UNIVERSITY OF SOUTHAMPTON

FACULTY OF LAW, ARTS & SOCIAL SCIENCES

School of Humanities

The Expression of Bilateral Asymmetry in the Hands and Humeri: A Methodological Comparison

by

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Thesis for the degree of Doctor of Philosophy

January 2009

UNIVERSITY OF SOUTHAMPTON

ABSTRACT

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The population-level preference for the use of the right hand is one of the defining characteristics of *Homo sapiens* and as such, its evolutionary origins within the human genus remain a topic of interest. Identifying hand preference in extinct hominin species is complicated by the difficulty in distinguishing markers of laterality in the bones of the upper limb. These difficulties are further compounded by the range of osteological methods available to study asymmetry and the under-representation of the bones of the hand in such studies.

To better understand the evolution of handedness within the hominin lineage, the effect of methodology on asymmetry expression must first be clarified, as this in turn influences our notions of handedness in individuals and groups. The current study took an inclusive approach to the measurement of upper limb asymmetry in both modern human and non-human primate samples. To assess the contribution that the bones of the hand can make to asymmetry research, data from the metacarpals and phalanges were compared with that from the humerus, a more commonly-studied region of the upper limb. Both metric and musculoskeletal stress marker (MSM) data were collected and compared in order to assess the comparability of asymmetry profiles generated by contrasting methodological approaches. Asymmetry was determined for a sample of modern human skeletons and a non-human primate sample comprising *Pan troglodytes schweinfurthii* and *Gorilla gorilla gorilla*.

Two key findings emerge from these analyses: 1) The expression of asymmetry differs, in terms of both direction and magnitude, between the bones of the hand and the humerus. Differences are also apparent between the metacarpals and phalanges. 2) Metric and MSM methods differ in the asymmetry profiles they generate, with the MSM method generally underestimating the magnitude of asymmetry present in a sample, relative to that identified by a metric approach. In addition, the various skeletal samples studied exhibit variation in their relative asymmetry profiles which can be attributed to potential differences in functional recruitment patterns in the upper limbs of these individuals.

Together, these findings clearly highlight the care that must be taken in analyses of asymmetry, due to the level of methodological variation present in currently inter-changeable approaches. The relatively neglected region of the hand has an important contribution to make to our understanding of asymmetry in the upper limb. The results of this study recommend the adoption of a more inclusive approach to the study of upper limb bilateral asymmetry, particular when inferences are to be made regarding handedness. By combining methodological approaches and incorporating data from across the upper limb, a more accurate picture of asymmetry expression will emerge and allow us to better understand the evolutionary development of this trait in our hominin ancestors.

CONTENTS

LIST OF TABLES

CHAPTER 2. MEASURING ASYMMETRY

CHAPTER 3. MATERIALS AND METHODS

CHAPTER 4. ANALYSIS OF OBSERVER RELIABILITY

CHAPTER 5. ÉCIJA DATA ANALYSIS

CHAPTER 6. GREENWICH DATA ANALYSIS

CHAPTER 7. NON-HUMAN PRIMATE DATA ANALYSIS

CHAPTER 8. DISCUSSION

LIST OF FIGURES

CHAPTER 1. ASYMMETRY AND HANDEDNESS

CHAPTER 2. MEASURING ASYMMETRY

CHAPTER 3. MATERIALS AND METHODS

CHAPTER 4. ANALYSIS OF OBSERVER RELIABILITY

CHAPTER 5. ÉCIJA DATA ANALYSIS

CHAPTER 6. GREENWICH DATA ANALYSIS

CHAPTER 7. NON-HUMAN PRIMATE DATA ANALYSIS

DECLARATION OF AUTHORSHIP

I, ……**Lisa Anne Cashmore**……………………………………………,

declare that the thesis entitled

The Expression of Bilateral Asymmetry in the Hands and Humeri: A Methodological Comparison

and the work presented in the thesis are both my own, and have been generated by me as the result of my own original research. I confirm that:

- this work was done wholly or mainly while in candidature for a research degree at this University;
- where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
- where I have consulted the published work of others, this is always clearly attributed;
- where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
- I have acknowledged all main sources of help;
- where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;
- parts of this work have been published as:

Cashmore *et al.* (2008). The evolution of handedness in humans and great apes: A review and current issues. *Journal of Anthropological Sciences* 86: 7-35.

Cashmore & Zakrzewski (2009). The expression of asymmetry in hand bones from the medieval cemetery at Écija, Spain. In: Lewis, M.E. and Clegg, M. (eds). *Proceedings of the Ninth Annual Conference of the British Association of Biological Anthropology and Osteology*. British Archaeological Reports International Series 1918. Pp 79 – 92.

Cashmore (in press). Can hominin ‘handedness’ be accurately assessed? *Annals of Human Biology.*

Signed: ………………………………………………………………………..

Date:……………………………………………………………………………….

Acknowledgements

Although it is my name on the front page, it is safe to say that this thesis could not have been completed without the help, support and guidance of many others. Firstly, I would like to thank my supervisor Dr Sonia Zakrzewski for all her help and guidance over the years, but especially for her continued enthusiasm in the project. I'm sure there were many times when she despaired that I would never finish, but I hope that the end product has been worth the wait! I would also like to thank my advisor (and end-game supervisor) Dr John McNabb for all his help and encouragement during my time in Southampton and particularly during the final stages of completing this thesis. Dr Joanna Sofaer proof-read all the data analysis included in this thesis and I am grateful to her for her time and feedback. This thesis was partially funded by a studentship from the British Academy Centenary Project: From Lucy to Language - The Archaeology of the Social Brain and I would like to take this opportunity to thank Professors-In-Crime Gamble, Dunbar and Gowlett for having faith in me to begin with and their continued support for my research.

I would have been unable to carry out my data analysis without the generosity of a number of institutions and individuals who provided access to their skeletal collections. Thank you to Antonio Fernández Ugalde at the Museo Histórico Municipal de Écija for both allowing access to the extensive Écija collections and also his hospitality during my time in Spain. The Écija data collection was supported by a Small Research Project Grant from the British Association of Biological Anthropology and Osteoarchaeology (BABAO). Thank you to Dr Louise Loe and Ceri Boston at Oxford Archaeology for providing access to and assistance with the Greenwich Naval Hospital Cemetery collection. Thank you also to Mr Malcolm Harman for allowing access to the great ape material housed at the Powell-Cotton Museum and for regaling me with many interesting stories during my time there. I'd also like to thank the staff of the museum for providing cushions and a fan heater while I learnt the hard way why no-one attempts data collection there during the winter.

I would also like to thank the many friends and colleagues who have helped smooth the PhD process and make my time in Southampton all the more enjoyable. There are too many to single out here, but special mention must go to all the staff and students of the Archaeology department and particularly those in the Centre for the Archaeology of Human Origins (CAHO). I'm glad to have met so many great people in CAHO and have certainly enjoyed all the gossiping that ensued! I'd very much like to thank Emma Pomeroy for reading over an early draft of the Écija chapter and providing useful feedback. I'd also like to thank Sarah Inskip for being a wealth of knowledge on all things skeletal and providing lots of useful advice while I was getting to grips with the data collection process. A mention

should also go to all my fellow cottage dwellers over the years, especially Ross Thomas and Rebecca Bridgman who have been tireless sources of advice and all-round PhD-related wisdom. My long-time ally John Paul Newman deserves my praise for suffering with good grace all my various whinges and rants against the world. Outside the University of Southampton, I’d like to thank Osbjorn Pearson and Janet Cope for providing access to unpublished references. I’d particularly like to thank my fellow hand enthusiasts Emma Nelson and Natalie Uomini, who have been fantastic (and very generous) sources of information and discussion. Emma has kept me company at numerous conferences and I have her to thank for many a tipsy introduction to a respectable academic. Matt Grove continually gives me something to aspire to and that can only be a good thing.

A special mention must go to the great and the good at Wessex Lane Halls who took me off the streets and have given me a roof over my head and gainful employment as a warden for the last three years. The many good friends I’ve made in my time there almost makes up for all the 3am fire alarms. In particular, Tom Frost kindly took time out from righting the legal injustices of the world to proof-read the early chapters and to vainly try to end my love affair with the comma (you can judge his success for yourself).

To all those mentioned above (and those that I have not embarrassed by name) I am eternally indebted.

Finally, thank you a million times over to Omar, who has always been my hero.

Introduction

Asymmetry is crucial to functioning of biological molecules and is therefore considered as vital to the development of life on this planet (Gleiser & Walker, 2008). Despite this, vertebrates have traditionally been considered to be bilaterally symmetrical (Barr, 2001) with the animal body being comprised of numerous paired anatomical structures such as eyes, ears, arms, legs and internal organs. While a certain degree of symmetry is important for the smooth operation of these limbs and organs, upon further inspection it becomes clear that there is a great deal of asymmetry apparent within these pairs both in terms of their structure and their function. In fact, the presence of asymmetry in such systems serves to increase their efficiency and thus confers benefits to the organism (Marchant & McGrew, 1999; Rogers, 2002).

Homo sapiens are no different from the rest of the animal kingdom in exhibiting asymmetries within the paired structures of the body. While the presence of such asymmetries is by no means unusual, the nature of certain human structural and functional asymmetries *is* unique such as those found in the upper limb and cerebral cortices of the brain. From an evolutionary perspective interest has focused on asymmetries in the hemispheric organisation of the human brain related to language capabilities (e.g. Holloway & de la Coste-Lareymondie, 1982) plus those pertaining to control of the hands (e.g. Falk, 1980) and bilateral asymmetry in the bones of the upper limb (e.g. Trinkaus *et al.*, 1994). This interest has arisen due to language capabilities and population-level handedness being considered as specific to *H. sapiens* and not present within any other current living primate species (e.g. Corballis, 2003). Handedness, as it is expressed in modern humans, is the preference for the use of one hand across various tasks. In modern human groups right-handedness is the common condition with the large majority of individuals favouring the use of the right hand over the left, often cited at around 90% preference (Marchant *et al.*, 1995).

The uniqueness of these distinctly ‘modern’ traits has prompted researchers to investigate their origins and development within the hominin lineage leading to *Homo sapiens*. Understanding the emergence and progression of these traits will provide further insight into what makes our genus ‘human’ and shed light on the differences between ourselves and our closest non-human primate relatives. It has been suggested by some that handedness and language capabilities share a co-evolutionary origin, which has arisen from observation of a strong left hemisphere bias for both of these behaviours in the human brain and certain neuroanatomical links between the brain centres responsible for these actions (Falk, 1980; MacNeilage *et al.*, 1987; Crow, 1998; McManus, 1999; Corballis, 2003). If research into the evolution of behavioural lateralisation in hominins identifies a temporal discontinuity between the emergence of these traits then the validity of this co-evolutionary relationship would be called into question.

It is often necessary to study language capabilities indirectly in the fossil record through features such as vocal tract anatomy (Arensburg *et al.*, 1990; Martínez *et al.*, 2008), endocast anatomy (Holloway & de la Coste-Lareymondie, 1982), genetic markers (Krause *et al.*, 2007) and material culture (d'Errico *et al.*, 2003). However, fossilised traces of hand preference are much more readily observable in the hominin record through examination of asymmetry in the morphology of the upper limb skeleton. This has led to a continued interest in identifying direct evidence of handedness within the hominin lineage. In addition a large body of research has focused on pinpointing aspects of hand preference (and potentially handedness) in non-human primate species, particularly the great apes (see McGrew & Marchant, 1997). If hand preference akin to that seen in modern humans can be identified in non-human primates then this would call into question the uniqueness of this trait in *Homo* and its purported co-evolution with language. It would also change the focus of hominin handedness research as handedness would be expected to be present at or around the time of the last common ancestor of chimpanzees and humans.

The inimitable nature of human handedness and the implications of the timing and location of its emergence within hominin evolution make it vital that the expression of bilateral asymmetry in skeletal material can be assessed accurately. Although it is relatively straightforward to measure hand preference in living samples, its identification is much more problematic on the skeleton. For extinct hominins one of the main problems facing asymmetry research is the paucity of material available for study. Poor preservation and extremely limited numbers of paired upper limb bones make reliable assignments of asymmetry rare, particularly in the earlier stages of the evolution of the human genus. It is only with the emergence of *Homo neanderthalensis* that there is an increase in skeletal material suitable for study (Cashmore *et al.*, 2008). In modern human groups however, where sample size does not present the same logistical problem, identifying upper limb bilateral asymmetry is further complicated by certain methodological issues. There are a number of techniques available to quantify asymmetry which measure different aspects of long bone morphology, focusing on both external metric and cross-sectional geometric diaphyseal properties. In addition, analysis of the development of areas of muscle attachment to bone provides a means of determining asymmetric use of the arms and hands through the action of upper limb muscles. To date there have been few comparative studies of the outcomes of applying each approach to the assessment of asymmetry. It is therefore unclear the extent to which these methods, which are often applied interchangeably, present congruent asymmetry profiles for any given skeletal sample.

Studies of upper limb asymmetry tend to focus on measurements taken from the humerus bone. From a methodological viewpoint humeri are often readily available in skeletal collections and many measurements can be taken even if preservation is poor. For these reasons data on humeral asymmetry is often the basis for determination of hand preference in a given sample. The bones of the hand feature much more rarely in studies of asymmetry and handedness and existing research focuses exclusively on the second metacarpal (Garn *et al.*, 1976; Plato *et al.*, 1980; Roy *et al.*, 1994; Sarringhaus *et al.*, 2005; Lazenby *et al.*, 2008). By neglecting this region of the upper limb from scrutiny it is not possible to gain a comprehensive understanding of functional asymmetry and behavioural lateralisation in any species. At present it is not clear whether asymmetry represented in the commonly studied humerus would be congruent with that found in the bones of the hand. Evidence from a study of muscle activation during the bimanual manufacture of Oldowan stone tools indicates that the key muscle activity during this process is in the intrinsic muscles of the hands, i.e. muscles which originate and insert within the hand (Marzke *et al.*, 1998). This suggests that the bones and muscles of the hand are functionally recruited in different ways to that of the rest of the upper limb, and as such, should be investigated and incorporated in asymmetry research, particularly if the object of research is to determine hand preference.

To address the issues outlined above this thesis takes a methodological approach to the problem of reliably identifying markers of bilateral asymmetry and hand preference in upper limb skeletal material. This is approached by means of a comparison of asymmetry across anatomical regions and a comparison of two of the available techniques for determining skeletal asymmetry. The first comparison assesses the nature of asymmetry expression across the bones of the hand and how this compares to asymmetry in corresponding humeral material. Rather than focus solely on the second metacarpal, this approach utilises a number of measurements from both the metacarpals and phalanges. The second comparison explores the similarities and differences between some the available techniques for the measurement of upper limb bilateral asymmetry. This approach focuses on metric (i.e. external) bone properties taken from both the hands and humeri and compares the asymmetry profile obtained by this method with the asymmetry profile as determined from analysis of musculoskeletal stress marker development in both anatomical regions. To facilitate these comparisons, data has been collected from both modern human and non-human primate samples. While the non-human primate samples (comprising chimpanzees and gorillas) serve as control groups for the modern human material (due to the expected lower levels of identifiable asymmetry resulting from the functional constraints of locomotion imposed on the non-human primate upper limb), this study also provides an opportunity to further quantify the nature of skeletal asymmetry in species which have up until now received little attention (Sarringhaus *et al.*, 2005; Hopkins, 2008). These analyses aim to clarify both the contribution that the hands can make to our understanding of upper limb asymmetry and whether it is appropriate to continue to use the available methods for assessing skeletal bilateral asymmetry interchangeably.

