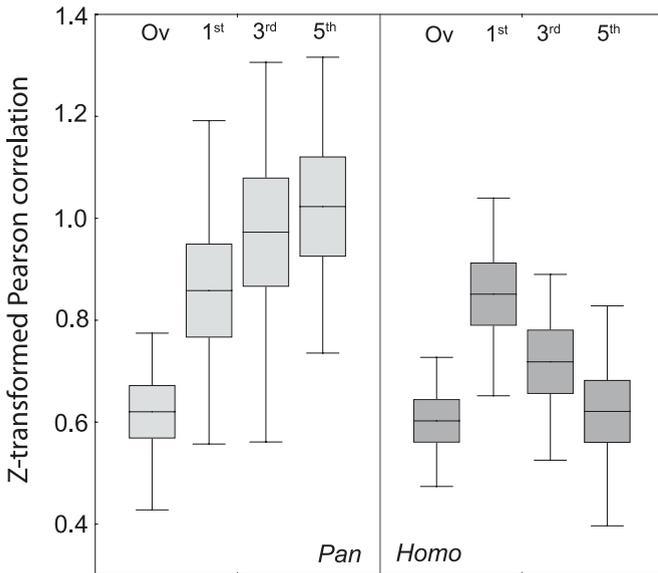
could reflect differences in the way the lateral digits and first digits develop (Montavon et al. 2008).

**EVOLUTIONARY RESPONSES TO SIMULATED SELECTION**

To test the prediction that matching patterns of phenotypic variation in the hand and foot phalanges lead to their correlated evolution, we subjected chimpanzee and human phenotypic VCV matrices to random selection gradient vectors ( $\beta$ 's, see Materials and Methods). For each selection vector, the evolutionary response vector,  $\Delta z$ , was divided into two homologous six-element response vectors, one for the hand and one for the foot. The dot product of the two normalized response vectors measures on a scale of  $-1$  to  $1$  the degree to which the hand and foot response vectors are parallel in multivariate space. Dot products near  $1$  imply that the evolutionary response of the hand and foot phalanges to selection is highly collinear, representing parallel evolutionary changes. Conversely, negative dot products indicate that the hand and foot response vectors diverged in multivariate space, reflecting evolutionary divergence in morphology.

The results of the simulation support the prediction that covariation between the hand and foot phalanges in *Pan* and *Homo* constrains their evolutionary responses along highly parallel trajectories in phenotypic space (Table 2). In both species, the average dot product of the hand and foot response vectors to 1000 random selection vectors is greater than 95% of the dot products among random six-element vectors, indicating that the hand and foot evolutionary responses are significantly more parallel than expected by chance. Moreover, when directional selection gradients acting on either the hand or foot are set to zero, reflecting relaxed selection on that autopod, the average dot product increases (Table 2). This increase is evidence for coevolution because even when one autopod is not targeted by selection directly, its multivariate mean shifts by association with the other autopod.

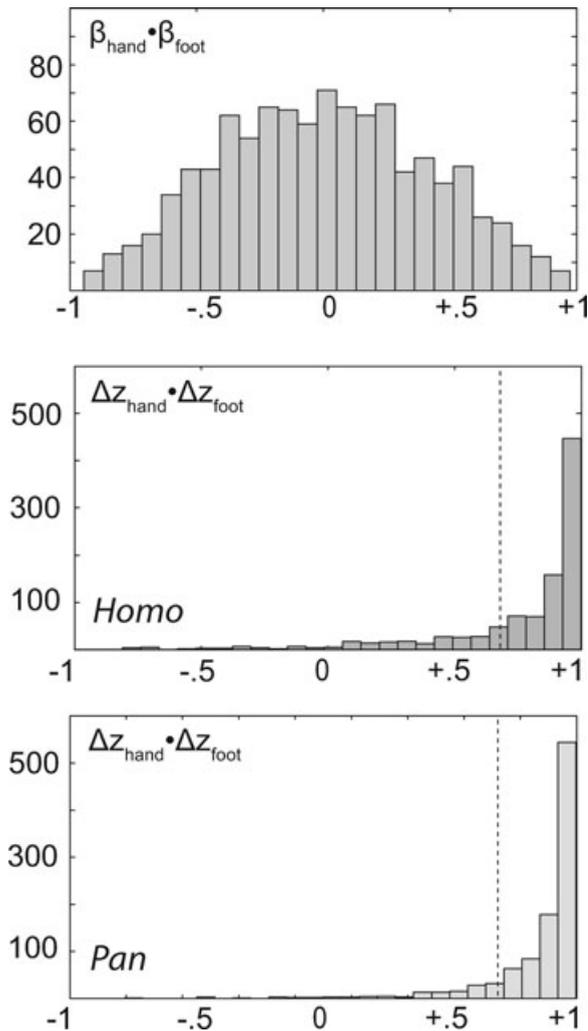
Figure 2 illustrates the frequency distribution of the 1000 response vector dot products in both species. The figure also



**Figure 1.** Average Fisher’s Z-transformed Pearson’s correlations in the autopods of *Pan* and *Homo* showing elevated phenotypic correlations among serially homologous traits in individual rays (first, third, and fifth rays) in relation to the average level computed for the entire dataset (Ov). Boxes show standard deviations and bars show the range of the bootstrapped data, respectively.

