Title:
Modularity and sexual dimorphism in human metacarpals

Journal Issue:
PaleoBios, 31(2)

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Publication Date:
2014

Permalink:
https://escholarship.org/uc/item/7xc156c2

Acknowledgements:
We thank the Phoebe A. Hearst Museum of Anthropology for research permission and access to the collection, which was greatly facilitated by Natasha Johnson. Thanks also to Tim White, Socorro Baez, and Josh Carlson in the Human Evolution Research Center at the University of California Berkeley. Many thanks also to C. Owen Lovejoy and Susan Smith for assistance with the measurement protocols, and to C. Owen Lovejoy for valuable discussion of the implications of our results. Thanks also to Mallory Watkins and Julia Addiss for assistance with data collection, and Sabrina Sholts, Theresa Grieco, and Whitney Reiner for their helpful feedback throughout the project, as well as to Sarah Amugongo and Phil Reno who thoughtfully reviewed an earlier version of this manuscript, improving it significantly.

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Keywords:
sexual dimorphism, modularity, metacarpals, Homo sapiens

Local Identifier:
ucmp_paleobios_24956

Abstract:
The shape of an animal's hands provides insight not only to its locomotory habitus but can also reveal information about the genetic and developmental sources that underlie its variation.

Detailed analyses of skeletal shape variation within a population can test hypotheses about the genetic, nongenetic, and epigenetic sources underlying that variation. Here, we report on the variation, patterns of correlation, and sexual dimorphism of human metacarpal size in order to better understand the evolutionary history of the hominid hand. Seven linear measurements were collected from unaffiliated adult Native Californians that lived between 3050 BP and 150 BP, correlations across digits were estimated and compared for the entire population, and for males and females. We also assessed sexual dimorphism in variance as well as for metacarpal length ratios.

Results indicate the thumb, or pollical metacarpal (MC1) measurements are only weakly correlated with those of the index through pinky fingers (palmar metacarpals, MC2-5), whereas all palmar metacarpals are more highly correlated with each other. The lower level of correlation between the pollical and palmar metacarpals accords with expectations from non-human developmental studies that indicate developmental modularity between these rays (and as a consequence, this results in developmental independence and the potential for selection to operate on the modules distinctly). Sexual dimorphism is observed in the absolute size of the metacarpals, and also in the degree of variation (males exhibit a greater range of variation) and level of correlation (females return lower correlations for the palmar metacarpal measurements). In contrast, metacarpal length ratios were not sexually dimorphic. The dimorphism in degree of variance and correlation raise new directions for research, while simultaneously bolstering the interpretation that human pollical and palmar metacarpals reflect two distinct developmental modules.

PaleoBios 31(2):1–20, December 9, 2014

Modularity and sexual dimorphism in human metacarpals

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The shape of an animal's hands provides insight not only to its locomotory habitus but can also reveal information about the genetic and developmental sources that underlie its variation. Detailed analyses of skeletal shape variation within a population can test hypotheses about the genetic, nongenetic, and epigenetic sources underlying that variation. Here, we report on the variation, patterns of correlation, and sexual dimorphism of human metacarpal size in order to better understand the evolutionary history of the hominid hand. Seven linear measurements were collected from unaffiliated adult Native Californians that lived between 3050 BP and 150 BP, correlations across digits were estimated and compared for the entire population, and for males and females. We also assessed sexual dimorphism in variance as well as for metacarpal length ratios.

Results indicate the thumb, or pollical metacarpal (MC1) measurements are only weakly correlated with those of the index through pinky fingers (palmar metacarpals, MC2-5), whereas all palmar metacarpals are more highly correlated with each other. The lower level of correlation between the pollical and palmar metacarpals accords with expectations from non-human developmental studies that indicate developmental modularity between these rays (and as a consequence, this results in developmental independence and the potential for selection to operate on the modules distinctly). Sexual dimorphism is observed in the absolute size of the metacarpals, and also in the degree of variation (males exhibit a greater range of variation) and level of correlation (females return lower correlations for the palmar metacarpal measurements). In contrast, metacarpal length ratios were not sexually dimorphic. The dimorphism in degree of variance and correlation raise new directions for research, while simultaneously bolstering the interpretation that human pollical and palmar metacarpals reflect two distinct developmental modules.

Keywords: sexual dimorphism, modularity, metacarpals, *Homo sapiens*

INTRODUCTION

The human hand is the result of many millions of years of evolution. It retains from the earliest tetrapods the basic configuration of five digits, and yet the size, relative proportions of these digits and their musculature have evolved to enable elaborate tool use free from obliged locomotion. The fossil record provides the evidence of this evolutionary history. Numerous scientists have attempted to infer when the uniqueness of the human hand arose and under what environmental conditions. The hand characteristics of the extinct *Australopithecus* **Dart, 1925** and *Homo erectus* **Dubois, 1891** imply that the fully modern human hand did not appear until after 2.5 Ma at the earliest, and possibly as late as 1.5 Ma (**Tocheri et al. 2008**). Although many features of the hand are derived (autapomorphic, although also shared with Neanderthals) (**Stern et al. 1995**), it is the shortening of the fingers relative to the thumb, visible in *Ardipithecus ramidus* **White et al., 1994** at 4.4 Ma and *Australopithecus afarensis* **Johanson, 1981** at ~3.0 Ma, that most characterizes the human hand and separates it from all other extant and extinct primates (**Tocheri et al. 2008**, **Reno et al. 2008**, **Lovejoy et al. 2009**).

Patterns of intraspecific variation in bone shape can provide insight to the underlying factors that contribute to that variation, and consequently, on its evolutionary history (e.g., **Hlusko 2004**). For example, **Grieco et al. (2013)** explored dental variation across six species of Old World monkeys and found evidence of developmental modularity commonly influencing both intra- and interspecific variation. **Young et al. (2010)** observed modular patterning (as elevated partial correlations in homologous versus nonhomologous elements) in the hindlimb elements of humans, apes, and monkeys. Here, we report on a brief study that takes a similar approach to variation within human metacarpals and discuss how these results inform on the larger questions of human hand evolution.

The developmental uniqueness of the thumb (digit 1) compared to the palmar fingers (index, middle, ring, and pinky fingers; digits 2 through 5 respectively) provides the mechanism on which evolutionary forces act in order to

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Citation: Morrish, K.R., and L.J. Hlusko. 2014. Modularity and sexual dimorphism in human metacarpals. *PaleoBios* 31(2). ucmp_paleobios_. ucmp_paleobios_24956
Permalink: http://escholarship.org/uc/item/7xc156c2

create the variety of primate hand proportions observed today. Specifically, the up-regulation of the homeobox genes *Hoxd13* and/or *Hoxa13* have been hypothesized as a possible means by which the thumb can be elongated while the rest of the palm is shortened, particularly in the metacarpals (**Reno et al. 2008**). Following on this, we hypothesize that human pollical metacarpal (MC1) measurements would demonstrate a lower level of correlation with the palmar metacarpals (MC2-5) than the correlations found between MC2-5.