Outline of chapters

Chapters 1 and 2 provide background to the topics of asymmetry and handedness research. Chapter 1 outlines the nature of asymmetry across the natural world, from basic biological molecules to the mammalian order. This chapter also outlines a particular asymmetry unique to humans, handedness, and explores the expression of this trait in hominins and non-human primates. Chapter 2 explores the most commonly applied osteological methods by which asymmetry can be assessed in skeletal material, in order to understand the expression of hand preference and handedness in archaeological samples of modern humans, non-human primates and fossil hominins. This chapter also compares regions of the upper limb from which asymmetry can be determined. Chapters 3 to 7 detail the methodologies used in the current study and the results of the data analysis. Chapter 3 outlines the skeletal samples analysed in the current study and the methods by which asymmetry was assessed. Chapter 4 details the results of analyses of inter- and intra-observer reliability performed on a subset of skeletal data. Chapters 5 and 6 provide the results of the data analyses performed on the modern human upper limb skeletal samples from the sites of Écija and Greenwich, respectively. Chapter 7 gives the results of the non-human primate data analyses, performed on a skeletal sample of chimpanzees and gorillas. The thesis concludes with Chapters 8 and 9: Chapter 8 contains a discussion of the findings of the current study and their implications for asymmetry and handedness research, with Chapter 9 outlining the conclusions and areas for future research.

Chapter 1. Asymmetry and Handedness

1.1. Introduction

At first glance, the natural world seems organised along symmetrical lines, with symmetry being associated with health, beauty and perfection. Upon closer inspection however, it appears that the world is inherently *asymmetric* (Close, 2000; Gardner, 2005). This chapter begins by briefly tracing the history of asymmetry within and across biological organisms and demonstrating how asymmetry and lateralisation are crucial to the functioning of the mammalian body.

Homo sapiens appear to be unique within the animal kingdom in terms of their cognitive development and use of complex syntactical language, and this uniqueness is in part a result of our asymmetric brain organisation. Asymmetry is also present in the structure and function of the human upper limb, with lateralisation in hand use reflected in a clear population-level preference in the use of the right hand across tasks. Handedness has long been of interest to researchers both in the field of psychology and palaeoanthropology, and for palaeoanthropologists in particular, attention has focused on when and where this trait emerged in hominin evolution. This chapter will also explore our current understanding of the nature of handedness in modern humans and how the various lines of evidence pertaining to hominin and non-human primates have addressed the issue of the evolution of handedness within the lineage leading to modern humans.

At this stage it is worth clarifying some of the terminology commonly used in the literature. The terms ‘asymmetry’ and ‘lateralisation’ are often used interchangeably, despite differences in their meaning. The term ‘asymmetry’ clearly refers to a deviation from symmetry.

- ‘Laterality’ is defined in the Oxford English Dictionary as “the dominance of the right- or the left-hand member of a pair of bodily organs as regards a particular activity or function”.
- ‘Asymmetry’ shall therefore be considered to refer to *structural* differences between two sides of an organ or component of the body and ‘laterality’ to refer to the *functional* differences between the sides of these structures.

Evidently the terms are strongly linked, but for the purposes of clarity the definitions of these terms as given above will be followed throughout the thesis.

1.2. Asymmetry in biological organisms

Asymmetry has been found at the molecular level of biological organisms, being identified in amino acids (Geschwind & Galaburda, 1987; Chothia, 1991; McManus, 2002). These molecules display chirality in their structure (i.e. an object is chiral if it differs from, and cannot be superimposed on, its mirror image) which results in D- (dextro/right-handed) and L- (laevo/left-handed) forms which not only differ in their structure (D- and L- amino acids are mirror images of each other) but also in their properties and function. For example, the D-limonene molecule smells of citrus, while the L-limonene version smells of pine (McManus, 2002). The important metabolism-regulating hormone thyroxine has also been found to be chiral, with L-thyroxine the naturally-occurring hormone and D-thyroxine the inactive form (*ibid.*), illustrating how asymmetry can be fundamental to the functioning of biological organisms.

Asymmetry appears to have quickly expanded beyond the microscopic level to influence structure and function at the organism-level, stretching back through vertebrate evolution. Perhaps the earliest evidence of behavioural lateralisation can be found approximately half a billion years ago. Of over 80 Middle Cambrian fossil trilobytes studied with predation injuries, 69% were found to have scars on their right side, suggesting a preference for direction of attack on the part of the predator (Babcock & Robinson, 1989). More recently, Dietl & Hendricks (2006) identify asymmetry in the coiling of Plio-Pleistocene marine snail shells, with dextral (right-twisting) and sinistral (left-twisting) shells. It is suggested that sinistral shells confer an advantage against predation from ‘right-handed’ crabs, but this may come at the cost of a reproductive disadvantage when compared to dextral snails. In modern animals, there is extensive evidence of laterality found across a wide range of species, from spiders (Ades & Ramires, 2002) to birds such as crows (Hunt, 2000; Emery & Clayton, 2004; Rutledge & Hunt, 2004) and parrots (Synder *et al.*, 1996; Synder & Bonner, 1999; Vallortigara *et al.*, 1999; Andrews & Rogers, 2002). Within the mammalian class, laterality has been identified in species as diverse as whales and dolphins (Clapham *et al.*, 1995; Marino & Stowe, 1997; Stafne & Manger, 2004; Woodward & Winn, 2006) to domestic cats (Pike & Maitland, 1997).

It is therefore clear that asymmetry (and the resulting lateralisation) of both molecules and organisms has a deep evolutionary history. The significance of asymmetric molecules is reflected in the variety of functions that can be achieved from structurally similar molecules however, the benefits of asymmetry and lateralisation for the individual organism are less clear. As Dietl & Hendricks (2006) point out, while an uncommon asymmetry in their sample of snails conferred a benefit against predation, this may have been at the expense of reproductive success. Disadvantages to lateralisation are explored by Rogers (2002). An example of this is lateralisation in the visual system, which could be considered disadvantageous as if it reduced the efficiency of recognition and response to predators, conspecifics and food resources (*ibid.*). However, as Rogers illustrates, there is evidence from a number of species that lateralisation in the visual system in fact leads to an increased ability to simultaneously process information, in addition to increased vigilance and quicker reaction times. Studies of the primate brain show increased cognitive capacity in lateralised individuals as a result of structural reorganisation of the brain, supporting this observation. Computational studies (Ringo, 1991; Ringo *et al.*, 1994) have proposed that as the brain increases in size there must necessarily be a fall in ‘connectivity’, i.e. the number of connections between neurons. This is because, with increased neuron numbers, the increased time and computational power required to maintain an increased number of connections negatively impacts computational speed. This is supported by the findings of a Magnetic Resonance Imaging (MRI) analysis of 43 primate brains conducted by Rilling & Insel (1999). They found decreased *inter*-hemispheric connectivity across the corpus callosum in the larger primate brains, but with increased *intra*-hemispheric connectivity. All the studies (Ringo, 1991; Ringo *et al.*, 1994; Rilling & Insel, 1999) agree that the increasing level of hemispheric specialisation seen in primates in particular is a likely result of the need to restructure hemispheric connectivity in the wake of increasing brain size. Further research is required however to test whether this trend can be identified in other large-brained mammals (Ringo *et al.*, 1994).

In non-human primates lateralisation of the hands has been found to increase speed and efficiency at manipulative tasks. McGrew & Marchant (1999) found that lateralised chimpanzees at Gombe, Tanzania (i.e. chimpanzees who preferred the use of one hand other the other) were more efficient at termite fishing (in terms of the amount of food gathered relative to effort) than those who did not exhibit any hand preference. While these lateralised behaviours confer advantages to the individual, Rogers (2002) also proposes group-level benefits of lateralisation. She suggests that lateralisation that extends to all members of the group or populations may provide the benefit of 'social predictability', that is the ability to know what other members of the group will do in certain situations, for example during a predator attack.

While asymmetry may have initially appeared in biological compounds as a result of variation in chemical bonding within molecules, it has ultimately led to the presence of asymmetries and lateralised behaviours which may confer adaptive benefits to both the individual and the group. The following section will show that *Homo sapiens* are no exception in this regard. In fact, a number of distinguishing human characteristics reflect the very unique nature of human asymmetry, in particular handedness and language capabilities. The remainder of this chapter will address one specific lateralised behaviour, handedness. The nature and expression of this trait within modern humans will be explored, alongside the evidence for when and where this trait first emerged in the course of hominin evolution.

1.3. Asymmetry in humans

With asymmetry clearly established across the animal kingdom, it should come as no surprise that asymmetry is also prevalent in the organisation of the body of *Homo sapiens*. Bilateral differences have been found in both the structure and function of the human viscera, for example in the kidneys (Shokeir *et al.*, 1993; Saito, 2003; Oh *et al.*, 2006), lungs (Grandmaison *et al.*, 2001; Roychoudhuri *et al.*, 2006), breasts (Hsieh *et al.*, 1991; Møller *et al.*, 1995; Manning *et al.*, 1997), testicles (Chang *et al.*, 1960; Bogaert, 1997), ovaries (Mittwoch, 1975; Barco *et al.*, 2003), as well as in the endocrine system

(Nelson, 1980; Gerendai & Halász, 1997; Werner *et al.*, 2005). Sensual asymmetry has also been well-documented, with left/right differences in both the visual system in terms of differences in what each eye sees, as well as eye dominance (Bradshaw, 1989; Springer & Deutsch, 1989), and the auditory system in terms of processing and perception (Coren & Porac, 1981; Pierson *et al.*, 1983; Springer & Deutsch, 1989; Lauter, 2007). There is also evidence for perceptual asymmetry in the tactile (Andrews & Watkins, 2002; Witelson, 1976; Smith *et al.*, 1977; Nilsson & Geffen, 1987; Schiff & Gagliese, 1994, but see Summers & Lederman, 1990) and olfactory senses (Andrews & Watkins, 2002*;* Abraham & Matthai, 1983; Werntz *et al.*, 1987).

The asymmetry exhibited by *H. sapiens* is not unique compared to the general pattern of vertebrate and mammalian evolution. However, there are aspects of human asymmetry that *are* unique, for example the population-level trend for the preferential use of the right hand[1] and asymmetries in the structure and organisation of the brain, reflected in left hemisphere dominance for language functions. Both of these features are considered distinguishing traits of our species (e.g. Corballis, 2003). It is not the presence of asymmetry alone that makes the human brain unique (Vallortigara & Bisazza, 2002) however, rather the nature and expression of that asymmetry. At the macroscopic level, size differences between the hemispheres have been identified, with the right hemisphere tending to be larger (Wada *et al.*, 1975) and heavier (LeMay, 1976) than the left. Petalial asymmetry has also been identified (LeMay, 1976; Holloway & de la Coste-Lareymondie, 1982; Watkins *et al.*, 2001; Phillips & Sherwood, 2007). Petalias are defined as the "greater protrusion of one cerebral hemisphere relative to the other as expressed at the frontal and occipital poles of the brain" (Phillips & Sherwood, 2007: 2398). In *H. sapiens*, the dominant pattern is for a left hemisphere occipital protrusion versus a right hemisphere frontal protrusion (Holloway & de La Coste-Lareymondie, 1982) (see Figure 1.1, below).

Specific asymmetries have been identified in both the frontal and temporal lobes and are believed to be closely linked to language organisation. The work of Paul Broca (Broca, 1863) was instrumental in assigning language functions to the left hemisphere. He discovered that lesions in the inferior frontal gyrus (one of the major 'folds' of the frontal lobe, and the area that became known as 'Broca's area') resulted in a speech aphasia, but with no detriment to language comprehension, leading Broca to conclude that this region of the frontal lobe was responsible for speech production. Later in the 19th century, Carl Wernicke challenged the assumption that there was only one centre for language in the left hemisphere (Wernicke, 1874). He described an aphasia caused by damage to an area of the temporal lobe in the language dominant hemisphere, most commonly the left hemisphere. Damage to

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[1] In addition to 'handedness', modern humans also exhibit 'footedness', with approximately 80% of individuals showing a right-foot preference (Coren & Porac, 1981; Carey *et al.*, 2001; McManus, 2002). Research into 'footedness' is far less extensive than that of handedness (Peters, 1988), and there is ongoing discussion regarding the nature of the inter-relationship between hand preference and foot preference (Peters, 1988; Berdel Martin & Machado, 2005).

this area (subsequently named the ‘Wernicke’s area’) led to an aphasia quite different to that described by Broca. There was no associated motor paralysis, although the content of the patient’s speech would be disorganised and nonsensical. In addition, despite no discernible hearing defects, the patient was unable to understand or repeat what was said to him/her. Wernicke proposed that this area of the temporal lobe is involved in the comprehension of language and works in parallel with the Broca’s area, the two areas being connected by a neural pathway known as the arcuate fasciculus (Kolb & Whishaw, 1996) (see Figure 1.2, below). Together, this research led to the left hemisphere being considered as the ‘language hemisphere’.

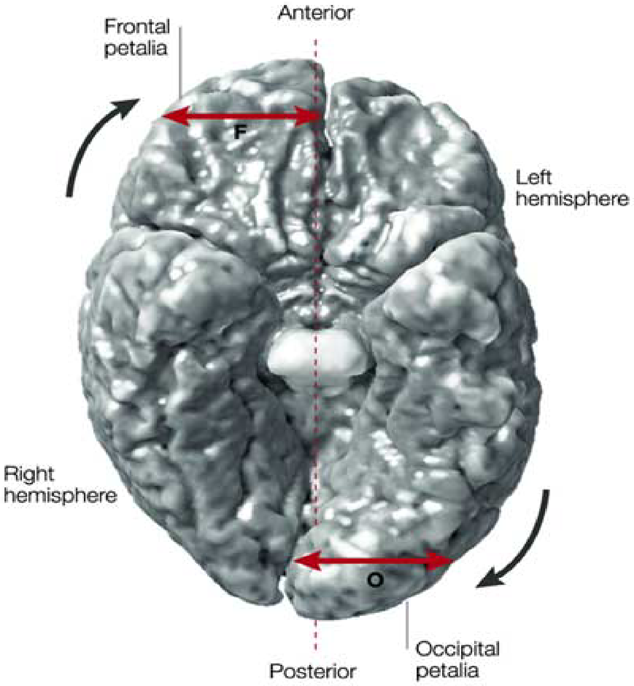


Figure 1.1. A representation of petalial asymmetry in the frontal lobe (F) and occipital lobe (O) of the modern human brain. Taken from Toga & Thompson (2003).

These functional asymmetries between the hemispheres are also reflected in related structural asymmetries. For example, the Sylvian fissure (also known as the lateral sulcus), which separates the frontal and temporal lobes and extends through both the Broca’s and Wernicke’s areas, has been found to be asymmetric in terms of the steepness of its slope, being gentler in the left hemisphere than in the right hemisphere (Geschwind & Levitsky, 1968; Toga & Thompson, 2003). The degree of slope of the Sylvian fissure is negatively correlated with the volume of the planum temporale (LeMay, 1976; Toga & Thompson, 2003), which is one of the key temporal lobe components of the Wernicke’s area (Kolb & Whishaw, 1996). Additionally, certain features of the planum temporale (PT) also display asymmetry, such as the volume of the PT, which has been found to be greater in the left hemisphere relative to the right (Toga & Thompson, 2003).

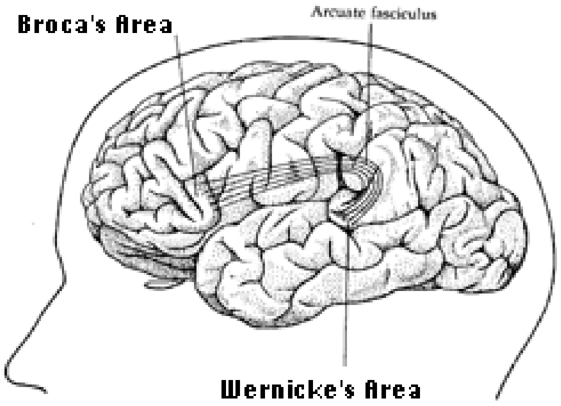


Figure 1.2. A representation of the left hemisphere of the modern human brain, with the regions of the Broca's area, Wernicke's area and arcuate fasciculus highlighted. Accessed at www.indiana.edu/~primate/brain.html.