**Table 2.** Average dot product of hand and foot evolutionary response vectors in *Pan* and *Homo* Average dot products between the hand and foot evolutionary response vectors are given for three different selection regimes (1000 random selection vectors, 1000 vectors selection acting only on hand, and 1000 only on foot). All average dot products are significantly greater than expected by chance, as determined using the distribution of dot products between 10,000 pairs of random six-element vectors.

	<i>Homo</i>	<i>Pan</i>
Random	0.765	0.874
Hand selection	0.917	0.917
Foot selection	0.820	0.930



**Figure 2.** Frequency distribution of dot products between the hand and foot halves of the selection vectors ( $\beta_{\text{hand}} \cdot \beta_{\text{foot}}$ ) and evolutionary response vectors ( $\Delta z_{\text{hand}} \cdot \Delta z_{\text{foot}}$ ) in *Pan* and *Homo*. All vectors were normalized to a length of 1.0 prior to computing the dot product. The dashed vertical line in the response vector plots shows the 95% significance level for dot products between random six-element vectors (0.67).

illustrates the frequency distribution of dot products between the two halves of the selection vectors ( $\beta$ ) acting on the hand and the foot, respectively. The selection vector dot products are normally distributed with a mean of 0, and approximately half the dot products are negative. In other words, in half the simulated selection episodes, the hand and foot multivariate means are being “pushed” in divergent directions in multivariate space. Even so, the overwhelming majority of hand and foot evolutionary responses to these selection pressures remain highly parallel in both taxa, as illustrated by the extremely left-skewed distribution of response vector dot products (Fig. 2, selection vector distribution skewness = 0.068, *Homo* response vector skewness =  $-2.27$ , *Pan* response vector skewness =  $-3.36$ ). Thus, as predicted, the

evolutionary response of the hand and foot to selection pressures tends to be highly positively correlated, regardless of the direction of selection.

### RECONSTRUCTING SELECTION HISTORY

To test the third prediction, that the evolution of fingers and toes was correlated, we evaluated the likelihood that hand and foot phalanges coevolved under similar selection pressures, versus one evolving as a by-product of selection acting on the other. Specifically, we estimated the magnitude and direction of selection required to produce human-like digits from an ancestral population with chimpanzee-like morphology and VCV structure (Table 3, Fig. 3). Results show that even though selection pressures acting on homologous traits in the hand and foot mostly have the same direction, all but one of the pressures on the hand of the LCA are weaker than those acting on homologous phalangeal traits in the foot (Fig. 3). In fact, the average absolute selection strength acting on foot traits is over twice the average in the hand, even though mean-standardized phenotypic differences ( $\Delta z$ ) are similar (Table 3). These differences are especially strong in phalangeal length variables (Fig. 3). At the most extreme, the standardized strength of selection on the length of the proximal phalanx in the big toe is over 50 times greater in magnitude than its homolog in the thumb.

The reconstructed selection gradients were also used to estimate the proportion of observed phenotypic differences between *H. sapiens* and a chimpanzee-like LCA resulting from direct and indirect selection (see Materials and Methods). For hand traits, the change in mean attributed to indirect selection on homologous foot traits is on average three times larger than the contribution from direct selection on the hand traits themselves, and vice-versa (Table 3). Further, indirect selection pressures on the foot had their largest effect on the length of the manual phalanges, particularly the thumb. In this digit, the change in mean attributable to selection acting on the length of the hallux proximal phalanx is almost 30 times larger than the effect of selection acting on the thumb directly. The reconstructed selection histories of the hand and foot thus suggest that although the hand phalanges in early hominins were under direct selection to some extent, more of their phenotypic change over the course of hominin evolution can be attributed to selection acting on homologous traits in the foot.