We also explored these data for evidence of sexual dimorphism. Sexual dimorphism in the relative lengths of the index and ring fingers of the human hand was recognized well over 100 years ago (e.g., **Whiteley and Pearson 1899**, **Lewenz and Whiteley 1902**). More recently, **Manning and colleagues (2000)** found lower mean length ratios of the second to fourth digit in male hands compared to females, and hypothesized this to be linked to relative exposure of testosterone and estrogen during development. **Zheng and Cohn (2011)** used a mouse model of second and fourth digit ratios to pinpoint the developmental origin of this dimorphism: a balance between androgen and estrogen signaling early in prenatal development, primarily influencing the length of the fourth digit. Given these previous examples of sexual dimorphism in finger lengths, we explored how evidence of developmental modularity may or may not be reflected in the differences between men and women.

A third goal of our study was to evaluate correlations between various metacarpal linear dimensions in an effort to understand the range of morphological variation in a given human population—Native Americans—that have not yet been incorporated into this specific literature. An expanded knowledge of the range in human metacarpal variation is a valuable addition to the ongoing study of the human hand variation and evolution more generally.

MATERIALS AND METHODS

All available right and left metacarpals of 41 individuals (18 male, 23 female) were measured (individuals listed in Appendix Tables 29, 30, pp. A18–19). These individuals are part of the human osteological collections of the Phoebe A. Hearst Museum of Anthropology (PAHMA) at the University of California Berkeley and range in archeological/geological age from 3050 BP to 150 BP (**Breschini et al. 1986**, **Bennyhoff et al. 1987**, **Jones and Klar 2007**).

Ten linear measurements were taken from each metacarpal, following **Bush et al. (1983)**, **Trinkaus (1983)**, **Smith (2000)**, **Green and Gordon (2008)**, **Lovejoy et al. (2009)** and **Kivel et al. (2011)**. Detailed description of our measurement protocol is presented in the Appendix (pp. A13–17). Three people trained in identifying metacarpal bony landmarks and with extensive data-collection experience took the measurements. Intra- and inter-observer error ranged from 2.17% to 0.037%, with a mean error of ±0.485% of the average measurement.

Of the 41 measured individuals, all had complete sets of all five metacarpals on which all ten linear measurements could be collected. Any metacarpal that was broken to the extent that one or more of the ten measurements could not be taken precluded the bone and/or individual from being included in our study. The right hand was ultimately chosen for analysis because the highest number of complete sets of all five metacarpals was found to be right hands for both male (18) and female (23) individuals (41 total). Individuals included in our analysis had all 10 of their right hand metacarpals in tact, allowing for 65 measurements to be collected from each individual's right hand.

Basic descriptive statistics and coefficients of variation were calculated in Microsoft Excel® (2010 Microsoft Office®). Correlations and their 95% confidence intervals were calculated using JMP© 9.0.0 (2010 SAS Institute Inc.) using the restricted maximum likelihood approach. The various metacarpal length ratios for males and females were first assessed for equal variances using an F-test and then the means were compared via a t-test with assumed unequal variances through the data analysis tool in Excel® (2010 Microsoft Office®). Figure 2 was generated using GNU Image Manipulation Program© 2.8.10 (2013 Spencer Kimball, Peter Mattis and the GIMP Development Team).

RESULTS

Table 1 reports the summary statistics for the length of the metacarpal, all of which are statistically significant from each other (male and female lengths were compared in a two-sample t-test assuming unequal variances, $p<0.01$). Male and female digit ratios were compared in a two-sample t-test assuming equal variances and were not significant ($p\sim0.07$). These latter measurements, also shown in Figure 1 in histogram form, demonstrate the overlap between males and females. Summary statistics for the other measurements of metacarpal head, base, and midshaft features are provided in the Appendix (Appendix Tables 23–28).

Table 2 reports on the correlation estimates for the length of the metacarpals. There is a high correlation between the lengths of MC2, MC3, MC4, and MC5. In contrast, MC1 has a lower correlation with the other metacarpals. This pattern is not as strongly evident in

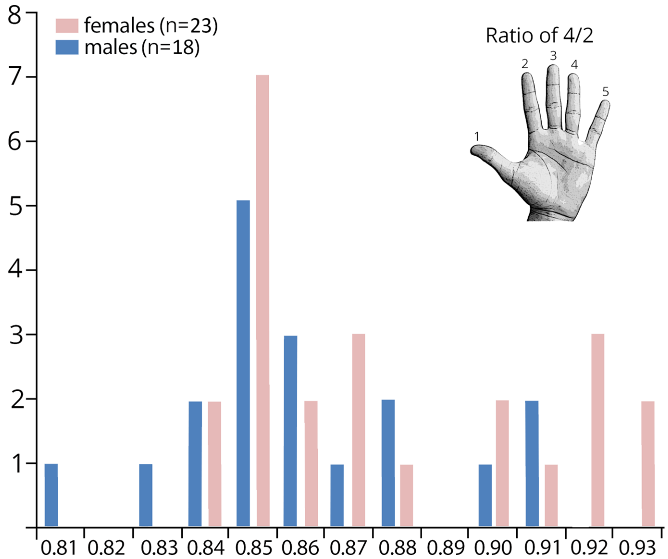

Figure 1. Histogram of the ratio of fourth versus second metacarpal lengths in males and females from a population of Native Californians.

measures of the metacarpal base, head, and some of the midshaft metrics (Appendix Tables 1–12).

Both sexes (Tables 3–4) showed the same pattern of integration between MC1 and the palmar metacarpals as was observed in the whole population (Table 2). However, we observed sexually dimorphic degrees of correlation among the palmar metacarpals, in which four of the six palmar correlations for females were below the male 95% confidence intervals. We also find it of note that the higher male correlations are found in conjunction with an overall higher degree of variation (see the coefficient of variation estimates, Table 1). The dimorphic pattern of correlation is not seen in metrics for metacarpal base, head, and midshaft features, which exhibit low correlation values and wide 95% confidence intervals (Appendix Tables 1–12).

About half of the ratios of metacarpal lengths of males and females were found to have equal variances, and none of the means were determined to be statistically significantly different, i.e., we found no statistical evidence of sexual dimorphism in any of the metacarpal length ratios including the hypothesized dimorphic MC4:MC2, although the female estimated means tend to be lower than are those of the males (Appendix Tables 13–22).