The unique nature of handedness and language in modern humans remains a source of fascination for researchers, especially their evolutionary origins in our hominin ancestors. Language capabilities leave little trace in the fossil record and as such are a difficult topic to study. Handedness leaves a much clearer skeletal and archaeological signature and therefore lends itself more readily to scrutiny. It has been proposed that handedness and language share not only a neurological link but also a co-evolutionary origin (e.g. Falk, 1980; MacNeilage *et al.*, 1987; Crow, 1998; McManus, 1999; Corballis, 2003), suggesting that an understanding of the evolution and development of hand preference in humans could also inform regarding the development of language skills. Whether or not this is possible, the way in which hands were used by hominins has a significant bearing on our understanding of the manufacture and use of lithic technologies and material culture. The hands and handedness, therefore, remain an important part of our modern identity and a component of our evolutionary history. The following sections will explore the nature and expression of human handedness, and will address the evidence for hand preference in both hominins and non-human primates, in order to shed light on the evolution of this distinct facet of human behaviour.

1.3.1. Human hand preference

'Handedness' refers to the tendency to preferentially and predominantly use one hand for all tasks. Handedness can be considered as not only a preference for the use of one hand over the other, but also increased skill in the use of the preferred hand (Steele, 2000a). Handedness is considered to be unique to modern humans from the observation that approximately 90% of individuals across all groups studied have shown a right-hand dominance (Marchant *et al.*, 1995). It is the ubiquity of this trait across all human societies that has made handedness of such interest to researchers, particularly in light of the proposed links between laterality of hand function and language capabilities (e.g. Crow, 1998;

McManus, 1999; Corballis, 2003). For these reasons, the term ‘handedness’ shall subsequently be used only to refer to the modern human condition of population-level right-hand dominance. Preferential use of one hand over another in other species shall be referred to as ‘hand preference’ unless it can be proven to be similar to hand use seen in modern humans.

The developmental origins of handedness are uncertain, but a prenatal emergence of hand preference has been proposed. Hepper *et al.* (1990) used ultrasound to ascertain the hand preference of 224 foetuses engaged in thumb-sucking behaviour. They found a significant right-hand preference for thumb-sucking, with 95% of foetuses sucking the right thumb. Butterworth & Hopkins (1993) found that, in a group spanning an age range of neonate to 3 months, there was a hand bias towards the right-side in 60 to 80% of subjects, compared to 15 to 20% bias towards the use of the left hand. Shafer (1993) also supports the presence of a hand preference in early childhood. In her study of 28 children aged two years to five years, she found that 93% of subjects showed a right hand preference, compared to only 3.5% of subjects with a left hand preference.

In addition, there is some skeletal evidence to suggest that a preference for the use of the right hand is present early in life. Steele & Mays (1995) found that, in the infant and juvenile skeletons from the medieval cemetery site at Wharram Percy, Yorkshire, while there was a trend for the left humerus to be longer than the right humerus in a sample of perinatal infants, right arm bones were found to be longer than those of the left arm in the larger juvenile sample (ranging from less than 2 years of age to 18 years old). However, the right-side dominance is not as strong in the juvenile sample as that found in the Wharram Percy adult sample. The authors take this to indicate the development of a right-arm preference in this sample from birth to adulthood, resulting from the cumulative effect of asymmetric mechanical loading over time.

A number of theories have been proposed to explain why modern humans display handedness (Steele & Uomini, 2005). These theories range from the asymmetric effects of life-long mechanical loading favouring the right arm (e.g. Steele & Mays, 1995) to those which consider left-handedness to be the result of a pathological process (e.g. Geschwind & Galaburda, 1987, but see Searleman *et al.*, 1989 for critique of this theory). The observation that handedness appears, to some degree, to run in families (Carter-Saltzman, 1980; McManus, 1991; McManus & Bryden, 1992) has led researchers to explore the extent to which this trait is genetically determined. The main proponents of this position have been Annett (1972, 2002) and McManus (1985a,b). Annett’s ‘right-shift’ (RS) theory works on the assumption that hand preference is unimodally distributed within a population (i.e. there is a continuum of hand skill). The presence of a RS+ phenotype results in a shift towards right hand skill preference, with the RS- phenotype resulting in the absence of a shift to the right in terms of skill. RS+ is the dominant form, so only a combination of RS-/RS- will lead to the RS- phenotype. The McManus ‘symmetric bimodal’ model is similar, but presumes a bimodal distribution of hand preference, with few truly ambidextrous individuals. In this model there are two alleles, D (Dextral) and C (Chance). The presence of DD will always lead to a right-hand preference, with CC resulting in an equal chance of left- or right-hand preference. The presence of DC will lead to a left-hand preference in 25% of individuals. McManus suggests this model as an explanation for the general discordance found in studies of monozygotic and dizygotic twin handedness (e.g. McManus & Bryden, 1992), with twins often exhibiting different handedness. In the McManus model each CC or DC twin has the same chance of being either left-or right-handed. Both the Annett and McManus models agree that one genotype is not responsible for handedness, but results in a predisposition towards a right-hand preference.

Despite the number of studies citing the 90% right-hand preference to 10% left-hand preference ratio in humans, these proportions may be best considered average values, with a number of meta-analyses suggesting that proportions of left-handedness vary across samples. Hécaen & de Ajuriaguerra (1964) found reported percentages of left-handedness ranging from 1% to as much as 30% in some populations. This finding was later supported by Marchant & McGrew (1998), McManus (1991) and Faurie *et al.* (2005). McManus’ meta-analysis found variation in left-handedness from 1.5% to approximately 20% across 88 studies. While McManus (1991) suggests that small sample sizes and age effects have led to differences in the proportion of left-handedness found in these studies, Marchant & McGrew (1998) support the notion that methodological inconsistencies across these studies account for the variation reported.

There is also evidence of significant spatial variation in the proportions of left-handedness, with a number of studies identifying clear geographical variability in proportions of left-handedness (Harris, 1990; Connolly & Bishop, 1992; Perelle & Erhman, 1994; Viggiano *et al.*, 2001; Fagard & Dahmen, 2004; Coudé *et al.*, 2006; Raymond & Pontier, 2004; Greenwood *et al.*, 2007; Leask & Beaton, 2007). As might be expected, these studies vary widely in aspects of experimental design, sample profile, methodology and analysis. This affects the comparability of these studies, making the true degree of geographical variation in handedness difficult to isolate. To address some of these problems Raymond & Pontier (2004) conducted a meta-analysis of studies containing hand preference for throwing and hammering activities (which are likely to be present across cultures and indeed, across species) and found clear variation between the 14 countries represented in the data in terms of the proportion of left-handedness for throwing and hammering. This supports the presence of true geographical variation in handedness proportions, most likely representative of cultural differences between the samples studied. Anecdotal evidence has previously indicated that cultural biases may have historically reduced the proportion of left-handers in certain groups (McManus, 2002), which has gained support from Porac *et al.* (1980) who suggest that an observed temporal increase in left hand preference for writing in their study is likely to have come about from a reduction in the practice of forcing young left-handed children to write with their right hand. However, Raymond & Pontier (2004) also identified significant handedness variation within some countries, suggesting that it may not be possible to entirely exclude methodological effects from such analyses.

Hand preference has been most commonly determined through self-reporting questionnaires such as the Edinburgh Handedness Inventory (Oldfield, 1971) and the Waterloo Handedness Questionnaire (Steenhuis & Bryden, 1989). Subjects specify their hand preference for a series of skilled and unskilled unimanual tasks to give an overall composite hand preference. Concerns have been raised about the utility of handedness questionnaires (McManus, 1999) as these questionnaires are subjective in their nature, assuming a limited range of hand functions (e.g. hand-writing), all of which are given equal weighting. Hand skill can be measured through a number of means, such as the Annett pegboard task (1970) and the more complex grooved pegboard task (Bryden & Roy, 2005). These tasks measure the time it takes to move pegs between holes in a board. The Wathand Box Test (Bryden *et al.*, 2000) is more similar to the hand preference questionnaires, with subjects being scored for the hand they use to perform a series of unimanual tasks. Finger tapping and grip strength tests can be used to measure muscular aspects of hand use and preference.

With so many measures of hand preference and skill available, our understanding of handedness can become confused. A number of researchers have addressed these methodological issues by combining approaches. Some researchers (Peters, 1998; Corey *et al.*, 2001; Brown *et al.*, 2004) have attempted to link measures of hand skill and hand preference by using underlying factors that are the same for both variables and are less ‘specific’, such as musculature, motor control and task experience. Brown *et al.* (2006) found that the best predictive models of handedness were those that combined preference measures and performance measures reflecting different aspects of motor performance. As might perhaps be expected, an inclusive approach, incorporating many aspects of hand function, is likely to be the best and most accurate way to assess hand preference. Other researchers (Marchant *et al.*, 1995; Marchant & McGrew, 1998) propose the adoption of a more ethological approach to assessing handedness, placing more emphasis on how the hands are used in everyday life. This approach is based on observations of not just object manipulation but also more spontaneous activities such as communication and gesturing. Both unimanual and bimanual activities are recorded.

In conclusion, although there is clear variability in the distribution of handedness between groups, the underlying foundation of right-hand preference remains strong. What remains unclear however, is the extent to which methodological factors mask, or indeed exaggerate, the true nature of variation in hand preference. Longitudinal studies of handedness (e.g. Porac *et al.*, 1980) and those of preliterate societies (Marchant *et al.*, 1995; Faurie *et al.*, 2005) suggest that there is a strong cultural component to handedness which requires further investigation in order to better understand the distribution of handedness and the ways in which its expression can be influenced. These observations have implications for the evolution of hand use and preference in the genus *Homo* and how we interpret data from extinct species. The study of great ape hand preference has the potential to be particularly illuminating in this respect as the cultural factors which appear to influence hand use in humans can be assumed to be reduced in these species. The following section will explore the expression of hand preference in our closest great ape relatives, to assess the extent to which hand preference in great apes mirrors that seen in modern humans and what can therefore be inferred about hand use in hominins.

1.3.2. Great ape hand preference

As our closest living relatives, the great apes can provide insight into the evolutionary development of hand preference in our ancestors. If a population-level hand preference akin to what is found in modern humans can be identified in non-human primates then this will point to an early evolutionary origin for the lateralisation of limb use. This will also have implications for the evolutionary coupling of handedness with language capabilities. If handedness can be identified outside the human genus then this would cast doubt on the notion that language capabilities (which are not present in non-human primates) and handedness co-evolved over the course of human evolution. However, if no population-level hand preference is found in great apes attention will then focus on extinct members of the genus *Homo* to provide answers to the questions of handedness origins. This section outlines the evidence regarding great ape handedness, in what remains a controversial area of research. This research focuses on studies of live subjects. Studies relating to skeletal asymmetry in great apes are considered in section 2.2.4.

Chimpanzees (*Pan troglodytes*) have been the most frequent focus of research into great ape hand preference (Sarringhaus *et al.*, 2005), although there is no clear consensus on the exact nature of hand preference in this species. The extensive research carried out on chimpanzee hand preference has identified a number of factors that appear to influence the expression of hand preference in chimpanzees (and great apes more generally) such as posture, tool-use and task complexity, in addition to aspects of data analysis and methodology (Cashmore *et al.*, 2008). The following sections will focus on what appears to be one of the main factors producing an observable effect on great ape hand preference distribution, namely the research setting of a study, as there appears to be a difference between studies of captive apes versus those observed in a natural context.

One of the first quantitative studies of hand preference in a captive sample was carried out by Finch (1941). Hand preference for obtaining suspended food was rated for thirty chimpanzees across 800 trials. Overall, 30% subjects showed a right hand preference, 30% showed a left hand preference, and 40% showed ‘ambiguous’ hand use, suggesting an even distribution of left- and right-hand preference.

More recent studies of captive chimpanzees have continued to identify this rather mixed pattern of individual-level hand preference, with studies indicating both left- and right-hand preferent individuals (e.g. Hopkins, 1993, 1994; Hopkins & Leavens, 1998; Hopkins *et al*., 2002, 2003, 2005; Hopkins & Cantalupo, 2005). Perhaps the most intriguing finding from these studies is the presence in these groups of what has been proposed to be a population-level hand preference or 'handedness' of the type seen in modern human groups

The majority of studies of wild chimpanzees have also identified individual lateralisation in tasks involving tool-use such as nut-cracking, termite fishing and fruit pounding, with individuals displaying either left- or right-hand preferences (e.g. Boesch, 1991; Sugiyama *et al.*, 1993; McGrew & Marchant, 1996, 1997; McGrew *et al.*, 1999). While this trend is often statistically significant for tasks involving tool-use, the same pattern is not identified for food processing tasks (Fletcher & Weghorst, 2005; Marchant & McGrew, 2007) where the general trend is towards ambilaterality (i.e. no statistically significant differences between the left and right hands) (e.g. Marchant & McGrew, 1996; McGrew & Marchant, 2001). Marchant & McGrew (2007) however, report that the majority of chimpanzees in their study sample from the Mahale Mountains National Park were ambilateral for ant fishing, which requires tool-use. The authors propose that the reason for this trend is the arboreal nature of the task, which requires one hand to be used for postural support during fishing, with hands often being swapped due to fatigue. Despite the presence of individual lateralisation in wild chimpanzee groups there has been little evidence to suggest a group-level or population-level bias towards hand preference similar to that identified in captive samples, with most studies failing to identify directional hand preference extending to the whole group (e.g. Marchant & McGrew, 1996; McGrew & Marchant, 1997, 2001; McGrew *et al.*, 1999; Fletcher & Weghorst, 2005).

In contrast to the majority of studies on wild chimpanzees, both Humle & Matsuzawa (2008) and Lonsdorf & Hopkins (2005) have identified what they determined to be population-level handedness in their wild samples. Lonsdorf & Hopkins (2005) studied a sample of 17 chimpanzees from the Gombe National Park, Tanzania and for termite-fishing they found that 12 out of the 17 individuals displayed a left-hand preference, which constituted a statistically significant population-level effect. Lonsdorf & Hopkins suggest that previous failures to identify population-level trends in wild subjects are a result of small sample sizes in studies of this nature. Interestingly, Lonsdorf & Hopkins (2005) also suggest that the direction of hand preference is influenced by the nature of the task, e.g. termite-fishing elicits left-hand preferences, while nut-cracking and wadge-dipping appear to elicit right-hand preferences, which the authors suggest could be a result of a combination of genetic hereditability of hand preferences, plus motor and cognitive differences between the tasks. Humle & Matsuzawa (2008) also find evidence for a population-level hand preference in their sample from Bossou, Guinea. While this study focused on tool-using activities (ant-dipping, algae-scooping, pestle-pounding and nut-cracking), the authors found that the general trend was towards right-hand dominance for all tasks. Both the results of these studies, plus those from captive chimpanzee studies indicate that tool-using behaviours are those most likely to elicit a strong individual hand preference, or indeed a group-level hand preference. This observation mirrors the finding of an ethological study of modern human hand use (Marchant *et al.*, 1995), which only identified strong right-handedness for unimanual tool-using tasks. Consensus is lacking however, regarding the direction of such lateralisation, suggesting that the trend is still a weak one. The term ‘population-level handedness’ should be used with caution, with the phrase ‘group-level hand preference’ perhaps more appropriate for discussion of trends of hand use in non-human primate species. In addition, further exploration of the difference in lateralisation between tool-using and non-tool-using tasks is necessary in order to better understand the emergence of handedness in the human genus.