### Discussion

The novel evolutionary developmental biology framework employed here supports the prediction that a common genetic/developmental “blueprint” in fingers and toes limits their capacity to vary independently, producing similar patterns of phenotypic variation in the size and shape of the fingers and toes. In turn, these correlated patterns of variation affect the degree to which

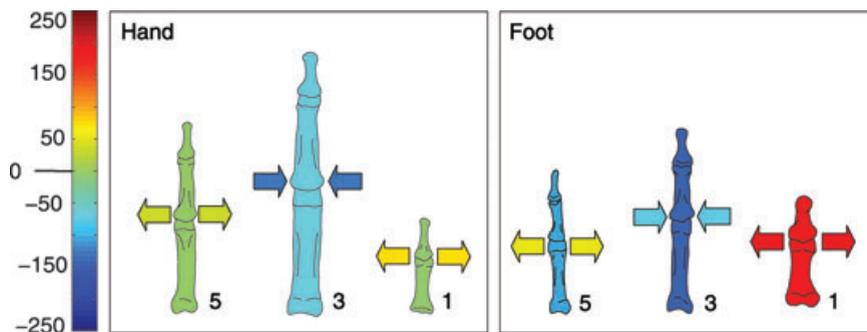
**Table 3.** Selection strength and direct/indirect selection on the digits of *Pan–Homo* LCA. P1L, first phalangeal length; P1W, first phalangeal width; P3L, third phalangeal length; P3W, third phalangeal width; P5L, fifth phalangeal length; P5W, fifth phalangeal width.  $\beta$  represents the standardized selection strengths required to produce observed phenotypic differences ( $\Delta z$ ) in the autopods between a *Pan*-like ancestral population and the derived *Homo* condition. All data are mean-standardized and dimensionless. To the right,  $\Delta z$  is partitioned into direct and indirect effects of selection acting on each character (Direct) and its serial homolog (Homolog), respectively, as well as the summed effect of indirect selection acting on elements in the same (Within autopod) or homologous autopod (Across autopod).

	$\beta$	$\Delta z$	Direct	Homolog	Within autopod	Across autopod
Hand						
P1L	-3.40	0.20	-0.04	1.15	-0.20	0.44
P1W	77.89	0.51	0.41	0.40	-0.28	0.38
P3L	-83.09	-0.26	-0.31	-0.58	0.02	0.04
P3W	-119.73	-0.05	-0.35	-0.12	0.09	0.21
P5L	9.48	-0.22	0.04	-0.47	-0.29	0.02
P5W	25.23	0.05	0.13	0.25	-0.28	0.20
Foot						
P1L	181.45	0.13	1.06	-0.02	-0.67	-0.26
P1W	163.99	0.38	0.58	0.19	-0.08	-0.11
P3L	-151.39	-0.42	-0.75	-0.32	0.62	-0.29
P3W	-61.68	-0.01	-0.33	-0.24	0.41	-0.10
P5L	-104.97	-0.41	-0.65	0.04	0.55	-0.32
P5W	74.36	0.15	0.39	0.09	-0.07	-0.17
Hand abs. average	53.13	0.21	0.21	0.50	0.19	0.22
Foot abs. average	122.97	0.25	0.63	0.15	0.40	0.21

the hand and foot digits can evolve independently, as demonstrated by the selection simulation. In other words, in these species, variational constraints imposed by development translated into constraints on the evolvability of the hand and foot digits. Further, our data suggest that these developmental constraints caused hominin fingers to evolve largely as a by-product of stronger selection pressures acting on toes. Simply put, the shorter fingers and longer, more robust thumbs of humans likely evolved because of selective pressures on their respective homologues in the foot.

It is important to note that our data do not reflect a universal constraint on the independent evolvability of digits in primates, or

vertebrates in general. Indeed, several species of primates (e.g., aye-ayes, *Colobus*) and other vertebrates (e.g., bats) show that developmental constraints on variation in digital size and shape can be overcome to produce morphological divergence in fingers and toes, likely through the effect of a few key genes and/or regulatory elements that are uniquely expressed in each limb (e.g., *Pitx1*, *Tbx5*; Logan and Tabin 1999; Takeuchi et al. 2000). Rather, our data suggest that in some evolutionary contexts, a shared developmental/genetic basis can and does cause sets of phenotypic traits to coevolve. For humans and their hominin ancestors, such a context may have been the transition to bipedalism, in which selection on hand digits was relaxed following their



**Figure 3.** Standardized intensity of selection on the digits required to produce *Homo sapiens*-like fingers and toes, assuming a *Pan*-like ancestral morphology and variance/covariance structure. The color of the digits reflects the magnitude of selection acting on phalangeal length variables. The colored arrows reflect the intensity and direction of selection acting on phalangeal width variables. All magnitudes obtained from mean-standardized raw data.