DISCUSSION

As far back as Lewenz and Whiteley (1902), correlation patterns indicating a higher degree of integration in the palm compared to the thumb were observed in humans. Our data confirm this pattern of higher correlations between the palmar metacarpals and reduced correlation between the palmar and pollical metacarpals, but more specifically demonstrate that the overall length of the metacarpals reflects this pattern more distinctly than do the other metacarpal measurements. In this paper, we posed the hypothesis that this observation may be due to *Hox* gene patterning—a reflection of developmental modularity, as has been hypothesized and demonstrated in other taxa (Wagner et al. 2007, Young et al. 2010). However, there is an equally plausible alternative explanation.

There has been a long-standing debate among anatomists as to whether or not the first ray of the hand and foot is comprised of three phalanges and is lacking a metapodial, or if it has a true metapodial and lacks one of the three phalanges. Reno et al. (2010) reviewed this debate, the evidence behind it, and added more detailed information about the location of metapodial growth plates across tetrapods. They found that non-therian tetrapods have growth plates at both ends of the metapodials, whereas all therians have growth plates at the distal ends of MC2-5 and at the proximal end of MC1—a synapomorphy that evolved after the mammalian phalangeal formula (Reno et al. 2010).

Our results on the human pattern of correlation cannot distinguish between these two possible explanations. Therefore, we conclude that population level variation in humans, despite our highly derived tool-making manipulative ability, follows the expected therian pattern, be it the result of differences in the regulation of patterning genes or, perhaps more likely, the result of factors that influence the different timing of the MC1 distal growth plate fusion relative to the MC2-5 proximal growth plate fusion.

We found that in this population of Native Californians, the sexually dimorphic levels of correlation within the hand are only statistically significant for the palmar metacarpals, suggesting that the mechanism by which these higher correlations are achieved influences only the palmar metacarpals and not the pollical metacarpal. In other words, this finding confirms the observation of developmental processes that are specific to the shape and size of the palm, independent of the thumb. This distinction provides further evidence of developmental modularity of some type—a pollical metacarpal module and a palmar metacarpal module that can be independently influenced by sexually dimorphic factors. Just as sexually dimorphic finger length ratios have been linked to varying levels of androgen exposure in utero in both men and women (Manning et al. 2000, Robertson et al. 2008, Zheng et al. 2011), the same can be supposed for metacarpal features that exhibit the correlation pattern observed in this study.

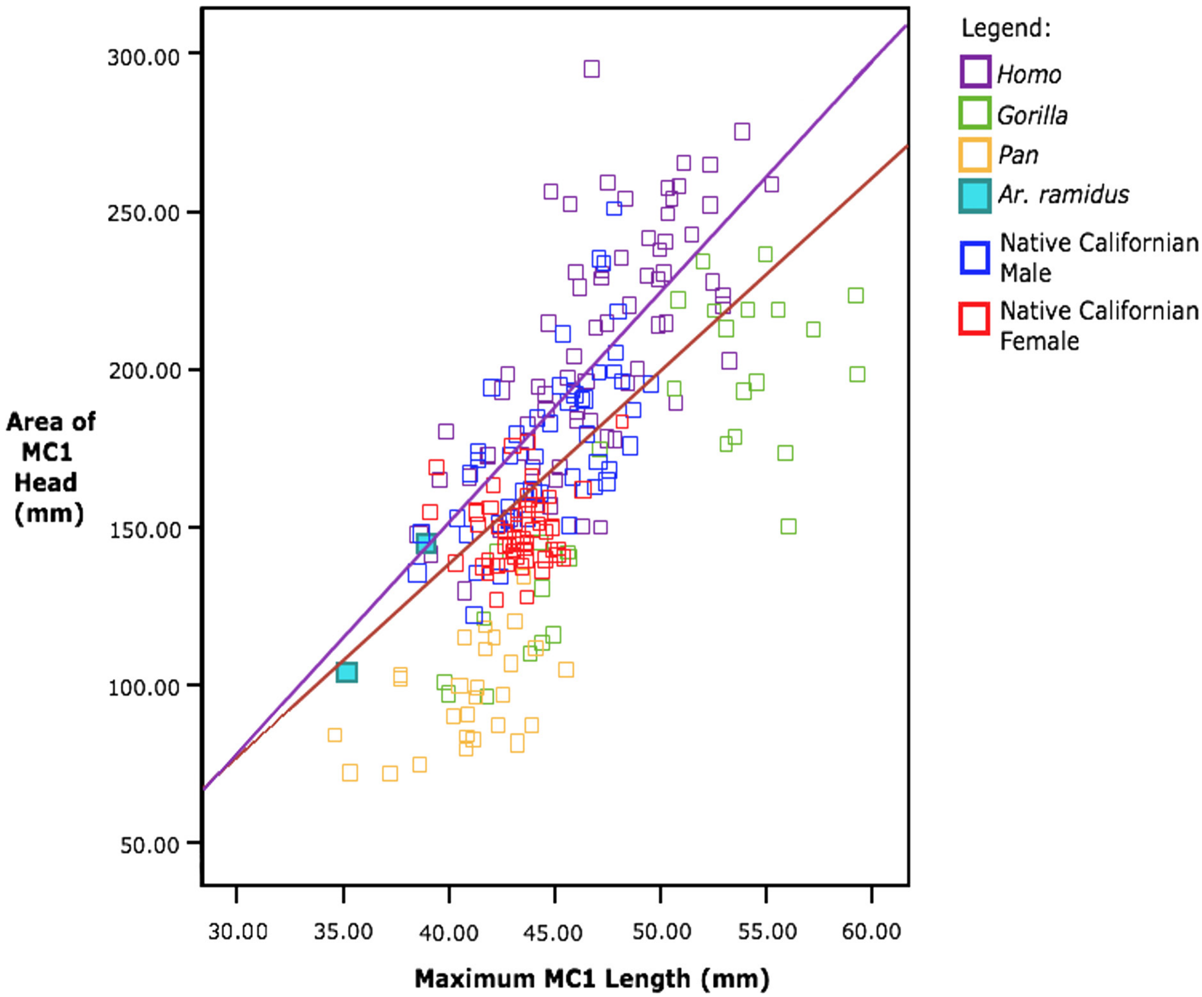

Figure 2. Mc1 Head Size in African Apes, Humans, and *Ar. ramidus*. Scatterplot of the product of mediolateral head [width] and dorsopalmar head height versus maximum bone length. This figure is modified from the Lovejoy et al. (2009) Figure S20 (SOM:22), with Native Californian data superimposed as the blue (male) and red (female) points (original published data is marked in purple as "Homo," with regression line in purple). The Native Californian population's regression line is indicated with a brown line.