The distribution of hand preference has also been studied in gorillas, although without the same focus on tool use seen in chimpanzees. Byrne & Byrne (1991) examined hand preference for foliage processing in a group of wild mountain gorillas and found that subjects displayed hand preferences for certain tasks, but no population-level trends were identified. Shafer (1993) investigated hand preference for various manual activities (such as eating, gesturing, throwing and touching self or others) in 47 captive gorillas from five American zoos. Shafer found that 72% of subjects showed a right hand preference, compared to 26% with a left hand preference. Interestingly, only manipulation of small objects elicited lateralisation in every subject. These results suggest a population bias for handedness in this particular gorilla group, an unusual finding in this primate species. Shafer speculates that the amount of time spent by gorillas in a bipedal position may influence the degree of lateralisation in this group, although McGrew & Marchant’s (1997) observation that captivity (and therefore increased human contact) may increase right hand preferences in primates must also be considered as a possible explanation for this data until these results can be replicated. Vauclair & Fagot (1993) have also studied hand preference in captive gorillas (*Gorilla gorilla*), this time for food reaching and moving a plastic sliding panel to access food items. While there was an equal distribution of hand preference for the reaching task (3 with a right preference, 3 with a left preference and 4 with no preference), there was a significance population-level left hand preference for the panel-sliding task. Caution must be exercised when interpreting results from such a small sample of captive subjects, where the handedness of the experimenters and those involved with housing the ape has not been taken into consideration. These results do however raise the interesting possibility of population-level hand preference being present in great ape groups for certain complex manual activities. What is unclear at this stage is whether or not the results from these studies reflect a true population-level hand preference in these groups of gorillas, or more simply an artefact of experimental design.

Research on hand preference in orangutans (*Pongo pygmaeus*) has been limited compared to other great ape species and has provided mixed results on the nature of lateralisation in this genus (Hopkins, 1993; Hopkins *et al.*, 2003; O'Malley & McGrew, 2006). Hand preference for eating (one-handed and two-handed) and tool manufacture/modification was studied in a group of eight captive orangutans (O'Malley & McGrew, 2006). No population-level lateralisation was found for any of the tasks observed (including the additional use of the feet and mouth in these tasks) although significant hand preference was observed in both the eating and tool-based tasks for less than half of the subjects. When data from the various tasks were pooled, three subjects were found to have a left-hand preference and three subjects exhibited a right-hand preference. These results support conclusions drawn from other great ape studies, namely that while individual-level lateralisation is common, there is no strong evidence for population-level hand preference.

Research into hand preference in our closest primate relatives presents a complex picture which can be difficult to interpret. Individuals differ on the level of lateralisation they display, which may in part be related to the task used to elicit hand preference. There also appear to be clear differences, both between and within species on whether or not 'population-level' hand preference is present. This finding appears to be very much influenced by methodological and statistical factors, and in chimpanzees in particular, setting (i.e. whether captive or wild subjects are used) seems to be one of the largest contributing factors. Where there seems to be consensus, however, is in the notion of individual lateralisation, with most studies identifying hand preference for individual subjects. This is clearest for tool-use. In an evolutionary context these results can be taken to support the observation that population-level right-handedness is unique to *Homo sapiens* and that this trait emerged within the human genus, although individual, task-specific hand preference is likely to have been a feature found in the last common ancestor of chimpanzees and humans.

1.3.3. Hominin hand preference

While the measuring of hand preference and hand use in modern human groups is relatively straightforward, section 1.3.2 has shown that this is not the case for non-human primate groups, and it is by no means clear to what extent hand preference is present in great apes. More comparative work is required to clarify the situation. In comparison to the situation in extant populations, identifying hand preference in extinct species is particularly difficult. This is in part due to the paucity of material available for study and the necessity of using skeletal material and material culture (such as stone tools and parietal art). Despite these limitations, attempts have been made to assess hand preference in extinct hominin species. The following section outlines the available evidence (both from skeletal and material cultural sources) pertaining to hominin hand preference and discusses some of the problems with attempting to identify this trait in extinct populations.

1.3.3.1. Skeletal evidence for hominin hand preference

The African Plio-Pleistocene provides sparse skeletal evidence for the presence of hominin hand preference. While the functional anatomy of the *Australopithecus* hand has been studied in detail (e.g. Bush *et al.*, 1982; Alba *et al.*, 2003; Ricklan, 1987; Stern & Susman, 1983; Susman, 1994, 1998; Marzke, 1997), hand preference (and upper limb asymmetry in general) in this genus has seldom been addressed. As is the case throughout the fossil record, small sample sizes and fragmentary remains hamper the study of asymmetry. Postcranial remains attributed to *Australopithecus afarensis* (AL 483-1) contain a pair of 2nd metacarpals (Drapeau *et al.*, 2005). These metacarpals are extremely well preserved and provide a rare opportunity to collect metric data. Comparison of measurements of metacarpal length and midshaft, distal and proximal diameters found no consistent pattern of asymmetry between the metacarpals, with a combination of right-side dominant, left-side dominant and symmetrical dimensions identified. The degree of asymmetry between the left and right metacarpals was not excessive, ranging from 0.3% to 4.5%. Although this comparison is limited it does not support the presence of clear unidirectional asymmetry in the 2nd metacarpal. At this stage it would be unwise to extrapolate to the rest of the upper limb in this individual, or other members of *A. afarensis*.

The largest collection of hand bones from this period comes from Hadar in Ethiopia and has been assigned to *A. afarensis* (Bush *et al.*, 1982), however, as this collection comprises at least 5 individuals (two of which are juvenile) and the bones were not found in anatomical association, no assessment of asymmetry was undertaken. Alba *et al.* (2003) have reanalysed the Hadar material and compiled a composite *A. afarensis* hand from the material, believing the bones likely to have come from a single individual. It has therefore not been possible to identify pairs of bones from which to make an assessment of asymmetry. It is, however, possible to see that reconstructions of this nature have the potential to allow future asymmetry calculations to be attempted, if allowances were made for measurement error. With regards to the upper limb, the AL 288-1 *A. afarensis* skeleton ("Lucy") retains fragmentary humeri and ulnae (Senut, 1981), although the asymmetry in these bones has not been studied to date.

The remarkably intact Stw 573 *Australopithecus* (potentially *A. africanus*) skeleton found at Sterkfontein, and dating to around 3.3 million years, appears to have a complete left arm and hand (Clarke, 1999) and adds renewed vigour to the search for the signature of hand preference in the hominin fossil record. At present, this specimen is in the process of being extracted from the Sterkfontein breccia, but Clarke believes that a complete right upper limb will also be found. If this is the case then Stw 573 will provide an unparalleled opportunity not only to study the *Australopithecus* arm as a complete functional unit, but also to allow comparisons of upper limb bilateral asymmetry within the individual.

There is a noticeable lack of postcranial material associated with the species proposed to be the first tool-makers (e.g. Haeusler & McHenry, 2007). The discovery of the OH 7 (*Homo habilis*) fossils in 1960 (Leakey *et al.*, 1964) provided the first instance of a set of hominin hand bones found in the same context as early Oldowan stone tools. Such was the importance of the association between the hand bones and the tools that the name given to this newly identified species, *H. habilis,* reflected how the role of stone tool-use was perceived as integral to the evolution of the hominin lineage. Napier (1962) reported the presence of hand bones from a juvenile and an adult from Bed I at Olduvai Gorge as being part of this new species of *Homo*. Although it was not possible to make attributions of hand preference to such a small sample, Napier highlighted the very modern morphology of the bones, suggesting that a modern pattern of hand-use would also have been likely in the new *H. habilis* species.

In contrast to the fragmentary nature of most early *Homo* remains, the relatively complete skeleton of the approximately 1.6 million year old KNM-WT 15000 *Homo ergaster* specimen (also known as the Nariokotome Boy) provides a rare opportunity to assess upper limb bilateral asymmetry in this species. KNM-WT 15000 is a juvenile skeleton (the exact age at death has been debated but has been suggested to be approximately 8 years [Dean & Smith, 2009; Dean & Lucas, in press]), but the state of preservation is such that asymmetry could be assessed in a number of bones (Walker & Leakey, 1993). Damage to the left scapula and the absence of a left humerus make asymmetry estimations impossible for these bones. The preservation of the clavicles is much better however, and a virtually complete pair exists. While there is very little difference in the lengths of the bones (right = 130.5mm, left = 130.4mm), there is a noticeable difference in the groove that houses the deltoid attachment (right = 22.0mm x 3.8mm, left = 17.0mm x 3.0mm). This has led Walker & Leakey (1993) to conclude that the Nariokotome Boy may have been right-handed. There are also faint markers which indicate the presence of attachments for the *pectoralis major* and *subclavius* muscles and the costoclavicular ligament, with these appearing to be more developed on the left than the right.

Aside from the missing (unfused) epiphyses, both ulnae of KNM-WT 15000 are also complete (Walker & Leakey, 1993). A bilateral difference exists in the lengths of the preserved bones. The right ulna (260.3mm) is longer than the left ulna (257.2mm), although the missing epiphyses must also be taken into consideration. Unfortunately, few hand bones have been recovered for the Nariokotome Boy, but Walker & Leakey (*ibid.*) have identified what they believe to be first metacarpals once again missing the unfused epiphyses. The left shaft is longer than the right shaft in this instance (right = 34.7mm, left = 35.2mm). The authors raise concerns with the accurate identification of these bones as first metacarpals due to their poor preservation and also with attributing these bones to KNM-WT 15000 due to the presence of other juvenile mammal material in the locale of these specimens. These measurements should therefore be treated with caution.

Despite the small number of comparable measurements available, the trend for the Nariokotome Boy is for the right upper limb to be bigger than the left upper limb and, for the clavicles at least, for muscle development to be greater on the right side. Taken together this suggests that this skeleton exhibited a general right arm preference. The juvenile status of this specimen must of course be taken into consideration when drawing conclusions about its asymmetry, but this example shows that assessments of upper limb bilateral asymmetry are possible in fragmentary fossil hominin remains.

The 1.77 million year old site of Dmanisi, Georgia is well-known for its collection of cranial and mandibular material representing one of the first movements of *Homo* out of Africa (Gabunia & Vekua, 1995; Gabunia *et al.*, 2000; Vekua *et al.*, 2002; Lordkipanidze *et al.*, 2005, 2006; Rightmire *et al.*, 2006). Postcranial material has also been recovered from the site (Lordkipanidze *et al.*, 2007). While few hand bones have been recovered, a pair of adult clavicles (missing the sternal and acromial ends) and a pair of subadult humeri (not complete) have been found. While these bones must be interpreted with caution due to their incomplete state and subadult status (for the humeri), no clear pattern of side dominance was identified in their metric properties.

The Sierra de Atapuerca in Spain has produced an extensive collective of hominin fossils from the Early and Middle Pleistocene of Europe (e.g. Arsuaga *et al.*, 1990; Carbonell *et al.*, 1995; Bérmudez de Castro *et al.*, 1997; Arsuaga *et al.*, 1999; Carretero *et al.*, 1999). The Lower Pleistocene site of Gran Dolina has produced fossils attributed to *Homo antecessor*, believed by some to be the last common ancestor of *Homo neanderthalensis* and *Homo sapiens* (e.g. Bérmudez de Castro *et al.*, 1997), while the Middle Pleistocene site of Sima de los Huesos at Atapuerca has produced large amounts of postcranial material belonging to *Homo heidelbergensis* (Carretero *et al.*, 1997). Despite the wealth of skeletal material, a lack of matched pairs of bones makes measurements of asymmetry unreliable at present.

With the appearance of *Homo neanderthalensis* larger amounts of preserved upper limb material begin to appear in the fossil record. Trinkaus *et al.* (1994) quantified the asymmetries in the paired humeri of eight Neanderthal individuals: La Chapelle 1, La Ferrassie 1, Neandertal 1, La Quina 5, Spy 2, Shanidar 1, Tabun 1, and Kebara 2 using humeral length, distal articular breadth, cortical and medullary areas. Trinkaus and colleagues found a right-side dominance for all individuals except Shanidar 1, although this specimen has a pathological right arm and associated disuse atrophy on the left arm. The arms of Neandertal 1 also show pathologies in the form of left arm lesions which may have partly contributed to the strong rightward asymmetry in this pair of humeri. A possible left-arm trauma can be attributed to a third fossil, La Quina 5, despite the absence of visible lesions. The remaining five individuals are considered as having non-pathological asymmetries, indicating they were subjected throughout their lifetimes to differential loading patterns which favoured the right arm

(Trinkaus *et al.*, 1994). The Neanderthal specimen from Le Régourdou also supports this trend for right-side dominance (Vandermeersch & Trinkaus, 1995), showing asymmetry in diaphyseal diameter in the clavicle and humerus plus medio-lateral diaphysis diameter for the ulna and radius. There is also a right-side dominance for radial neck diameter, proximal clavicular curvature, radial interosseus crest development, and ulnar radial facet height. These data support a general trend for right-side dominance in Neanderthals (Steele & Uomini, 2005).

This trend towards right-side dominant asymmetry is further evidenced in skeletal material from Upper Palaeolithic *H. sapiens*. In a large sample of skeletons from across Europe, North Africa and Asia, representing the early to late Upper Palaeolithic, Shackelford (2007) found a clear right-side dominance in humerus cross-sectional properties across all samples. Shackelford noted variation in the magnitude of asymmetry, both temporally and geographically (see section 2.2.2), suggesting that by the Upper Palaeolithic there may have been behavioural variability between groups of individuals. With larger samples of individuals it may be possible to identify such trends in the Neanderthals although their geographical range was reduced relative to early *H. sapiens*. A right-side dominant asymmetry has also been identified in humeral retroversion related to preference for using the right arm for throwing in a sample of Middle to Upper Palaeolithic *H. sapiens* from Europe (Rhodes & Churchill, 2009). When these data were compared with a small (N = 3) sample of Neanderthals it was found that the Neanderthals displayed less bilateral asymmetry in humeral retroversion relative to the anatomically modern humans. The authors tentatively conclude that this suggests a behavioural difference between the species with *H. sapiens* engaging in more habitual throwing behaviours than the Neanderthals.

Recent finds such as the *Homo floresiensis* specimens from the island of Flores, Indonesia (Brown *et al.*, 2004; Morwood *et al.*, 2005) provide new opportunities to study hand preference in hominin evolution. Research undertaken by Larson *et al.* (2007) on the *H. floresiensis* shoulder and upper arm and by Tocheri *et al.* (2007) on the wrist bones have confirmed the unusual and distinctly primitive nature of the upper arm, posing interesting questions about its tool-making capabilities in this species and the relationship between morphology and function in the wrist, suggesting that “the earliest hominins to use and make stone tools retained primitive hominin wrist morphology” (2007: 1745). To date only a few hand bones have been found belonging to this species (Morwood *et al.*, 2005) making the identification of asymmetry impossible at this stage. It can be hoped, however, that with further excavations on Flores a larger sample will eventually be available for study.

Hand preference in hominins can also be inferred from dental material. Bermúdez de Castro *et al.* (1988) identified striations on incisor and canine teeth which they attributed to the use of tools by Middle Pleistocene hominins. From striations on the buccal surface of 19 teeth found at the Atapuerca site of Sima de los Huesos, Bermúdez de Castro *et al.* (*ibid*.) inferred that these hominins were predominantly right-handed, as the location and orientation of the striations suggested that material of some nature was being held between the teeth and cut or scraped with the right hand. This assertion was further supported by experimental replication of this activity which identified the same striation patterns as found on the Sima de los Huesos teeth (Bermúdez de Castro *et al*., *ibid.*). A study by Fox & Frayer (1997) studied the teeth of Neanderthal individuals from Krapina and found a similar right-handed pattern of non-dietary striations in six out of seven of the individuals who showed a side preference (and 90% of all documented cases they reviewed). In a control sample, the authors noted striations of a similar morphology to those found in the Neanderthal teeth in a sample of bear teeth from the Krapina site. They found no particular pattern of side dominance in the bear teeth sample, suggesting that, in fact, the hominin teeth striations were non-dietary in origin. Striations purportedly made by flint tools have also been described by Pitts & Roberts (1997) on two teeth believed to have come from the same individual (attributed to *H. heidelbergensis*) from the site of Boxgrove, West Sussex. The striations on teeth were interpreted as being made by a flint implement being held in the right hand, similar to that seen at Atapuerca and Krapina.