“emancipation” from functional constraints related to arboreal locomotion (Darwin 1871; Richards 1986; Marzke 1996).

If hominin hands and feet evolved in a correlated manner, then one expects to find evidence for similar and contemporaneous changes in the proportions of hand and foot digits in the hominin fossil record. There are at present too few complete and associated hand and foot remains to paint a definitive picture of digital proportions in early hominins. Recently published hand and foot remains from *Ardipithecus ramidus*, dated to 4.4 million years ago, suggest a remarkably ape-like digital morphology (Lovejoy et al. 2009a,b). Based on the authors’ body size estimate for partially complete specimen ARA-VP-500 (~50 kg), the lateral manual and pedal phalanges of *A. ramidus* are only marginally shorter than modern chimpanzees, but substantially longer and more curved than extant humans. No first ray proximal phalanges have been found in association with this specimen, but first metapodials suggest incipient increases in length and robusticity for these digits. Assuming *Ardipithecus* is an early hominin, its digital proportions are commensurate with our model of coevolution, and further suggest that major anatomical changes in digital proportions occurred after the emergence of facultative bipedal locomotion.

Available fossil data from younger species suggests that by at least 3.5 million years ago, australopiths possessed broadly similar proportions in their hands and feet, with a mosaic digital pattern intermediate between African apes and extant humans. For instance, a partial articulated foot recovered at Hadar, Ethiopia, shows that the hallux of *A. afarensis* was relatively more robust, and although evidence related to hallucial length is more equivocal, the fossil footprints at Laetoli, Tanzania, indicate that the hallux was also relatively longer than in *Pan* (Latimer et al. 1982; Berge et al. 2006). In contrast, the Hadar partial foot possessed lateral toes with marked sagittal curvature and a relative length shorter than chimpanzees, but 30%–40% longer than modern humans (Latimer et al. 1982; Susman et al. 1984). Similarly, hand remains from Hadar show that the thumb had also increased in relative length and robusticity (Alba et al. 2003); and although fossil lateral phalanges cannot be unequivocally attributed to individual digits, evidence from Hadar and a juvenile specimen from Dikika, Ethiopia, suggests the lateral manual digits in *A. afarensis* were also curved, and intermediate in relative length between chimpanzees and humans (Bush et al. 1982; Marzke 1983; Alemseged et al. 2006).

Unfortunately, there are not enough complete and associated hand and/or foot phalanges in early *Homo* to infer reliably digital proportions, although 1.5 million year old footprints from Ileret, Kenya, indicate that *H. erectus* had fully modern digital proportions (Bennett et al. 2009). In addition, many other derived postcranial features in early *H. erectus*—including proximal limb proportions—are similar to modern *Homo* (Bramble and Lieber-

man 2004). Based on this indirect evidence, it is reasonable to hypothesize that hominin hand and foot proportions were essentially modern by 1.8–1.5 million years ago.

Evidence for coevolution of fingers and toes in hominin evolution has interesting implications for interpreting the relationship between the evolution of bipedalism and the origins of stone tool technology. One longstanding hypothesis is that the derived proportions of human toes and fingers are independently evolved, sequential adaptations, with selection for the origins of bipedalism freeing the hands from locomotor constraints and making possible selection for tool-making and manipulative capabilities (Darwin 1871; Marzke 1996). However, our data indicate that evolutionary changes in the toes associated with bipedalism caused matching evolutionary changes in hand anatomy that actually may have facilitated the emergence and development of stone tool technology. Specifically, multiple lines of evidence (developmental, fossil, and archaeological) suggest two general stages in the coevolution of obligate bipedalism and stone tool technology.

In the first stage, seen in the australopiths (but possibly older), strong directional selection on the hallux may have favored longer and more robust first digits that were almost modern in morphology (Fig. 3, Table 3). At the same time, weaker selection in the lateral toes favored the intermediate condition observed in the lateral fingers and toes of australopiths (Table 3). Functionally, increased hallucial length and robusticity would have improved performance during bipedal walking, by providing both better resistance to increased load-bearing on the medial aspect of the foot, and a rigid lever necessary for propulsion during toe-off (Root et al. 1977). At the same time, moderately longer, curved toes would not have compromised the australopith foot’s ability to walk (but not run) long distances effectively (Rolian et al. 2009), and would have permitted the retention of arboreal behaviors, as evidenced by morphological adaptations elsewhere in the skeleton (Susman et al. 1984; Stern 2000).