We also find it of note that the higher male correlations are found in conjunction with an overall higher degree of variation, a result we had not anticipated but that poses more questions than it answers. For one, are males more variable in other anatomical regions as well? Hanihara and Ishida (2005) present a large-scale comparison of human dental variation on a worldwide scale. They report that intraregional variance in tooth size is not systematically higher in males than females, but rather varies by population (Hanihara and Ishida 2005). For example, while the Far East, Australia, and Sub-Saharan African populations have higher male than female variance, the Pacific, South/West Asia, and European populations are characterized by more variance in females. The New World populations had a male variance of 0.956 and a female variance of 0.945, a difference that is much less distinct than found in most other populations. A much more extensive study that explores skeletal variation across multiple anatomical regions needs to be undertaken to determine whether or not skeletal anatomies vary differentially or if there is a similar pattern across all of the anatomy. If the former case is supported, these different patterns of dimorphism may elucidate how genetic and non-genetic influences vary during skeletal development. If the latter scenario is supported, then these patterns of intra-population variation could add to our repertoire of phenotypes used to better understand the evolutionary histories of these various human groups.

Forensic scientists are continually looking for methods that enable the distinction between male and female skeletal remains (**Breedlove 2010**). Although Breedlove concluded that the 4D:2D ratio was not a suitable predictor of an individual's phenotype, to our knowledge there has yet to be a study to examine the effectiveness of MC4:MC2 for determining the sex of an individual. While our results demonstrate a lack of statistical difference between males and females, a visual inspection of the male and female histograms suggests that it might be possible for the MC4:MC2 ratio to be combined with other skeletal observations to form a stronger body of evidence when confirming the sex of a deceased individual (Fig. 1).

The third goal of our research was to expand the range of assessed human metacarpal variation to include Native Californians. Our data are superimposed on a previously published figure (**Lovejoy et al. 2009**) that includes several hominoid species as well as fossil hominids (Fig. 2). The Native Californian data extend the range of human variation further into the upper ranges of the *Pan* **Oken, 1816** and *Gorilla* **Geoffroy, 1852** clouds, as well as with the upper *Ar. ramidus* data point. The biological implications of this extended range of variation for our own species suggests that much more research into the evolutionary underpinnings of this variation can be explored even within just this one taxon, as noted previously in our discussion about the different patterns of male and female variance.

Following on this evolutionary context, our results have implications for the interpretation of variation found within the hominid fossil record. Functional morphological analyses of hominid hand trait variation play an important role in our understanding of the paleobiology of our extinct ancestors (e.g., **Kivell et al. 2011**). The discovery of *Australopithecus sediba* **Berger et al., 2010** brought international attention to the association of thumb-to-finger ratios with tool use and tool production (**Kivell et al. 2011**). The pattern of sexual dimorphism we found in this population of Native Californians may indicate that such interpretations could be confounded by the presence of sexual dimorphism. It is therefore recommended that the attachment of specific behaviors, such as tool use and production, to single or small sample sizes of fossil hominid hands be done with caution. Conclusions drawn on the latter could be strengthened, but more likely weakened by an increased understanding of the range of variation in human hand morphology within our global population, local populations, and sex populations. Additional research is needed to identify how extensive this pattern of sexual dimorphism may be across humans, extinct hominids, and other apes.

ACKNOWLEDGEMENTS

We thank the Phoebe A. Hearst Museum of Anthropology for research permission and access to the collection, which was greatly facilitated by Natasha Johnson. Thanks also to Tim White, Socorro Baez, and Josh Carlson in the Human Evolution Research Center at the University of California Berkeley. Many thanks also to C. Owen Lovejoy and Susan Smith for assistance with the measurement protocols, and to C. Owen Lovejoy for valuable discussion of the implications of our results. Thanks also to Mallory Watkins and Julia Addiss for assistance with data collection, and Sabrina Sholts, Theresa Grieco, and Whitney Reiner for their helpful feedback throughout the project, as well as to Sarah Amugongo and Phil Reno who thoughtfully reviewed an earlier version of this manuscript, improving it significantly.

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SUPPLEMENTARY INFORMATION

Appendix contents:

BIVARIATE CORRELATION ANALYSES

Appendix Table 1. Bivariate correlation analyses for base height for the female individuals including Correlation Values and 95% upper and lower Confidence Intervals

				Confidence Interval	
Metacarpal	by	Metacarpal	Correlation	Lower 95%	Upper 95%
MC1		MC2	0.3480	0.0532	0.5870
MC1		MC3	0.3882	0.0995	0.6166
MC1		MC4	0.0136	-0.2879	0.3127
MC1		MC5	0.4372	0.1575	0.6519
MC2		MC3	0.4970	0.2312	0.6938
MC2		MC4	0.2677	-0.0355	0.5258
MC2		MC5	0.4116	0.1269	0.6336
MC3		MC4	0.3402	0.0444	0.5812
MC3		MC5	0.4783	0.2078	0.6808
MC4		MC5	0.5410	0.2873	0.7237

Note. Correlations marked in grey demonstrate statistically significant sexual dimorphism (Female Correlation Value falls outside Male Confidence Intervals).

Appendix Table 2. Bivariate correlation analyses for base height for the male individuals including Correlation Values and 95% upper and lower Confidence Intervals

				Confidence Interval	
Metacarpal	by	Metacarpal	Correlation	Lower 95%	Upper 95%
MC1		MC2	0.4658	0.1268	0.7074
MC1		MC3	0.3445	-0.0180	0.6269
MC1		MC4	0.3964	0.0421	0.6621
MC1		MC5	0.5198	0.1963	0.7413
MC2		MC3	0.6791	0.4221	0.8351
MC2		MC4	0.5984	0.3035	0.7886
MC2		MC5	0.5340	0.2151	0.7500
MC3		MC4	0.5472	0.2328	0.7580
MC3		MC5	0.4747	0.1381	0.7131
MC4		MC5	0.3506	-0.0111	0.6311

Note. Correlations marked in grey demonstrate statistically significant sexual dimorphism (Male Correlation Value falls outside Female Confidence Intervals).

Appendix Table 3. Bivariate correlation analyses for base width for the female individuals including Correlation Values and 95% upper and lower Confidence Intervals

				Confidence Interval	
Metacarpal	by	Metacarpal	Correlation	Lower 95%	Upper 95%
MC1		MC2	0.4648	0.1911	0.6714
MC1		MC3	0.1859	-0.1212	0.4605
MC1		MC4	-0.0278	-0.3254	0.2748
MC1		MC5	0.2839	-0.0179	0.5384
MC2		MC3	0.5059	0.2424	0.6999
MC2		MC4	0.3262	0.0286	0.5706
MC2		MC5	0.1273	-0.1799	0.4119
MC3		MC4	0.2340	-0.0714	0.4992
MC3		MC5	0.0063	-0.2946	0.3060
MC4		MC5	-0.1925	-0.4659	0.1145

Note. Correlations marked in grey demonstrate statistically significant sexual dimorphism (Female Correlation Value falls outside Male Confidence Intervals).