Bax & Ungar (1999) also urge caution when interpreting patterns of tooth striations. Their study compared striations on the teeth of 66 individuals from modern populations where subsistence strategy was known and found no relationship between striation orientation and hand preference (although it should be noted that the authors assumed a right-hand dominance for the individuals represented in the study). The lack of a significant relationship was also evidenced for the modern populations where tools were known to be scraped along the incisors. The results led Bax & Ungar (*ibid*.) to question the link between hand-use and tooth striations unless the hominins studied were using their teeth in different ways to modern humans as represented in their study.

This section has shown that there are clear problems with identifying hand preference in the hominin skeletal record. One of the main problems is the obvious paucity of material available for study. Many species are represented by few and fragmentary hand bones, and for some species (e.g. *Homo rudolfensis*) there appears to be no hand bones at all (or indeed upper limb bones in general). During excavation, if it cannot be determined that all bones come from the individual being studied, the ability to determine asymmetry is affected. When suitable material is available for study, the lack of paired bones makes an assessment of individual asymmetry challenging. For the hand bones especially, ordering and siding of bones can prove problematic, particularly for the phalanges (Case & Heilman, 2006). Despite this there is potential for studying the development of asymmetric hand use over the course of hominin evolution. With the current available material, a right-side dominance in metric and muscle properties has been shown for the Neanderthals. The evidence for hand preferences is less clear for the earliest members of the human genus, although it can be tentatively concluded from the evidence that a right-side dominance was present in *Homo* prior to the emergence of the Neanderthals. When this move towards a right-hand preference occurred is unclear based on the skeletal evidence alone.

1.3.3.2. Lithic evidence for hominin hand preference

Evidence of material culture is particularly abundant in the archaeological record of hominin evolution, and is most commonly represented by stone tools. Material culture represents the actions of individuals and perhaps more importantly groups of individuals. As bilateral use of the hands is necessary for the production of material cultures, analysis of artefacts and artworks provides an indirect means of identifying lateralisation and hand preference in the archaeological record (Steele & Uomini, 2005). Of all the available lines of material culture evidence, the remnants of stone tool manufacture and use are by far the most prevalent. Despite this, studies of hand preference in the manufacture and use of tools is not common and conclusions have been drawn from a relatively small number of studies. The most commonly cited study of hand preference in stone tool manufacture comes from Toth (1985). In his study, Toth uses the orientation of cortex on flakes detached from a core as an indicator of the hand preference of the knapper. This is based on the assumption that a right-handed knapper will rotate a core clockwise (anti-clockwise for a left-handed knapper) and this will be reflected in the position of the cortex remaining on detached flakes. This, of course, will only work for those flakes taken from the outer surface of the core. Toth's experimental findings have been interpreted as supporting the presence of preferential right-handed knapping at the Lower Pleistocene site of Koobi Fora, Kenya (1.9 – 1.4 ma) and the Middle Pleistocene site of Ambrona, Spain (0.4 – 0.3 ma).

Although widely cited, Toth's methodology has attracted criticism. Analysing the flakes produced by a group of modern-day knappers, Pobiner (1999) found that handedness as indicated by flakes did not necessarily correspond with the hand preferences reported by the knapper. When flakes from multiple knapping sessions were compared, it was found that hand preference (as identified from the flakes) changed from session to session for some knappers. Two knappers produced equal amounts of right- and left-handed flakes, and one of the right-handed knappers only produced left-handed flakes in certain sessions. In addition, this method does not take account of the fact that many tools are not made using the core rotation technique identified by Toth. Bifacial flaking, for example, is ignored (John McNabb, pers. comm.). The nature of these results, as well as their inconsistency, suggests that examining the orientation of cortex on flakes is unlikely to be a reliable method of assessing hand preference in the lithic record.

In response to some of the problems found in Toth (1985), Rugg & Mullane (2001) outlined a methodology that uses the degree of skew in the cone of percussion of knapped flakes to identify the hand preference of the knapper. The use of direct percussion to remove flakes for a stone core leaves identifiable traces on the core and the detached flake. The cone of percussion is, as the name suggests, a cone-shaped feature from which ripples extend, originating at the point at which the core was struck. The hypothesis tested was that hand preference would influence the direction from which the core was struck and therefore it would be possible to identify the hand preference of the individual knapping from the angle of the cone of percussion. Rugg & Mullane found that 75% of their sample could be accurately sided by this method when the hand preference of the knapper was known. Although the sample size (N = 75) was small, this methodology has potential to add to the techniques available for the analysis of hand preference in stone tool manufacture.

The identification of hand preference in tool manufacture has also been attempted through different means by Posnansky (1959) and Cornford (1986). Posnansky (1959) suggested that asymmetry in the position of the median ridge on a handaxe could be used to identify hand preference. Posnansky found that this asymmetry made the tool easier to use either in one hand or the other, and examination of a Lower Palaeolithic collection found 31% to be right-handed, 17% left-handed and 45% symmetrical (plus 7% which could not be assigned to a category). Cornford (1986) found asymmetry in long sharpening flakes at the La Cotte de St Brelade site in Jersey, presumed to have been knapped by Neanderthals. The method of producing these sharpening flakes led Cornford to suggest that asymmetry in the position of the bulbar surfaces could be used to ascertain the hand preference of the knapper. The right-side bias in the position of bulbar surface facet on the flakes in this sample suggested that between 71% and 84% of the flakes were made by right-handed people. Despite their rather cursory nature, both these studies suggest potential methods of identifying knapper and tool-user hand preference.

Taken together, the results of these studies tentatively suggest the dominance of the right hand in tool manufacture as far back as early Oldowan tools. However, the methodological and interpretative issues associated with these analyses mean that definitive statements regarding hand lateralisation in lithics manufacture cannot reasonably be made. Despite these concerns, the studies outlined above highlight a number of interesting potential avenues for further research regarding identifying handedness in the lithic record, assuming that methodological procedures are more tightly controlled.

1.3.3.3. Parietal art evidence for hominin hand preference

Parietal art (i.e. rock art), while not enjoying the same spatial or temporal distribution as hominin lithic material, provides an interesting avenue for assessing hand preference, particularly in Upper Palaeolithic populations dating back approximately 30,000 years or more (Valladas *et al.*, 2001). Representations of the hand, either as hand prints or hand stencils, are one of the most enduring and numerous of all forms in parietal art. Hand prints are created by covering the palmar surface of the hand with a paint substance and creating a ‘positive’ print of the hand on a surface. Hand stencils are created by placing the hand upon a surface and then applying pigment (either by blowing paint through a tube, spitting or using a brush) around the hand to create a 'negative' print of the hand. Hand prints can therefore be considered to represent an impression of the dominant hand, whereas the hand stencils are likely to represent an impression of the non-dominant hand, if we assume that the 'artist' needed his or her dominant hand to assist with the painting process. However, it has been suggested (Pager *et al.*, 1991) that 'positive' hand prints can feasibly be made by both the dominant or non-dominant hand, whereas the 'negative' stencils are likely to have been made with the non-dominant hand, thus leading Pager *et al.* (*ibid*.) to propose that hand prints are not a reliable indictor of hand preference.

Despite this, from the collections of hand prints/stencils where an assignment of hand use has been made, the majority suggest a right hand preference (Steele & Uomini, 2005). Gunn (1998), for example, found that the ratio of right to left handprints was 4:1 (n = 193), with a 1:4 ratio for the hand stencils (n = 3431) at the Levi Range in Central Australia. This suggests an 80% right hand dominance at these sites.

In a study of living subjects, Faurie & Raymond (2004) investigated hand preference for hand stencil creation. They found no significant difference between the numbers of right hand dominant individuals in the modern sample and the comparative Upper Palaeolithic sample. A strong correlation was also found between the hand used for holding the paint-blowing tube and the dominant hand for writing and for throwing. Together this research supports the notion that a clear right-hand preference was established in Upper Palaeolithic populations prior to the appearance of rock art in Europe.

The orientation of animals in cave paintings may also provide a means of identifying hand preferences in the Upper Palaeolithic. Pager *et al.* (1991) found that in a study of a hundred school children, all the left-handed children drew animals that faced to the right, whereas all the right-handed children studied drew their animals facing to the left. Following from these results Willcox (1959) found that between 50.6% and 62.3% of the European and African rock art studied showed animals facing to the right, i.e. consistent with being drawn by a left-handed person. Such a high percentage of apparently left-handed individuals, when compared to other lines of evidence, suggests that, unless there is a unique activity represented by the paintings, the orientation of animals in rock paintings may not be the most reliable method for assessing hand preference in these populations.

The archaeological evidence for hand preference faces similar problems to the fossil skeletal material (Cashmore *et al.*, 2008). Although stone tools are preserved in greater quantities in the archaeological record than fossil remains, their indirect link to hand-use will only allow ambiguous conclusions to be drawn. Studies of lithic and rock art material have often been based on unreliable methods (e.g. Toth, 1985), or using methods which have yet to be replicated. However, where conclusions have been drawn they support the pattern of right-side dominance found in the skeletal material.

1.4. Conclusion

Asymmetry in structure and function is crucial for the functioning of biological organisms and *Homo sapiens* is no different in this regard. However, what appears to be unique to our species is how asymmetry has manifested itself in lateralisation within the brain and perhaps more obviously, in the use of the upper limb. Although there is some variation in the exact proportions of right- and left-hand preference in modern human groups, the dominant preference for the use of the right hand is evident in humans. What remains unclear is the strength of this right-hand preference in non-human species and how, where and when this preference emerged. The research that currently exists for hand preference in humans, non-human primates and hominins embraces a wide range of research questions and methodologies and therefore it is vital to be certain that the methods of measuring hand preference are appropriate for the research questions being addressed. The concept of ‘handedness’ is ripe for revision, but before this can occur, methodological issues must first be addressed. Our understanding of this distinctive human trait is complicated somewhat by the various methods available for its measurement. To fully understand the expression of handedness and how this trait evolved, it is necessary to understand how it can be assessed and quantified and the problems inherent in these methods. This is true for modern human groups, as well as primate and fossil hominin samples. The next chapter will explore the methods used to assess upper limb preference in skeletal material and what each method has contributed to our understanding of bilateral asymmetry. In addition, issues associated with these approaches will be discussed.

Chapter 2. Measuring Asymmetry

2.1. Introduction

The previous chapter highlighted the complexity of study into handedness and asymmetry across all species, and that identification of evidence for hand preference, particularly in extinct species, is challenging at best. As indicated in the preceding chapter, isolating asymmetry in skeletal material can be achieved through analysis of various aspects of bone robusticity or alternatively through analysis of muscle attachment site development. However, while it is clear that there is no one method available for making assessments of hand preference in skeletal material, the comparability of these various methods is less clear. Within the asymmetry literature, bone robusticity (metric and geometric) and muscle marker methods are often used interchangeably, with little discussion of the congruency of these approaches. The extent to which these methods can be shown to be consistent in their determination of asymmetry will ultimately impact on our understanding of hand preference in skeletal populations. To that end, this chapter explores metric, geometric and muscle marker methods in more detail to assess what these methods can tell us about the nature of upper limb bilateral asymmetry in extinct skeletal populations. Due to the nature of the literature, the predominant focus of this research is on anatomically modern human skeletons.

2.2. Asymmetry in bone robusticity

By far the most commonly applied technique for assessing upper limb bilateral asymmetry is through the determination of left and right differences in bone size and robusticity. These differences can be measured in terms of either external, metric bone properties (such as length, diameter, circumference) or cross-sectional, geometric properties (such as cortical area, second moment of area and polar moment of area). These methods are derived from the accepted wisdom that bone responds to the mechanical stress placed upon it through a process of modelling and remodelling. Over the course of a lifetime, the bones of the skeleton are subjected to many types of stress, mainly resulting from the actions of skeletal muscles and gravitational forces. Long bones in particular are subjected to bending stresses which are transmitted top-down through the body (in terms of weight) and bottom-up from the ground. The internal structure of a long bone is therefore organised to best withstand the stresses placed upon it. During periods of mechanical stress, compact bone (i.e. the hard outer layer of bone that comprises the diaphyseal shaft) will model/remodel (i.e. deposition of new bone or removal of existing bone) to increase the strength of the bone at the point where the stress is greatest (Knight *et al.*, 2003; Marieb, 2004). For this reason, long bones tend to be thickest at the diaphyseal midpoint where bending stresses are greatest (Marieb, 2004). The principle of bone adaptation to mechanical stress is often referred to as ‘Wolff’s Law’. Further principles can also be considered to be included under this heading:

- Trabeculae (small structures that form networks that provide structure to cancellous [spongy] bone) orientate along lines of stress to provide support to the bone.
- Both mechanisms of functional adaptation are self-regulating and are initiated by mechanical stress (Pearson & Lieberman, 2004).

Certain aspects of the application of Wolff's Law have been challenged, however (Cowin, 2001; Pearson & Lieberman, 2004; Ruff *et al.*, 2006). The originality of Wolff's work has been disputed, with some researchers suggesting that the principles that are collected under the banner of 'Wolff's Law' are in fact attributable to other researchers (Pearson & Lieberman, 2004), especially the work of W. Roux, who proposed the "concept of functional adaptation of osseous tissue" (Cowin, 2001: 1). What Wolff added to the 'Law' is the notion that trabeculae are formed during the growth of bone in the early stages of life and are orientated according to the stress placed upon the bone. Wolff also devised a mathematical model to explain this process (Pearson & Lieberman, 2004). Cowin (2001), however, demonstrates that the mathematical component of Wolff's Law is erroneous and also questions the validity of the using the word 'law' for what might be more accurately defined in scientific terms as a 'theory'. Therefore, caution must be exercised when using the term 'Wolff's Law' to describe such biomechanical processes. While 'Wolff's Law' is commonly used in the literature to refer to what might be better named 'Roux's Theory' (Cowin, 2001), it is necessary to be clear on the use of the exact meaning of terminology used, to avoid confusion and misinterpretation. If applied correctly, however, biomechanical principles can be used to address the issue of bilateral asymmetry in skeletal populations.

Following from this understanding of how bone responds to mechanical stress, differences in bone size and robusticity, as reflected in bilateral asymmetry, can be and have been used to infer behavioural characteristics of past populations based on the assumption that behavioural lateralisation will increase the level of bilateral asymmetry observed in the skeleton (Trinkaus *et al.*, 1994; Lieberman, 1997; Ruff, 2000; Steele, 2000a,b; Lazenby, 2002c; Auerbach & Ruff, 2006). The human arm is unique in the primate order in being free from the functional constraints of locomotion. Therefore it is expected that bilateral asymmetry in the bones of the upper limb will reflect differences in recruitment of the left and right arms in occupational activities. This can be compared to the low levels of asymmetry expected in the bones of the lower limbs, due to their more symmetrical recruitment in bipedal locomotion (Auerbach & Ruff, 2006; Drapeau, 2008). The following sections examine the use of metric and geometric bone properties to ascertain the nature of upper limb bilateral asymmetry in modern humans. These patterns are compared with data from the under-represented region of the hand, and also the corresponding evidence from non-human primate species. Issues surrounding the application of these approaches are then discussed.

2.2.1 Asymmetry in metric properties

Metric bone properties are those that represent the external dimensions of bone, such as length, breadth, diameter and circumference and data on these properties can be collected relatively easily and cheaply. Studies of asymmetry in metric properties in the human upper limb have focused almost exclusively on the bones of the arm, and the humerus in particular. This is likely due to the large numbers of paired arm bones present in archaeological contexts which allow comparative measurements to be taken. Relative to the bones of the arm, the bones of the hand are less commonly recovered from excavation and, due to their small size, may be more prone to taphonomic damage. Perhaps for these reasons, the relationship between mechanical loading and diaphyseal robusticity has been less frequently studied in the hand region.