Functionally, the marked increase in thumb length/robusticity and moderate decrease in finger length that paralleled changes in the australopithecine foot, likely improved the ability to produce grips between the thumb and lateral digits. Precision grasping, in which the tips of the thumb and fingers are brought into opposition, is a key determinant of manipulative ability in hominins (Napier 1962; Marzke 1997). All hominoids have the ability to grasp objects between the thumb and the lateral digits, but length discrepancies between their shorter thumbs and longer fingers causes them to oppose the thumb tip to the medial aspect of the index finger, much like humans hold a key (Marzke and Shackley 1986). In contrast, the derived australopith thumb to lateral digit length ratio would have significantly improved grasping performance by allowing the tips of the thumb and one or more lateral digits to be opposed, creating both a more secure and more precise grip during the handling of objects such as Oldowan choppers

and flakes (Marzke 1997). At the same time, a more robust thumb would have been better able to tolerate the large joint reaction forces resulting from more distal grips, by dissipating these forces over larger joint surface areas (Susman 1994).

It should be noted that other derived aspect of musculoskeletal anatomy in hominin hands were likely also important in improving performance during precision grasping (e.g., hypertrophic thumb muscles, apical tufts on the distal phalanges, modified carpal morphology enabling thumb to fifth finger opposition; Lewis 1989). Nonetheless, changes in manual digital proportions that enabled digit tips to be brought into opposition may have been a prerequisite for the development of precision gripping capability in australopiths. Also, although pedal changes associated with facultative bipedalism probably provided australopiths with hands capable of producing and using Oldowan stone tools by at least 3.5 million years ago, it should be noted that manufactured stone tools do not appear in the archaeological record until about 1 million years later (Marzke 1983, 1997). Australopiths may have lacked the cognitive capacity for manufacturing tools and/or their technology was entirely nonlithic.

The second hypothesized stage in the coevolution of bipedalism and lithic technology occurred with the emergence of *Homo* around 2 million years ago. The evolutionary transition from *Australopithecus* to *Homo* has recently been interpreted in part as a shift from a partly arboreal, facultative biped, to an obligate terrestrial biped that regularly engaged in long-distance trekking and running (Bramble and Lieberman 2004; Lieberman et al. 2006). Biomechanical studies of locomotion have shown that the uniquely derived short lateral toes of *Homo* may have evolved in the context of this transition in order to reduce mechanical work in the digital flexors during running (Rolian et al. 2009), and/or to reduce the bending moments acting on the phalanges (Preuschoft 1969). If so, then directional selection on the lateral toes around 2 million years ago for locomotion may have caused parallel changes in the fingers that provided further performance benefits for manipulation. Increased brain size, both relative and absolute, in early *H. erectus* along with changes in manual proportions possibly even contributed to further technological advances in the Developed Oldowan and Acheulean industries (Wynn 1979, 1981; Marzke and Shackley 1986).

In short, there are several reasons to believe that selection on the foot caused correlated changes in the hand during human evolution, that selection on the hallux was stronger and preceded selection on the lateral toes, and that these changes in manual digital proportions may have facilitated the development of stone tool technology. More fossil and archeological data are necessary to test these hypotheses, especially from the first few million years of the hominin fossil record and in early *Homo*. Additional developmental genetic data will also be useful to determine when

and how, from a mechanistic perspective, such parallel changes in digital morphology occurred. To our knowledge, the evolution of manual digital proportions that improve dexterity, but initially evolved as by-products of selection on the toes, represents the first empirically validated case of a preadaptive morphological feature in human evolution (Gould and Lewontin 1979; Gould and Vrba 1982). From a theoretical standpoint, this interpretation challenges the assumption that all skeletal traits in extinct and/or extant hominins have a strictly adaptive origin, and highlights the need for more integrative research in paleoanthropology, combining data from developmental genetics, evolutionary quantitative genetics, as well as from paleontology and archaeology.

#### ACKNOWLEDGMENTS

The authors wish to thank J. Chupasko, M. Harman, L. Jellema, and E. Westwig for granting access to specimens in their care, and the reviewers and editor for insightful comments on the manuscript. This work was supported by a National Science Foundation Doctoral Dissertation Improvement Grant (BCS 0647624), Canadian Natural Sciences and Engineering Research Council (NSERC) Graduate Scholarship, and CIHR Training Grant from Alberta Children's Hospital Institute for Child and Maternal Health to CR, and NSERC (number 238992) and Genome Canada grants to BH.

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Associate Editor: J. Wolf

## Supporting Information

The following supporting information is available for this article:

**Table S1.** Raw correlations (below diagonal) and partial correlations (above diagonal) among the 12 autopod variables in *Homo*.

**Table S2.** Raw correlations (below diagonal) and partial correlations (above diagonal) among the 12 autopod variables in *Pan*.

Supporting Information may be found in the online version of this article.

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