Appendix Table 4. Bivariate correlation analyses for base wdth for the male individuals including Correlation Values and 95% upper and lower Confidence Intervals

				Confidence Interval	
Metacarpal	by	Metacarpal	Correlation	Lower 95%	Upper 95%
MC1		MC2	0.5676	0.2669	0.7676
MC1		MC3	0.4032	0.0570	0.6628
MC1		MC4	0.2173	-0.1485	0.5308
MC1		MC5	0.3615	0.0082	0.6346
MC2		MC3	0.6323	0.3583	0.8061
MC2		MC4	-0.0656	-0.4104	0.2956
MC2		MC5	0.4923	0.1671	0.7209
MC3		MC4	0.1746	-0.1916	0.4981
MC3		MC5	0.5953	0.3054	0.7842
MC4		MC5	0.1720	-0.1942	0.4961

Note. Correlations marked in grey demonstrate statistically significant sexual dimorphism (Male Correlation Value falls outside Female Confidence Intervals).

Appendix Table 5. Bivariate correlation analyses for head height for the female individuals including Correlation Values and 95% upper and lower Confidence Intervals

				Confidence Interval	
Metacarpal	by	Metacarpal	Correlation	Lower 95%	Upper 95%
MC1		MC2	0.4340	0.1537	0.6497
MC1		MC3	0.3300	0.0329	0.5735
MC1		MC4	0.4331	0.1526	0.6490
MC1		MC5	-0.0527	-0.3476	0.2516
MC2		MC3	0.7683	0.6083	0.8683
MC2		MC4	0.6854	0.4848	0.8174
MC2		MC5	0.4123	0.1278	0.6341
MC3		MC4	0.7198	0.5351	0.8388
MC3		MC5	0.4040	0.1180	0.6281
MC4		MC5	0.4903	0.2228	0.6892

Note. Correlations marked in grey demonstrate statistically significant sexual dimorphism (Female Correlation Value falls outside Male Confidence Intervals).

Appendix Table 6. Bivariate correlation analyses for head height for the male individuals including Correlation Values and 95% upper and lower Confidence Intervals

				Confidence Interval	
Metacarpal	by	Metacarpal	Correlation	Lower 95%	Upper 95%
MC1		MC2	0.4885	0.1622	0.7185
MC1		MC3	0.5433	0.2341	0.7528
MC1		MC4	0.4790	0.1502	0.7124
MC1		MC5	0.5461	0.2378	0.7544
MC2		MC3	0.7545	0.5462	0.8749
MC2		MC4	0.7804	0.5888	0.8889
MC2		MC5	0.6781	0.4261	0.8324
MC3		MC4	0.8385	0.6889	0.9196
MC3		MC5	0.6777	0.4255	0.8322
MC4		MC5	0.5948	0.3047	0.7839

Note. Correlations marked in grey demonstrate statistically significant sexual dimorphism (Male Correlation Value falls outside Female Confidence Intervals).

Appendix Table 7. Bivariate correlation analyses for head width for the female individuals including Correlation Values and 95% upper and lower Confidence Intervals

				Confidence Interval	
Metacarpal	by	Metacarpal	Correlation	Lower 95%	Upper 95%
MC1		MC2	0.5023	0.2378	0.6974
MC1		MC3	0.6105	0.3798	0.7697
MC1		MC4	0.5862	0.3469	0.7538
MC1		MC5	0.5714	0.3272	0.7441
MC2		MC3	0.7268	0.5455	0.8431
MC2		MC4	0.6323	0.4098	0.7838
MC2		MC5	0.6196	0.3923	0.7756
MC3		MC4	0.6732	0.4673	0.8098
MC3		MC5	0.6237	0.3979	0.7783
MC4		MC5	0.5981	0.3629	0.7616

Note. Correlations marked in grey demonstrate statistically significant sexual dimorphism (Female Correlation Value falls outside Male Confidence Intervals).

Appendix Table 8. Bivariate correlation analyses for head width for the male individuals including Correlation Values and 95% upper and lower Confidence Intervals

				Confidence Interval	
Metacarpal	by	Metacarpal	Correlation	Lower 95%	Upper 95%
MC1		MC2	0.6775	0.4252	0.8321
MC1		MC3	0.6732	0.4188	0.8296
MC1		MC4	0.7858	0.5980	0.8918
MC1		MC5	0.7678	0.5681	0.8822
MC2		MC3	0.7619	0.5582	0.8789
MC2		MC4	0.6261	0.3493	0.8024
MC2		MC5	0.7143	0.4820	0.8528
MC3		MC4	0.8165	0.6504	0.9081
MC3		MC5	0.7254	0.4995	0.8590
MC4		MC5	0.7987	0.6198	0.8987

Note. Correlations marked in grey demonstrate statistically significant sexual dimorphism (Male Correlation Value falls outside Female Confidence Intervals).

Appendix Table 9. Bivariate correlation analyses for midshaft height for the female individuals including Correlation Values and 95% upper and lower Confidence Intervals

				Confidence Interval	
Metacarpal	by	Metacarpal	Correlation	Lower 95%	Upper 95%
MC1		MC2	0.3990	0.1121	0.6245
MC1		MC3	0.4125	0.1281	0.6343
MC1		MC4	0.2663	-0.0370	0.5247
MC1		MC5	0.3484	0.0536	0.5873
MC2		MC3	0.5798	0.3383	0.7496
MC2		MC4	0.6902	0.4917	0.8204
MC2		MC5	0.5983	0.3633	0.7618
MC3		MC4	0.5809	0.3398	0.7503
MC3		MC5	0.4073	0.1218	0.6305
MC4		MC5	0.5111	0.2489	0.7034

Note. Correlations marked in grey demonstrate statistically significant sexual dimorphism (Female Correlation Value falls outside Male Confidence Intervals).

Appendix Table 10. Bivariate correlation analyses for midshaft height for the male individuals including Correlation Values and 95% upper and lower Confidence Intervals

				Confidence Interval	
Metacarpal	by	Metacarpal	Correlation	Lower 95%	Upper 95%
MC1		MC2	0.5109	0.1912	0.7326
MC1		MC3	0.6035	0.3169	0.7891
MC1		MC4	0.1993	-0.1668	0.5172
MC1		MC5	0.5109	0.1911	0.7326
MC2		MC3	0.7116	0.4778	0.8513
MC2		MC4	0.6070	0.3218	0.7911
MC2		MC5	0.4555	0.1207	0.6973
MC3		MC4	0.4642	0.1315	0.7029
MC3		MC5	0.5297	0.2159	0.7444
MC4		MC5	0.1592	-0.2069	0.4861

Note. Correlations marked in grey demonstrate statistically significant sexual dimorphism (Male Correlation Value falls outside Female Confidence Intervals).