Studies that have focused on upper limb asymmetry have identified a trend towards right-side dominant asymmetry in a number of metric traits. The anatomist Arnold (1844, cited in Stirland, 1993) was one of the first to identify a right-side dominant asymmetry in humerus length. This finding has subsequently been supported by the work of Schultz (1937) and Latimer & Lowrance (1965), which also identified right-side dominant asymmetry in terms of bone length and weight. More recently Stirland (1993) compared humeral asymmetry in medieval populations from a Norwich cemetery and the crew of the *Mary Rose*, Henry VIII's flagship. Asymmetries were determined for seven metric humeral properties plus greater tubercle width. This measurement was taken to represent the dimensions of the muscle attachment sites for the *supraspinatus*, *infraspinatus* and *teres minor*. Stirland found that all asymmetries identified in both samples favoured the right-side. However, there was a clear difference in asymmetries between the samples with the Norwich sample showing significant asymmetries in six of eight measurements (the exceptions being proximal breadth and distal breath), but the *Mary Rose* sample was only significantly asymmetric for greater tubercle width. While Stirland suggests that the asymmetry in the Norwich sample reflects the modern human tendency for right-handedness, she believes that the increased symmetry in the *Mary Rose* humeri is a result of the presence of professional archers in this sample who were likely to have experienced strong mechanical loading in both arms.

As indicated in section 1.3.1, Steele & Mays (1995) found right-side dominant asymmetry in their sample from the medieval cemetery at Wharram Percy. For the adults studied there was significant right-side dominant asymmetry for humerus, radius and ulna length, plus for humerus and radius length combined (i.e. a proxy for arm length). The results from Wharram Percy were compared with those of other medieval, Anglo-Saxon and modern European samples, where Steele & Mays found similar levels of right-side dominant asymmetry.

A recent study by Blackburn & Knüsel (2006) has taken an innovative approach to determining the link between upper limb skeletal asymmetry and hand preference. The authors compared individuals' self-reported hand dominance with a measure of humeral distal epicondylar breadth taken on the same individuals. The distal humeral epicondyles can be easily palpated through the skin and the measurement taken on live samples is expected to differ little from the skeletal measurement. The authors found that despite 84% of their sample (sample N = 50) being self-reported right-handers, only 58% of individuals displayed epicondylar breadth larger on the right-side. Hand dominance equated to skeletal asymmetry for 68% of individuals overall. A comparison of epicondylar breadth in the living sample with a sample an Anglo-Saxon sample found similar levels of right-side dominant asymmetry, although the samples significantly differed in their proportions of left-side dominant individuals (*ibid.*). These findings pose interesting questions about the relationship between skeletal asymmetry and (self-reported) hand dominance in modern samples, which in turn has important implications for how we interpret evidence for hand preferences in extinct groups. However, it is worth bearing in mind the small sample sizes included in this study. Additionally, only one metric dimension was assessed, which may not accurately reflect the precise nature of asymmetry in the upper limb, particularly as articular surface dimensions have been demonstrated to be less susceptible to asymmetric loading than diaphyseal dimensions (Ruff, 2000; Lieberman *et al.*, 2001). The approach proposed by Blackburn & Knüsel (2006) is a promising one and one that requires further exploration. While an overall right-side dominant asymmetry in metric properties has been identified across many studies, it is still not clear how this maps on to hand preference in living samples, either self-reported or experimentally determined.

2.2.2. Asymmetry in geometric properties

Since the 1970's there has been a move towards the increasing use of geometric bone properties to determine patterns of functional loading in the upper limb and the distribution of bilateral asymmetry. The geometric approach measures the cross-sectional dimensions of long bone diaphyses and uses engineering concepts to model the bone as a beam to determine aspects of bone strength and its ability to resist stress. As indicated in section 2.2 (above), long bones are most commonly subjected to bending stresses, but as a beam, bone is also subjected to a number of other stresses, such as compression, twisting and shear stresses (see Figure 2.1, below).

As with the example in section 2.2, it is assumed that bone responds to such stresses by strengthening the bone (through modelling and remodelling) at the points of greatest strain. Therefore, it is proposed that, by measuring cross-sectional properties of long bone diaphyses, it is possible to determine the nature of the stresses and strains the bone was subject to during its lifetime. By extension, by comparing left- and right-side bone cross-sectional dimensions it will be possible to identify differences in the stresses experienced, for example, by each arm. From this inferences can then be made regarding behavioural lateralisation in the upper limb.

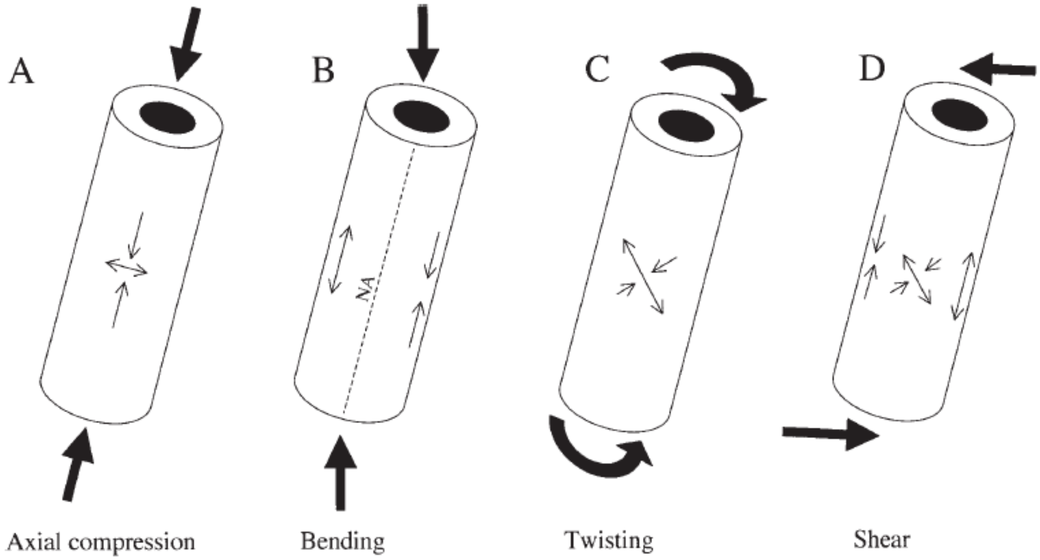


Figure 2.1. The various stresses that long bones are subject to: (A) compression, (B) bending, (C) twisting and (D) shear stress. The bold arrows represent the stress applied to the bone; the thin arrows indicate the strains experienced by the bone. Taken from Pearson & Lieberman (2004).

More recently, with increased availability of the equipment necessary to collect cross-sectional data in a non-destructive manner (i.e. radiography or computer tomography), the geometric approach has been favoured over the traditional metric approach. Geometric principles have also been favoured over metric ones as it is believed that they more accurately reflect functional responses of bone to stress (Ruff *et al.*, 2006). A number of geometric properties can be determined from cross-sectional dimensions. A list of these dimensions and their mechanical significance are outlined in Table 2.1 (below) and represented visually in Figure 2.2 (below).

Based on these properties a number of studies in recent times have addressed the issue of upper limb bilateral asymmetry in human skeletal populations (e.g. Ruff & Jones, 1981; Trinkaus *et al.*, 1994; Lazenby, 1998; Ruff, 2000; Mays, 2002; Nystrom & Buikstra, 2005; Rhodes & Knüsel, 2005; Auerbach & Ruff, 2006; Marchi *et al.*, 2006; Shackelford, 2007; Sládek *et al.*, 2007; Kujanová *et al.*, 2008; Maggiano *et al.*, 2008b). One of the first quantitative studies to employ this approach examined humeral response to strenuous activity in living samples (Jones *et al.*, 1977). Jones and colleagues compared cortical thickness (measured from x-ray films) in a sample of long-term professional tennis players and found that a significant increase in cortical thickness (and a corresponding decrease in medullary cavity width) in the ‘playing’ arm of subjects relative to their ‘non-playing’ arm. The authors concluded from this that activity can be assumed to modify diaphyseal properties. While this conclusion has been criticised by Bertram & Swartz (1991) on the grounds that many of the subjects were suffering from injury or pain in their playing arms, Haapasalo *et al*. (2000) found that in their sample of Finnish male professional tennis players total cross-sectional area was significantly greater in the playing arm compared to the non-playing arm. However, there was clear variation in the proportions of cortical area and medullary cavity at various points along the humerus. No significant changes were noted in bone density between the arms. Haapasalo and colleagues interpret the variation in loading at the different points of measurement as reflecting differences in loading at these locations, thus supporting the notion that variability in mechanical loading (and therefore behavioural variability) will be observable on the skeleton.

Symbol	**Dimension**	**Mechanical relevance**
TA	Total subperiosteal area	Combined area of cortical bone and medullary cavity
CA	Total cortical area	Correlate of resistance to compressive or tensile loading
I_{max}	Maximum second moment of area	Correlate of maximum bending strength
I_{min}	Minimum second moment of area	Correlate of minimum bending strength
I_x	Second moment of area, x axis	Correlate of bending strength about x axis
I_y	Second moment of area, y axis	Correlate of bending strength about y axis
J	Polar second moment of area	Correlate of torsional strength, sum of any perpendicular second moments of area

Table 2.1. Cross-sectional dimensions of long bone diaphyses used to determine bone's response to stress. Modified from Stock & Shaw (2007). Additional information taken from Ruff (2000).

Subsequent studies have applied this principle to examine bilateral asymmetry in the upper limb within the context of behavioural lateralisation. Of these the general trend has been towards the identification of right-side dominant asymmetry (e.g. Ruff & Jones, 1981; Trinkaus *et al.*, 1994; Auerbach & Ruff, 2006; Shackelford, 2007; Sládek *et al.*, 2007; Kujanová *et al.*, 2008). This trend has been used to infer temporal and spatial changes in behavioural patterns. For example, Shackelford (2007) analysed regional variability in postcranial robusticity in Upper Palaeolithic individuals from across Europe, Africa and Asia. The European sample displayed the strongest asymmetry, particularly in second moment of area (J). Temporally, early Upper Palaeolithic skeletons were found to exhibit more bilateral asymmetry than late Upper Palaeolithic skeletons. Shackelford suggests that that the increased humeral robusticity seen in more recent skeletons (reflected in reduced bilateral asymmetry) may reflect a change in subsistence strategies and technologies after the Last Glacial Maximum. Trinkaus *et* *al.* (1994) found a similar temporal change in their comparative sample of humeri from Neanderthals, anatomically modern humans and extant tennis players. They found that Neanderthals clearly exhibited greater bilateral asymmetry than the modern human sample, but a similar degree of asymmetry as the extant tennis player sample, all favouring the right-side. The authors take these results to indicate the presence of activity-induced mechanical change in their samples, particularly in the Neanderthal and tennis player samples. This conclusion is supported by the observation that pathological Neanderthal individuals (i.e. where trauma/disease had inhibited the use of one arm) exhibited extremely large bilateral asymmetry, from 112% to 215% difference between left and right measurements resulting from the increased use of one arm relative to the lack of use of the opposite arm. A traumatic origin for extreme upper limb asymmetry has also been suggested for the pattern of strong left-side dominant asymmetry observed in a Neolithic skeleton studied by Lieverse *et al.* (2008) and the strong right-side dominant asymmetry in an Upper Palaeolithic skeleton examined by Churchill & Formicola (1997).

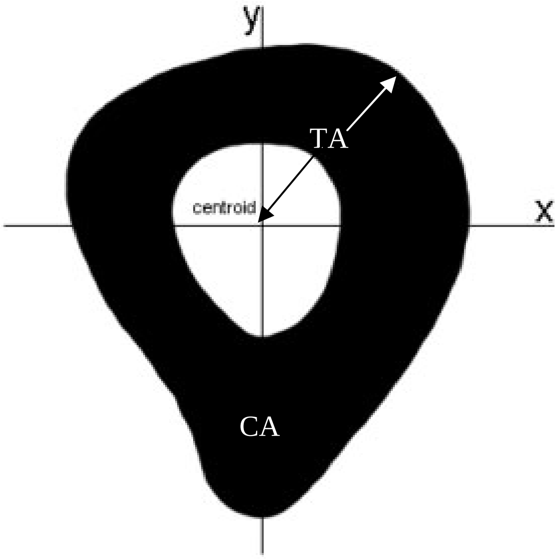


Figure 2.2. A femoral midshaft cross-section, with points of measurement for the dimensions in Table 2.1 indicated. Modified from Stock & Shaw (2007).

Research into upper limb bilateral asymmetry, which has utilised both metric and geometric bone properties, has returned a remarkably consistent pattern of asymmetry across various human groups studied, namely a trend for right-side dominant asymmetry. Given the obvious anatomical relationship between external and cross-sectional bone properties (Stock & Shaw, 2007) it is not surprising that there is congruency between the studies. Variation between samples has been interpreted as reflecting behavioural differences between the groups compared, however disparity between the methods should also be considered as a factor.

2.2.3. Asymmetry in the hands

Despite the use of upper limb bilateral asymmetry research to inform regarding hand preferences in skeletal samples, very little research has focused on the presence of asymmetry in the bones of the hand, and what research exists is primarily centred on the second metacarpal. In an early study, Garn *et al.* (1976) identified bilateral asymmetry in the geometric properties (bone area, cortical area and percentage cortical area) of the 2nd metacarpal of 227 patients with chronic renal failure. Of these 227 individuals, 208 were self-reported right-handers and the remaining 19 self-reported left-handers. For both groups bone area and cortical area was found to be significantly greater on the right-hand side, but percentage cortical area was greater on the left-hand side. The authors highlight the fact that the size of the differences between the left and right sides is small, and it is worth noting that the study sample are all suffering from chronic renal failure which results in a degree of bone loss (*ibid.*). However, the results suggest that self-reported hand preference is not closely linked to bone robusticity. A follow-up study by Plato *et al.* (1980) compared hand preference, as determined by grip strength, with measures of combined cortical thickness (the difference between the total and medullary widths), total area, cortical area and percentage cortical area in the second metacarpal. The results of this study mirrored those of Garn *et al.* (1976), namely that dimensions of the right hand were found to be larger than those of the left hand, with the exception of percentage cortical area (for left-handers) and metacarpal length (for 'ambidextrous' subjects), although these differences were not statistically significant in all cases. In particular, those subjects categorised as left-handed did not show significant differences between left- and right-hand measurements, despite an underlying tendency towards right-side dominance. Plato *et al.* (1980) suggest that there is an underlying tendency for the right-hand bones to be larger irrespective of hand preference, but that a left-hand preference may reduce the level of observable asymmetry by increasing the amount of bone present in the left hand.

These early findings have been criticised on methodological grounds, in particular the small number of left-handed individuals studied, the inclusion of pathological subjects, the use of grip strength measures to determine hand preference and the exclusion of second moments of area as a variable (Roy *et al.*, 1994). To address these concerns, Roy *et al.* (1994) studied asymmetry in a series of cross-sectional properties of the second metacarpal in a sample of 992 subjects. Hand preference was self-reported for each subject. Roy *et al.* found that right-handed subjects displayed significantly larger geometric properties in the right 2nd metacarpal, with left-handed subjects having significantly larger left 2nd metacarpal dimensions. Interestingly, the magnitude of the asymmetry was equivalent for both the right- and left-side dominant individuals. In addition, right-handed individuals were found to have significantly larger 2nd metacarpal length measurements. The corresponding trend was not found in the left 2nd metacarpal for left-handed individuals. The authors therefore argue against any inherent tendency for the right hand to display greater robusticity than the left hand and instead suggest that mechanical loading influences the cross-sectional properties of the hand bones in the same manner as other limb bones, where this trend has already been identified.

More recently, the work of Lazenby (Lazenby, 1998, 2002a; Lazenby *et al.*, 2008) has been particularly informative regarding the nature of bilateral asymmetry in various aspects of second metacarpal skeletal morphology. Lazenby (1998) assessed bilateral asymmetry in a wide range of second metacarpal cross-sectional properties in a 19th Century Canadian cemetery sample and found that right-side dimensions were significantly larger than left-side dimensions for all measurements except medullary area and percentage cortical area, although of course hand preferences in this sample cannot be known. Lazenby also indicates that despite the right-side dominant trend, approximately 14% to 26% of individuals exhibited larger left-side metacarpal properties, noting that this is at odds with the literature on hand preference in living populations. Without knowing the life histories of the individuals in the sample studied it is not possible to know what factors influenced the expression of asymmetry, although a strong mechanical loading component is likely to be involved. Cortical thickness across both the medio-lateral and antero-posterior planes in the right second metacarpal relative to the left in the same Canadian cemetery sample also appears to show bilateral asymmetry (Lazenby, 2002a).