Appendix Table 11. Bivariate correlation analyses for midshaft width for the female individuals including Correlation Values and 95% upper and lower Confidence Intervals

				Confidence Interval	
Metacarpal	by	Metacarpal	Correlation	Lower 95%	Upper 95%
MC1		MC2	0.3175	0.0190	0.5641
MC1		MC3	0.2411	-0.0639	0.5049
MC1		MC4	0.5658	0.3198	0.7404
MC1		MC5	0.3381	0.0420	0.5796
MC2		MC3	0.4960	0.2300	0.6931
MC2		MC4	0.5080	0.2451	0.7014
MC2		MC5	0.3461	0.0511	0.5856
MC3		MC4	0.6376	0.4171	0.7872
MC3		MC5	0.2362	-0.0690	0.5010
MC4		MC5	0.4422	0.1636	0.6555

Note. Correlations marked in grey demonstrate statistically significant sexual dimorphism (Female Correlation Value falls outside Male Confidence Intervals).

Appendix Table 12. Bivariate correlation analyses for midshaft width for the male individuals including Correlation Values and 95% upper and lower Confidence Intervals

				Confidence Interval	
Metacarpal	by	Metacarpal	Correlation	Lower 95%	Upper 95%
MC1		MC2	0.5205	0.2037	0.7386
MC1		MC3	0.4493	0.1129	0.6932
MC1		MC4	0.4750	0.1451	0.7099
MC1		MC5	0.5813	0.2859	0.7758
MC2		MC3	0.8151	0.6478	0.9074
MC2		MC4	0.4398	0.1013	0.6871
MC2		MC5	0.4745	0.1444	0.7095
MC3		MC4	0.4867	0.1600	0.7174
MC3		MC5	0.6294	0.3540	0.8043
MC4		MC5	0.5514	0.2449	0.7577

Note. Correlations marked in grey demonstrate statistically significant sexual dimorphism (Male Correlation Value falls outside Female Confidence Intervals).

Appendix Table 13. Two-sample t-test assuming unequal variance for the ratio of MC1 by MC2

	males	*females*
Mean	0.669	0.677
Variance	0.001	0.001
Observations	18	23
Hypothesized Mean Difference	0	
df	28	
t Stat	-0.795	
P(T<=t) one-tail	0.217	
t Critical one-tail	1.701	
P(T<=t) two-tail	0.433	
t Critical two-tail	2.048	

Appendix Table 14. Two-sample t-test assuming unequal variance for the ratio of MC1 by MC3

	males	*females*
Mean	0.691	0.695
Variance	0.002	0.001
Observations	18	23
Hypothesized Mean Difference	0	
df	27	
t Stat	-0.376	
P(T<=t) one-tail	0.355	
t Critical one-tail	1.703	
P(T<=t) two-tail	0.710	
t Critical two-tail	2.052	

Appendix Table 15. Two-sample t-test assuming unequal variance for the ratio of MC1 by MC4

	males	*females*
Mean	0.777	0.773
Variance	0.002	0.001
Observations	18	23
Hypothesized Mean Difference	0	
df	27	
t Stat	0.359	
P(T<=t) one-tail	0.361	
t Critical one-tail	1.703	
P(T<=t) two-tail	0.722	
t Critical two-tail	2.052	

Appendix Table 16. Two-sample t-test assuming unequal variance for the ratio of MC1 by MC5

	males	*females*
Mean	0.837	0.837
Variance	0.002	0.001
Observations	18	23
Hypothesized Mean Difference	0	
df	29	
t Stat	0.009	
P(T<=t) one-tail	0.496	
t Critical one-tail	1.699	
P(T<=t) two-tail	0.993	
t Critical two-tail	2.045	

Appendix Table 17. Two-sample t-test assuming unequal variance for the ratio of MC2 by MC3

	males	*females*
Mean	1.033	1.027
Variance	0.000	0.001
Observations	18	23
Hypothesized Mean Difference	0	
df	38	
t Stat	0.767	
P(T<=t) one-tail	0.224	
t Critical one-tail	1.686	
P(T<=t) two-tail	0.448	
t Critical two-tail	2.024	

Appendix Table 18. Two-sample t-test assuming unequal variance for the ratio of MC2 by MC4

	males	*females*
Mean	1.162	1.143
Variance	0.001	0.002
Observations	18	23
Hypothesized Mean Difference	0	
df	38	
t Stat	1.614	
P(T<=t) one-tail	0.057	
t Critical one-tail	1.686	
P(T<=t) two-tail	0.115	
t Critical two-tail	2.024	

Appendix Table 19. Two-sample t-test assuming unequal variance for the ratio of MC2 by MC5

	males	*females*
Mean	1.251	1.237
Variance	0.002	0.002
Observations	18	23
Hypothesized Mean Difference	0	
df	36	
t Stat	1.067	
P(T<=t) one-tail	0.147	
t Critical one-tail	1.688	
P(T<=t) two-tail	0.293	
t Critical two-tail	2.028	

Appendix Table 20. Two-sample t-test assuming unequal variance for the ratio of MC3 by MC4

	males	*females*
Mean	1.125	1.112
Variance	0.001	0.001
Observations	18	23
Hypothesized Mean Difference	0	
df	36	
t Stat	1.568	
P(T<=t) one-tail	0.063	
t Critical one-tail	1.688	
P(T<=t) two-tail	0.126	
t Critical two-tail	2.028	

Appendix Table 21. Two-sample t-test assuming unequal variance for the ratio of MC3 by MC5

	males	*females*
Mean	1.212	1.205
Variance	0.001	0.001
Observations	18	23
Hypothesized Mean Difference	0	
df	38	
t Stat	0.608	
P(T<=t) one-tail	0.273	
t Critical one-tail	1.686	
P(T<=t) two-tail	0.547	
t Critical two-tail	2.024	

Appendix Table 22. Two-sample t-test assuming unequal variance for the ratio of MC4 by MC5

	males	*females*
Mean	1.077	1.083
Variance	0.001	0.001
Observations	18	23
Hypothesized Mean Difference	0	
df	37	
t Stat	-0.651	
P(T<=t) one-tail	0.260	
t Critical one-tail	1.687	
P(T<=t) two-tail	0.519	
t Critical two-tail	2.026	

SUMMARY STATISTICS

Appendix Table 23. Summary statistics for metacarpal head width

		MC1	MC2	MC3	MC4	MC5	MC4/MC2
all	N=	41	41	41	41	41	41
	avg	12.57	9.78	10.18	9.40	8.65	0.97
	stdv	1.00	1.27	1.04	0.69	0.94	0.11
male	N=	18	18	18	18	18	18
	avg	13.00	10.05	10.54	9.70	9.02	0.98
	stdv	1.21	1.28	1.10	0.66	0.92	0.10
female	N=	23	23	23	23	23	23
	avg	12.23	9.57	9.90	9.16	8.36	0.97
	stdv	0.65	1.26	0.92	0.64	0.86	0.11