Lazenby *et al.* (2008) address the issue of ‘articular constraint’, namely that articular surfaces respond to mechanical loading through reorganisation of trabeculae in bone epiphyses. If this is the case, then it is expected that trabecular bone will exhibit asymmetry in the same way as cortical bone. Micro-CT scanning of second metacarpals from the Canadian cemetery sample utilised in Lazenby (1998, 2002a) found that this was indeed the case in this sample, with the head of the right second metacarpal exhibiting significantly greater volume of trabeculae relative to a number of dimensions, such as bone volume, ratio of trabeculae area to bone volume, number of trabeculae and connectivity of trabeculae. In comparison, while midshaft and distal articular surface dimensions showed a general right-side dominant asymmetry this was less than in the trabecular dimensions, particularly for the articular surface properties. This study suggests that trabecular bone has an important role to play in our understanding of functional asymmetry in both the hands and the arm. Lazenby *et al.* (2008) suggest that this method could be particularly applicable to hominin hand bone remains, as differences in the structural organisation of trabeculae in the dominant metacarpal (plate-like) differs from that seen in the non-dominant metacarpal (rod-like), suggesting that it could be possible to identify hand dominance in non-paired hand bones. However, as the authors point out, further research on human and non-human primates is first required.

While early research on metacarpal asymmetry suggested a rather mixed pattern of asymmetry in the hands, subsequent research has addressed earlier methodological concerns and pointed towards a pattern of right-side dominance. The extent to which mechanical loading influences this pattern is unclear, as is whether this trend is represented across the whole hand. The discrepancy between skeletal asymmetry and real-world hand preference highlights the need for further work to clarify the precise nature of the relationship between these two traits.

2.2.4. Asymmetry in the non-human primate upper limb

Perhaps as a result of the observation that the non-human primate forelimbs are primarily symmetrically recruited in locomotor activities and are therefore likely to exhibit less asymmetry than the upper limbs of humans, there has been little research carried out into the extent and direction of any asymmetry in the non-human primate arm. Early comparative work suggested that, relative to humans, great and lesser apes displayed no clear tendency for right-side dominant asymmetry in metric skeletal properties, with the magnitude of asymmetry in these species reduced compared to that of humans (Schultz, 1937). Dhall & Singh (1977) addressed the issue in rhesus macaques and found side dominance in arm muscle and bone weights for the majority of individuals studied. The trend in this sample was towards a right-side dominance, with six of nine individuals showing asymmetry towards the right, and three showing asymmetry towards the left. This trend towards right-side dominant asymmetry in rhesus macaque forelimbs has been identified in much larger sample of rhesus macaques by Falk *et al.* (1988) and Helmkamp & Falk (1990). Falk *et al.* (1988) found right-side asymmetry in metric properties of the humerus, ulna, radius and second metacarpals, although this asymmetry was only statistically significant for measurements taken on the humerus and ulna. The authors note that the measurements for which asymmetry was significant (humeral supracondylar ridge length, humeral diameter measured at the intertubercular groove, ulna length, olecranon process length) represent locations of muscle attachments, and as such, right-side asymmetry in these measurements could represent increased functional recruitment of the muscles in the right arm relative to the left. This conclusion is tempered by Helmkamp & Falk (1990) who suggest that the right-side dominant asymmetry seen in rhesus macaques may be more reflective of ontogenetic factors due to the identification of clear sex and age differences in asymmetry in their sample.

A small study of skeletons of chimpanzees from Gombe National Park allowed Morbeck *et al.* (1994) to measure asymmetry in the limb bones of individuals with known life histories. For the six individuals studied, their results indicate a fluctuating pattern of individual asymmetry in metric and geometric skeletal properties of the arm bones, with no clear association with observed hand preference during life. Asymmetry was also assessed in a larger skeletal sample (N = 11) from Gombe for which hand preference was not known. This analysis also found a rather mixed pattern of asymmetry, with metric properties tending towards left-side dominance and geometric properties favouring right-side dominant asymmetries.

Sarringhaus *et al.* (2005) compared asymmetry in total subperiosteal area (TA) in the humerus, 2nd metacarpal and femur of a sample of wild-shot chimpanzees. They found a statistically significant left-side dominant asymmetry for the humerus and a right-side dominant asymmetry, albeit a non-significant one, for the second metacarpal. As the authors note, it is likely that the smaller number of individuals in the metacarpal sample was the cause of the non-significant result as the proportion of right-side dominant metacarpals was the same as the left-side dominant humeri. Proportions of left-side and right-side dominant femora were roughly equivalent and therefore not statistically significantly different. This is interpreted as reflecting the directional nature of asymmetry in the upper limb. The results of this study can be interpreted as indicating a functional component to asymmetry in the upper limb of this chimpanzee sample. Sarringhaus *et al.* suggest that the left-side dominant asymmetry seen in the humeral TA may result from recruitment of the left arm in providing postural support, freeing the right hand to engage in object manipulation, thus accounting for the right-side dominant asymmetry observed in the second metacarpal.

The limited data available on non-human primate upper limb asymmetry paints a mixed picture of asymmetry, particularly in the great apes species. It may be possible that differences inherent in the metric and geometric approaches have led to variable asymmetry patterns, however the mixed pattern of upper limb asymmetry identified by Sarringhaus *et al.* (2005) hints at a more complicated explanation. The difficulty in determining the exact nature of lateralised hand preferences in living ape groups (see section 1.3.2) suggests that identifying distinct and universal trends in skeletal asymmetry is unlikely. More research is certainly required to further illuminate this issue.

2.2.5. Issues with metric and geometric approaches

Despite the ubiquity of metric and geometric approaches in the asymmetry literature a number of issues surround their application. Questions remain over the most appropriate method for analysis of long bone robusticity and asymmetry. While many researchers favour the geometric approach as the being the most appropriate (e.g. Ruff *et al.*, 2006) metric methods are still applied by some, particularly as this method can be a quick way of collecting data without requiring equipment that is often expensive and specialised (Stock & Shaw, 2007). It is therefore necessary to ask whether these approaches are congruent. It is also crucial to query whether external measurements do indeed accurately reflect mechanical loading in the upper limb, and the extent to which they reflect ontogenetic or environmental factors. Trinkaus *et al.* (1994) compared metric and geometric measures of bilateral asymmetry in modern human and Neanderthal humeral samples. They found that asymmetry as determined from metric properties (humerus length and distal articular breadth) was reduced relative to that seen in corresponding geometric measurements. Trinkaus *et al.* (1994) take this finding to indicate that geometric bone dimensions are more representative of biomechanical forces on long bone diaphyses than more traditional metric measurements. However, further studies that have compared cross-sectional properties with 2nd metacarpal length (Roy *et al.*, 1994) and 2nd metacarpal distal articular surface (Lazenby *et al.*, 2008) suggest that it is mainly the magnitude of the asymmetry that differs between the methods rather than the direction of the asymmetry. Therefore, while caution must be exercised when interpreting results of metric studies, this approach can still be applied to the determination of skeletal asymmetry where appropriate.

Demes (2007) challenges the assumption that the structural organisation of bone is 'optimised' so that bone can offer the maximum mechanical resistance with the minimum amount of bone substance. Bending stresses are believed to be the stresses most commonly experienced by long bones, meaning that for second moments of area (see Table 2.1) "the plane with the greatest area moment should be aligned with the plane in which the bone is habitually bent during activity" (Demes, 2007: 717). However, as suggested by Demes *et al.* (1998, 2001) and Lieberman *et al.* (2004), evidence from *in vivo* bone strain studies in monkey and ovine samples indicates that, in fact, these planes are not aligned. Ruff *et al.* (2006) propose that *in vivo* studies measure bones that have already experienced mechanical loading and therefore have changed the orientation of the neutral bending axis. However, Demes (2007) offers mathematical corrections that can bring misaligned axes back in line.

Weiss (2005) has compared humeral cross-sectional properties in skeletal samples that were expected to differ substantially in activity regimes (prisoners of war from Quebec vs suburbanites from New Mexico) and found that both samples were statistically similar in terms of both bone robusticity and bilateral asymmetry. While there may be certain environmental and ontogenetic factors influencing humeral morphology in these samples, Weiss advises caution when extrapolating directly from cross-sectional data to activity patterns. Additionally, these findings suggest that care must be taken when inferring behaviours in archaeological samples, favouring the exploration of 'broad' rather than 'narrow' research questions.

Overall, these studies raise issues about how we interpret and understand the bone's response to stress, and to accept geometric principles without subjecting them to the same scrutiny as metric principles risks misinterpretation of the available data. Demes (2007) cautions that bone adaptation is not a straightforward process and other 'osteogenic' factors that influence bone modelling and remodelling should be considered, such as age and body mass, as well as hormonal and genetic factors (Pearson & Lieberman, 2004). But bearing these concerns in mind, the relationship between activity and functional appears to remain, allowing further comparisons of behavioural variability in skeletal populations. However, it is important to also consider the types of activity that elicit bone remodelling, i.e. whether strenuous activity is more likely to result in observable bone remodelling relative to continual, low-level activities (Pearson & Lieberman, 2004).

In conclusion, although there are differences between the metric and geometric methods available to study the effects of mechanical loading on bone dimensions, in terms of determining upper limb bilateral asymmetry, there is a general agreement on the trend towards right-side dominant asymmetry. While ontogenetic and environmental factors may exert a degree of influence on these properties, the continued identification of right-side dominant asymmetry in upper limb properties suggests a real effect of functional lateralisation in the use of the arms in the samples studied. Furthermore, it can be seen from section 2.2 that the main focus on skeletal asymmetry research has been on the bones of the hominin arm, with little work addressing the nature of asymmetry in the bones of the hand, or in non-human primate species in general. Where such research has been undertaken, results are generally consistent with expectations. Studies of the human 2^{nd} metacarpal indicate a trend for right-side dominant asymmetry, suggesting a certain influence of hand preference on skeletal asymmetry. For non-human primates, the small number of studies so far carried out support a much more ‘mixed’ pattern of asymmetry which less clearly favours the right-side. Together, these findings highlight the need for more research in these areas to clarify the nature of asymmetry expression throughout the hands in both modern human and non-human primate skeletons. Additionally, more detailed understanding of asymmetry in the non-human primate upper limb as a whole can help to address issues surrounding the extent to which lateralised behaviours influence bilateral asymmetry in the upper limb, in both human and non-human primate samples.

2.3. Asymmetry in musculoskeletal stress markers

As with the external and cross-sectional bone dimensions discussed in section 2.2, analysis of musculoskeletal stress marker (MSM) development also has the potential to provide information on upper limb bilateral asymmetry in skeletal samples. This is because strenuous muscle activity is thought to result in bone remodelling taking place at sites of muscle-to-bone and tendon-to-bone attachment. Increased activity at these sites leads to an increase in the number of capillaries that supply the periosteum (covering around the outer bone surface), and this increased blood flow in turn stimulates osteon (the basic functional units that make up compact bone) remodelling (Hawkey & Merbs, 1995). Attachment site remodelling can lead, in some instances, to bone forming (osteophytic) processes which are reflected in the rugose appearance of bone in the area of muscle attachment. At other times, particularly if a muscle if regularly stressed beyond its natural capabilities, bone remodelling takes the form of bone erosion/reabsorption (osteolytic processes). On these occasions repeated stress causes muscle fibres to tear. These fibres must reattach to the periosteum, but this reattachment may disrupt the normal blood flow to the bone which can, in severe cases, lead to bone necrosis. If muscle stress continues and the periosteum is unable to heal then substantial pitting of the bone’s cortical surface may result (*ibid*.).

Variation in the development of MSM across and between bones has therefore been considered reflective of differences in the activity of the muscles corresponding to these MSM, based on the assumption that “degree and type of [muscle] marker are related directly to the amount and duration of habitual stress placed on a specific muscle” (Hawkey & Merbs, 1995: 324). From this assumption, the analysis of MSM development has been commonly used to make determinations of occupation patterns and sociocultural divisions of activity in skeletal populations (Dutour, 1986; Hawkey & Street, 1992; Hawkey & Merbs, 1995; Munson Chapman, 1997; Capasso *et al.*, 1998; Churchill & Morris, 1998; Peterson, 1998; Robb, 1998; Steen & Lane, 1998; Lovell & Dublenko, 1999; al-Oumaoui *et al.*, 2004; Eshed *et al.*, 2004; Molnar, 2006; Weiss, 2007). This approach can also be used more specifically to identify and assess bilateral asymmetry, particularly in the upper limb. The following section reviews the contribution MSM analysis has made to the understanding of upper limb bilateral asymmetry in skeletal populations and some of the issues associated with this approach. At this stage it is worth noting the varying terminology used in the literature. Kennedy (1998) for example, promotes the use of the term ‘markers of occupational stress’ (MOS), taken to include MSM and skeletal robusticity markers (RM), as well as osteoarthritis, pressure facets, enthesopathies (tendinous attachments) and syndesmoses (ligamentous attachments) (Wilczak & Kennedy, 1998). In this study the term ‘musculoskeletal stress marker’ (MSM) will be used to refer to bone surface markers created as a non-pathological response to biomechanical loading stress on the muscles. Pathological responses to stress (e.g. enthesopathies and syndesmoses) will be referred to as such. This use of terminology does not assume that occupation is the only influence on muscle marker development (Hawkey & Merbs, 1995).

Early studies that addressed MSM development in the upper limb (e.g. Dutour, 1986; Angel, 1987; Kelley & Angel, 1987) were often qualitative in nature, comprising descriptions of the location and nature of extreme MSM expression often (but not always) with accompanying photographic evidence. From such accounts somewhat ‘anecdotal’ evidence for upper limb MSM asymmetry can be gleaned, suggesting a trend towards right-side dominant asymmetry. For example, from Dutour (1986) it can be seen that enthesopathies were more commonly identified on the bones of the right arm than the left, and when present bilaterally were more pronounced on the right side relative to the left. A qualitative approach has also be used to assess muscle development in species of *Homo* other than *H. sapiens*, for which only fragmentary remains are preserved (e.g. Walker & Leakey, 1993, for the Nariokotome *H. ergaster*, KNM-WT 15000). However, with the development of a visual scoring system for the assessment of MSM development (Hawkey & Merbs, 1995), it has been possible to reduce (to a certain extent) the subjectivity of MSM assessment and to increase the potential for inter-study comparisons. The Hawkey & Merbs (1995) method consists of categorising MSM expression into one of three groups (robusticity marker, stress lesion and ossification exotosis) and then, within each category, MSM were scored on a 0 to 3 scale, where 0 = no expression and 3 = strong expression, with 1 and 2 representing intermediate states.