Appendix Table 24. Summary statistics for metacarpal head height

		MC1	MC2	MC3	MC4	MC5	MC4/MC2
all	N=	41	41	41	41	41	41
	avg	12.76	13.32	13.68	12.38	11.24	0.93
	stdv	0.81	1.01	0.87	0.76	0.72	0.05
male	N=	18	18	18	18	18	18
	avg	13.22	13.73	14.05	12.69	11.63	0.93
	stdv	0.72	1.04	0.80	0.77	0.77	0.05
female	N=	23	23	23	23	23	23
	avg	12.40	13.01	13.39	12.14	10.93	0.94
	stdv	0.69	0.87	0.84	0.68	0.50	0.05

Appendix Table 25. Summary statistics for metacarpal base width

		MC1	MC2	MC3	MC4	MC5	MC4/MC2
all	N=	41	41	41	41	41	41
	avg	13.41	12.06	12.49	8.37	9.20	0.70
	stdv	0.95	1.06	1.00	0.84	0.69	0.09
male	N=	18	18	18	18	18	18
	avg	14.00	12.38	12.92	8.60	9.65	0.72
	stdv	0.86	1.12	1.10	0.91	0.53	0.11
female	N=	23	23	23	23	23	23
	avg	12.94	11.81	12.17	8.19	8.84	0.70
	stdv	0.75	0.96	0.79	0.75	0.59	0.07

Appendix Table 26. Summary statistics for metacarpal base height

		MC1	MC2	MC3	MC4	MC5	MC4/MC2
	N=	41	41	41	41	41	41
all	avg	12.10	15.11	15.16	10.30	9.94	0.68
	stdv	0.77	1.22	1.04	0.85	0.81	0.05
	N=	18	18	18	18	18	18
male	avg	12.40	15.78	15.48	10.68	10.29	0.68
	stdv	0.91	1.28	1.15	0.94	0.65	0.05
	N=	23	23	23	23	23	23
female	avg	11.87	14.58	14.91	9.99	9.67	0.69
	stdv	0.55	0.86	0.90	0.64	0.84	0.05

Appendix Table 27. Summary statistics for metacarpal midshaft width

		MC1	MC2	MC3	MC4	MC5	MC4/MC2
	N=	41	41	41	41	41	41
all	avg	10.70	8.08	7.59	6.32	7.23	0.79
	stdv	0.95	0.72	0.64	0.62	0.90	0.06
	N=	18	18	18	18	18	18
male	avg	11.36	8.49	7.96	6.69	7.89	0.79
	stdv	0.79	0.66	0.57	0.55	0.77	0.07
	N=	23	23	23	23	23	23
female	avg	10.19	7.56	7.30	6.04	6.72	0.78
	stdv	0.73	0.60	0.55	0.52	0.63	0.06

Appendix Table 28. Summary statistics for metacarpal midshaft height

		MC1	MC2	MC3	MC4	MC5	MC4/MC2
	N=	41	41	41	41	41	41
all	avg	7.96	8.65	9.03	7.30	6.66	0.85
	stdv	0.72	0.76	0.77	0.91	0.70	0.07
	N=	18	18	18	18	18	18
male	avg	8.41	9.00	9.24	7.77	7.05	0.86
	stdv	0.70	0.73	0.76	1.09	0.62	0.09
	N=	23	23	23	23	23	23
female	avg	7.60	8.37	8.88	6.96	6.35	0.83
	stdv	0.50	0.67	0.76	0.55	0.60	0.06

METACARPAL MEASUREMENT DESCRIPTION

Maximum length (palmar view)

Maximum length (medial view)

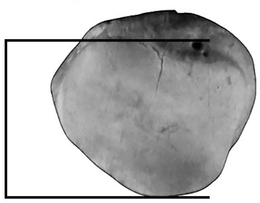
Measurement 1 (maximum length) shown here on a right metacarpal 1 (Mc1). Description: view bone laterally or medially, placing caliper stem parallel to diaphysis, take length of most proximal point to most distal point.

Articular length (palmar view)

Articular length (medial view)

Measurement 2 (articular length) shown here on a right Mc1. Description: place one needle of caliper at the center of the basal facet and the other at the most distal point on the bone's head. View from whichever angle maximizes accuracy.

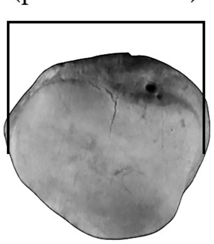
Base dorsopalmar height
(proximal view)



Base dorsopalmar height
(medial view)

Measurement 3 (base dorsopalmar height) shown here on a right Mc1. Description: the maximum dorsopalmar height of the MC base taken by resting the dorsal end of the bone on one jaw of the caliper and closing the caliper to meet a second point of contact on palmar aspect of the bone. Viewed proximally.

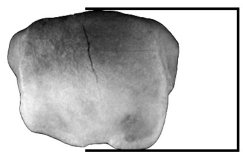
Base mediolateral width
(proximal view)



Base mediolateral width
(palmar view)

Measurements 4 and 5 (base mediolateral width) are the same measurement for the Mc1, therefore only measurement 4 is shown here on a right Mc1. Description: the maximum mediolateral width of the MC base taken by resting the medial end of the bone on one jaw of the caliper and closing the caliper to meet a third point of contact on lateral aspect of the bone. Viewed proximally.

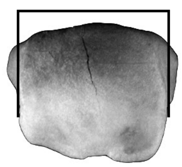
Head dorsopalmar height (distal view)



Head dorsopalmar height (medial view)

Measurement 6 (head articular dorsopalmar height) shown here on a right Mc1. Description: the maximum dorsopalmar height of the MC head articular surface taken by resting the palmar end of the bone on one jaw of the caliper and closing the caliper to meet a second point of contact on dorsal aspect of the bone. Viewed distally.

Head mediolateral width (distal view)



Head mediolateral width (palmar view)

Measurement 7 (head articular mediolateral width) shown here on a right Mc1. Description: the mediolateral width of the head articular surface taken at the dorsopalmar center of the head. Viewed distally.

Measurements 8 (head mediolateral dorsal width) and 9 (head mediolateral palmar width) were collected but not used for analyses.

Midshaft mediolateral width (palmar view)

Measurement 10b (palmar view midshaft mediolateral width) shown here on a right Mc1 (10a is viewed dorsally, but is the same measurement and therefore not shown here). Description: place bone on graph paper with diaphysis perpendicular to 'zero' line where apex of head touches. Mark the midshaft point on graph paper using half the articular value for that bone. Take maximum mediolateral midshaft width at this midpoint. Palmar view.

Midshaft dorsopalmar height (medial view)

Measurement 10d (medially-viewed midshaft dorsopalmar height) shown here on a right Mc1 (10c is viewed laterally, but is the same measurement and therefore not shown here). Description: place bone on graph paper with diaphysis perpendicular to 'zero' line where apex of head touches. Mark the midshaft point on graph paper using half the articular value for that bone. Take maximum dorsopalmar midshaft height at this midpoint. Medial view.

All photographs shown above are of the Mc1 of individual CA-Sis-239-9038 from the Phoebe A. Hearst Museum of Anthropology. All photography protocol was adapted from *Human Osteology* (White et al. 2012).

METACARPAL MEASUREMENT PROTOCOL

General:

— All measurements to be collected using electronic calipers.
— Zero the caliper.
— Identify and side each bone before taking measurements.
— Do not take measurements on bones that are severely damaged (broken in half, or either head or base missing) or appear to be juvenile (mark and double-check).

Specifics:

1) MAXIMUM LENGTH: view bone laterally or medially, placing caliper stem parallel to diaphysis, take length of most proximal point to most distal point.

2) ARTICULAR LENGTH: place one needle of caliper at the center of the basal facet (refer to picture for choosing center point for each metacarpal) and the other at the most distal point on the bone's head. View from whichever angle maximizes accuracy.

   Verbal descriptions for each metacarpal:
   — Mc1: the summit of the mediolateral convexity
   — Mc2: the trough's anteroposterior center
   — Mc3: the center of the carpal facet
   — Mc4: the center of the carpal facet
   — Mc5: proximal mediolateral midpoint of the dorsoventral convexity

3) BASE DORSOPALMAR WIDTH: the maximum dorsopalmar width of the MC base taken by resting the dorsal end of the bone on one jaw of the caliper—forming at least two points of contact—and closing the caliper to meet a third point of contact on palmar aspect of the bone. Viewed proximally.

4) BASE MEDIOLATERAL WIDTH (M): the maximum mediolateral width of the MC base taken by resting the medial end of the bone on one jaw of the caliper—forming at least two points of contact—and closing the caliper to meet a third point of contact on lateral aspect of the bone. Viewed proximally.

5) BASE MEDIOLATERAL WIDTH (L): the maximum mediolateral width of the MC base taken by resting the lateral end of the bone on one jaw of the caliper—forming at least two points of contact—and closing the caliper to meet a third point of contact on medial aspect of the bone. Viewed proximally.

6) HEAD DORSOPALMAR WIDTH: the maximum dorsopalmar width of the MC head articular surface taken by resting the palmar end of the bone on one jaw of the caliper—forming at least two points of contact—and closing the caliper to meet a third point of contact on dorsal aspect of the bone. Viewed distally.

7) HEAD ARTICULAR WIDTH: the mediolateral width of the head articular surface taken at the dorsopalmar center of the head. Viewed distally.

8) HEAD MEDIOLATERAL DORSAL WIDTH: the maximum mediolateral width of the head articular surface on the dorsal side of the bone. To measure, take dorsal view.

9) HEAD MEDIOLATERAL PALMAR WIDTH: the maximum mediolateral width of the head articular surface on the palmar side of the bone. To measure, take palmar view.

MIDSHAFT MEASUREMENTS: place bone on graph paper with diaphysis perpendicular to 'zero' line where apex of head touches. Mark the midshaft point on graph paper using half the ARTICULAR LENGTH value for that bone. Take the following four measurements:

10) Dorsal view: mediolateral width at midshaft.
11) Palmar view: mediolateral width at midshaft.
12) Lateral view: dorsopalmar width at midshaft.
13) Medial view: dorsopalmar width at midshaft.

ARTICULAR LENGTH MEASUREMENTS

Appendix Table 29. Articular length measurements of all complete **male** right hands (mm)

Individual	MC1	MC2	MC3	MC4	MC5
Sac-43-6691	44.37	69.79	67.90	60.32	55.23
CA-Sjo-144-7681	45.40	66.87	62.89	54.11	53.85
Sis-239-9043	47.17	69.32	66.01	58.73	54.35
Sjo-105-9801	42.82	64.32	63.09	54.88	51.95
Ala-13-10456	44.43	61.71	59.39	52.64	48.57
Mnt-281-8479	38.06	57.30	55.65	48.33	42.55
Ala-328-10239	45.62	65.97	63.54	55.84	52.52
Cco-138-10657	44.11	62.13	60.97	53.26	49.46
Ala-328-8566	44.82	65.20	63.47	57.22	52.95
Sis-249-9047	39.51	61.68	58.31	53.54	48.24
Ala-13-10461	42.07	63.15	60.67	53.22	50.34
Sca-1-1601	40.78	58.71	57.70	52.97	48.35
Mrn-76-12-2137	42.27	66.39	63.96	54.89	51.57
Ala-328-5283	37.21	56.91	57.62	51.66	48.73
CCo-138-5879	45.29	68.66	68.01	62.32	57.81
Cco-138-6124	40.40	60.48	57.45	51.99	47.11
Mrn-242-6508	39.40	68.76	66.41	58.70	53.75
Cco-138-6263	41.95	58.57	56.37	51.78	49.06

Appendix Table 30. Articular length measurements of all complete **female** right hands (mm)

Individual	MC1	MC2	MC3	MC4	MC5
Ala-13-10472	40.07	61.17	59.35	52.14	49.55
Ala-13-10473	41.42	66.89	64.10	56.73	51.08
Cco-138-10519	40.45	60.83	60.60	56.59	49.64
Cco-138-10521	42.56	61.56	58.42	52.45	49.54
Ala-328-8934	40.15	61.53	59.68	53.54	48.71
Ala-328-8952	40.62	58.48	58.96	53.77	51.71
Ala-328-8953	40.53	59.36	56.92	50.44	48.17
Mrn-168-8960	41.08	62.66	60.61	52.74	50.19
Sis-239-9038	42.20	63.12	61.16	53.64	49.32
Sis-239-9044	41.19	61.38	60.17	53.21	48.67
Mnt-281-9650	41.30	59.33	59.35	51.28	46.44
Sjo-106-9097	40.69	58.35	58.97	52.31	47.07
Cco-241-8560	41.99	63.63	57.98	54.51	50.92
Ala-328-10248	40.31	57.84	54.98	49.08	47.04
Ala-328-10214	39.24	59.13	56.13	50.17	47.34
Cco-138-10654	42.71	60.34	60.58	55.86	50.49
Cco-138-10675	42.17	60.77	60.11	54.51	48.45
Cco-138-10676	42.66	62.15	57.72	52.06	47.04
Ala-307-8274	39.88	61.42	59.03	53.24	50.63
Cco-138-9729	41.76	58.20	57.69	53.09	48.49
Ala-328-5391	40.44	58.61	58.29	53.64	48.12
Cco-138-6260	41.18	61.06	60.40	53.90	50.29
Mrn-242-6420	37.63	55.87	55.70	51.20	47.79