As might be expected from the application of a more involved assessment process, the pattern of upper limb bilateral asymmetry derived from studies using a Hawkey & Merbs (1995) methodology is also more complex, but overall appears to support the presence of right-side dominant asymmetry across skeletal samples (e.g. Hawkey & Merbs, 1995; Peterson, 1998; Molnar, 2006). An example of this complexity can be seen when comparing studies based on the same material. Peterson (1998) studied MSM expression in the upper limb of a Late Pleistocene Natufian sample from the Levant region and found that males in the sample had significantly more upper limb asymmetries than females and that these asymmetries favoured the right arm. Peterson interpreted these differences as reflecting male engagement in over-arm throwing while using weapons, which was influenced by a pre-existing right-handedness in the population. However, when Eshed *et al.* (2004) assessed and compared bilateral asymmetry in Natufian samples from many of the same sites as Peterson (1998) with Neolithic Levantine samples in order to analysis the effects of the transition to agricultural practices in this region, they did not find any statistically significant asymmetries in the upper limb for either males or females. Non-significant trends were found towards left-side dominant asymmetry in the Natufian males and right-side dominant asymmetry in the Neolithic males. Both female samples showed a trend towards left-side dominant asymmetry. Such contrasting findings from studies of the same samples suggest that care must be taken, not just in applying the Hawkey & Merbs (1995) method, but also in the application of statistical techniques for assessing asymmetry. In the example above there were differences in the way in which asymmetry was calculated and additional differences in how the degree of asymmetry and its ‘significance’ was assessed. While there is a certain degree of consensus that non-parametric statistics are the most appropriate for MSM comparisons (Churchill & Morris, 1998; Robb, 1998; Steen & Lane, 1998; Drapeau, 2008), techniques that are essentially parametric (e.g. the ranking of mean values) are still apparent (Hawkey & Merbs, 1995; Peterson, 1998). A consensus on these analytical issues is required to improve the comparability of this method especially as some studies have found no statistically significant asymmetries (Steen & Lane, 1998; Stirland, 1998; Eshed *et al.*, 2004; Molnar, 2006), although right-side dominant trends are occasionally identified.

The Hawkey & Merbs (1995) technique, however, is not the only one that has been applied to the assessment of MSM expression. A modification of the ordinal scoring technique has been proposed by al-Oumaoui *et al.* (2004). In their study of samples from the Iberian Peninsula the authors scored MSM as being either ‘present’ or ‘absent’. In addition a ‘consensus’ approach was taken to scoring, with all three authors agreeing on the category membership of each MSM. This approach was designed to remove some of the subjectivity that remains with an ordinal scoring technique, although the authors acknowledge that this method currently limits inter-study comparisons. Al-Oumaoui *et al.* (2004) found that all the samples in their study exhibited right-side dominant asymmetry using this technique, although they caution that one of the necessary consequences of this approach is an inability to draw detailed conclusions regarding activity patterns which will remove the tendency for “gratuitous speculation" (2004: 358) which can hamper MSM research. An approach suggested by Robb (1998) involves scoring individual MSM expression relative to the range of variation observable in a particular sample. Robb advocates creating a broad reference sample of skeletons within which the skeletons will be sorted and graded according to the development of a particular MSM from the smallest and least rugose, up to the largest and most rugose. From this the series can be divided into five categories representing the range of development for each MSM. This sorting and grading must be repeated for each MSM studied. Robb (1998) is keen to point out that equivalence can not be assumed between the scoring categories for different MSM. Additionally, it is important to select a relevant reference sample on which to base the grading process. A further classification system for MSM is proposed by Mariotti *et al.* (2004). They suggest that areas of MSM are classified as either 'entheses' (i.e. normal areas of attachment) scored in terms of rugosity, or 'enthesopathies', where the bone's response to muscular stress has become pathological. Enthesopathies can be further scored as 'osteophytic' or 'osteolytic'.

Wilczak (1998) suggests measuring the area of muscle insertion as an alternative to scoring relative MSM development. While this approach results in a loss of three-dimensional data regarding MSM morphology and rugosity it avoids the pitfalls associated with treating ordinal data as distinct numerical categories (see section 2.3.3) and the influence of underlying bone robusticity on MSM prominence (*ibid*.). The application of this technique to various samples of American skeletons found an overall trend towards right-side dominant asymmetry in the arm for all but one of the samples (the remaining sample showed an equal proportion of left-side and right-side dominant MSM). This approach has been further developed by Zumwalt (2005, 2006), who has used laser-scanning to incorporate three-dimensional data into surface area plots.

Further work is now clearly required to determine the applicability of alternative methods of assessing MSM expression. The proliferation of methods and analytical techniques available currently serve only to confuse the results of MSM analyses and reduce the objectivity and comparability of the method introduced to address those very problems.

2.3.1. Asymmetry in hand MSM

It is clear from the examples above that the predominant focus of MSM research in the upper limb has been the bones of the arm, the humerus, radius and ulna. The bones of the hand, by contrast, are noticeable by their absence from this arena. There are a number of possible reasons for this. It may result from the small size of the MSM found in the hand, meaning that they do not display enough variation to allow meaningful study to take place (Robb, 1998). It may also result from the lack of well-preserved hand bone material recovered from archaeological excavations and problems inherent in accurately siding finger bones. A small number of studies have made reference to MSM located in the hands, although descriptions are generally cursory and refer mainly to development of phalanx flexor attachments. In a study of a skeleton believed to belong to an Egyptian scribe from the Third Intermediate Period named Penpi, Kennedy *et al*. (1986) make brief reference to the presence of developed flexor ligament ridges on the proximal phalanges of the right hand of the skeleton. This is taken to indicate that Penpi's profession as a writer was likely to have resulted in increased development of the right phalanx flexor ligament attachments relative to those of the left hand due to a preference for the use of the right hand for writing. Unfortunately there is no accompanying photographic evidence to allow comparison of the left and right proximal phalanges. Lai & Lovell (1992) provide brief discussion of the hypertrophy of the *flexor digitorum superficialis* insertion sites on the intermediate phalanges of their sample of three male skeletons from the 18th - 19th century Canadian fur trade, possibly resulting from extended periods of paddling canoes. As with the Kennedy *et al.* (1986) paper this is a purely qualitative examination and as such there is no reference made to the presence of any asymmetry in these MSM.

Molnar (2006) takes a more quantitative approach to assessment of MSM development in the phalanges through use of the scoring method proposed by Hawkey & Merbs (1995). Molnar does not specify whether it is *flexor digitorum superficialis* or *profundus* MSM that are being studied (or both), or indeed which combination of digits were included in analysis, meaning that it is not possible to draw specific conclusions regarding flexor asymmetry. However it appears that asymmetry in the 'flexors' was generally low and not statistically significant. This follows the overall trend for low bilateral asymmetry in this sample, although there is a trend towards individual right-side dominant asymmetry.

A study by Cope (2007) examined asymmetry in a number of hand muscle MSM, the extensor *pollicis longus*, *abductor pollicis longus*, and *flexor pollicis longus*. These MSM were all measured at the point of origin on the radius and ulna, and data were not collected on the insertion sites in the hand. In addition, the attachment site of the radio-carpal ligament on the scaphoid bone of the wrist was also assessed. No statistically significant asymmetries were found for any of the MSM.

The examples given above highlight the fact that the MSM of the hands have been largely overlooked in studies of upper limb MSM development and bilateral asymmetry. These examples also indicate the potential for hand MSM to be informative regarding asymmetric use of the hands and corresponding hand preferences. Methodological concerns have yet to be addressed experimentally and therefore this region of the upper limb should not be excluded from MSM research. A number of studies have included the upper and lower arm origins of muscles which have a terminal insertion in the hands, but there are a number of muscles which are intrinsic to the hands which have not yet been studied. There is scope for expanding MSM research away from anecdotal and equivocal descriptions of phalanx flexors insertions to include both extrinsic and intrinsic muscle insertions across all the bones of the hand. Only by taking a more inclusive and systematic approach will it be possible to determine conclusively whether MSM in the hands can be reasonably included in upper limb asymmetry research.

2.3.2. Asymmetry in non-human primate MSM

There has been virtually no work undertaken to assess the expression of MSM in non-human primate species and therefore it is still unclear what this approach can tell us about upper limb bilateral asymmetry in non-human primates relative to metric or geometric approaches. Given the lack of clarity surrounding the nature of hand preferences in great ape species (see section 1.3.2), any information pertaining to lateralisation that can be gleaned from non-human primate skeletal material can only serve to illuminate this complex issue. Although not directly concerning asymmetry, Zumwalt *et al.* (2000) compared the size of MSM at four sites on the humerus, radius, femur and tibia across eight great ape and monkey species in order to identify differences relating to locomotor strategy. While this study did not find significant differences between species utilising different locomotor style, in part due to the correlation between MSM area and body mass, they did find a correlation between MSM area and diaphyseal bending strength, which indicated that arboreal species had lower bending strength at the diaphyseal midshaft than quadrupedal species. This study therefore suggests that MSM in the non-human primate upper do have potential be to informative regarding activity-related asymmetry. This potential has been investigated by Drapeau (2008), who compared bilateral asymmetry in MSM development in both the upper and lower limbs of a sample of gorillas, chimpanzees and modern humans. Using the Hawkey & Merbs (1995) scoring method, Drapeau found that all three samples displayed upper limb asymmetry, which was greatest in the human sample relative to the chimpanzee and gorilla sample. The level of asymmetry seen in the chimpanzee arms was greater than that of the gorillas. Both the chimpanzee and gorilla sample showed increased asymmetry in the forelimbs relative to the lower limbs. What these results suggest is that methods of analysing MSM are readily applicable to great ape samples and as such this approach, combined with analyses of other skeletal properties has the potential to provide valuable information to answers questions regarding the nature of limb and hand preferences in non-human primates.

2.3.3. Issues with MSM approach

The introduction and widespread use of a more formal identification system for MSM, such as that proposed by Hawkey & Merbs (1995) has reduced the degree of subjectivity inherent to analysis of this kind and improved the reliability of inter-study and inter-sample comparisons. There remain a number of problems inherent to this approach and to the concept of MSM analysis more generally. One issue with this approach is the tendency of some researchers to attempt to ‘quantify’ what is essentially a qualitative method. The Hawkey & Merbs (1995) method relies on ranking individual MSM on a 4-point scale, thus creating a set of ordinal data. Use of such a scale works on the statistical assumption that there is the same distance between an MSM scored as ‘1’ and an MSM scored as ‘2’ as there is between MSM scored as ‘2’ and ‘3’. For this reason some researchers have felt justified in the use of parametric statistics (such as the t-test, mean values and standard deviations) to identify differences between groups of data. However, a number of researchers have questioned such an approach as it cannot be assumed that the distance between scoring categories is the same as the numerical differences between 0, 1, 2 and 3, meaning that the use of values such as the mean and standard deviation are mathematically inappropriate (Robb, 1998; Stirland, 1998; Wilczak, 1998). As Stirland (1998) points out, the scoring categories A, B, C and D are as equally valid as numerical ones. This problem is further compounded by the use of 0.5 divisions of scoring categories (e.g. Peterson, 1998; Molnar, 2006; Eshed *et al*., 2004). Many researchers have addressed this problem through the use of non-parametric statistics which make different assumptions about the distribution of the data. Robb (1998) urges that caution is also necessary when applying non-parametric tests to MSM data as the use of such statistics can make patterns in the data more difficult to identify. Robb addresses this problem by focusing on only the expression of MSM across skeletal sites and between individuals, thus moving away from trying to determine specific activities to drawing more general conclusions about the organisation of activities. To answer these questions the use of multivariate statistics is proposed (*ibid.*). A nominal scoring system such as that advocated by al-Oumaoui *et al.* (2004) may be more appropriate for use with non-parametric statistics as individuals can only occupy one of two categories, making the distance between them irrelevant. However, Robb (1998) suggests that such an approach may obscure patterns present in MSM data and limit the scope for intra- and inter-individual comparisons. For these reasons, if statistical analyses are performed on MSM data the choice of appropriate tests is crucial to the outcome of the analyses.

One of the key assumptions implicit in MSM research as highlighted by Hawkey & Merbs (1995) is the relationship between function and morphology. The widely-held belief is that continual, strenuous muscle activity will lead to exaggerated MSM expression. This relationship, however, has been difficult to test experimentally. Using a sheep model, Zumwalt (2006) investigated the relationship between exercise and MSM development. This was done by exercising sheep in an experimental setting where the duration and stress of the exercise (running on a treadmill carrying additional weight) could be controlled. After the experimental period (90 days, of 1 hour exercise per day) the muscle attachment sites in the limbs of the exercise group were compared with control muscle attachment data (the *masseter* on the mandible) and with the corresponding muscle attachment sites from a control group of sedentary animals. Although muscle mass was found to be greater in the exercise group compared to the control group, no aspect of muscle attachment site morphology was found to statistically differ between the two groups. Zumwalt (2006) suggests that these findings could be explained by the mature age of the animals involved, the selection of an unsuitable exercise regime for eliciting MSM development, or an exercise regime that was not strenuous enough to promote MSM development; although the author also found no relationship between muscle size and MSM morphology in the sedentary control group. These results have been interpreted by Zumwalt as indicating that a clear relationship does not exist between MSM morphology and muscle size and activity. While the short time span of Zumwalt's study has been questioned (Weiss, 2003; Drapeau, 2008), research continues to find evidence for a relationship between bone robusticity and MSM development in skeletal material (Weiss, 2003). Further testing, both *in vivo* and osteologically, is of crucial importance in clarifying this key assumption underlying biomechanical and MSM studies.

Important questions have also been raised about the 'relevance' of using MSM development, and indeed skeletal modification in general, to draw conclusions about past populations and their activity patterns. Within the context of discussing degenerative joint disease (DJD), Jurmain (1991) questions the accuracy with which we can predict the nature of the stresses which have led to skeletal modifications in extinct populations as it is difficult to be sure which activities have lead to the bone modification witnessed. As Jurmain (1991) points out, even for those populations for which we have relatively large amounts of historical information (see Lai & Lovell, 1992 for an example of an 'osteobiographical' approach), the information we can glean about what kinds of stress they were under, plus its duration and severity, is limited. In fact, he suggests that "such data are wholly inadequate for making specific arguments regarding archaeological populations. We probably will never have sufficient data for making such specific arguments" (Jurmain, 1991: 249).

This problem is often compounded by an assumption of narrow functionality of muscles in MSM research (Robb, 1998; Stirland, 1998). There is a tendency for each muscle to be ascribed only one function, e.g. the *pectoralis major* = lifting, and the expression of this MSM thus interpreted within this context (e.g. Peterson, 1998). Clearly a muscle such as the *pectoralis major* is involved in a number of actions as a prime mover, synergist and antagonist. In addition, the act of 'lifting' forms part of many actions it is possible for an individual to engage in, making it difficult to assign MSM expression to a particular activity. Therefore a more 'inclusive' approach to MSM analysis, focusing on the expression of groups of MSM, both across the individual and across the group or sample, has been encouraged (Robb, 1998; Stirland, 1998; Wilczak, 1998). Additionally, there appear to be certain 'biases' permeating MSM interpretations, which may ultimately be limiting the efficacy of the method. Robb highlights the problem of imposing "culturally-defined gender categories" (1998: 363) on past populations, i.e. assuming that females in a population will be engaged in certain tasks such as cleaning, foraging and child care, while the males will be using weapons, hunting and farming. The expression of a particular MSM in an individual will often be attributed to a particular task, depending on whether that individual is male or female (*ibid.*). While it is often the case that gendered divisions of activity are present in a given society, it is unhelpful to readily engage with certain 'stereotypes' without confirmation from additional historical or archaeological sources.

In conclusion, differences in aspects of MSM analysis, both qualitative and qualitative, can make results difficult to compare, despite a general standardisation of methods of scoring MSM. As with the metric and geometric approaches (section 2.2) the region of the hand is often overlooked, as are non-human primates. By doing so, the opportunity to utilise a more inclusive approach to understanding MSM development and expression is also lost. Despite certain issues with the technique, the MSM approach has more to offer asymmetry studies if a more ‘realistic’ approach can be taken and the limitations of the method fully understood and acknowledged.

2.4. Comparative approaches to upper limb bilateral asymmetry

Despite the wide range of the work carried out in order to better understand the nature of upper limb bilateral asymmetry in skeletal populations, utilising metric/geometric and MSM approaches, there has been relatively little systematic research undertaken to determine the comparability of such approaches. Despite obvious links between muscle action and both external and internal bone dimensions (Pearson *et al.*, 2006; Stock & Shaw, 2007), questions remain regarding the extent to which it can said that both the approaches agree on the asymmetry they are measuring, particularly when applied to the same sample.

One direct attempt to answer this question has come from Maggiano *et al*. (2008a). They compared geometric properties of the bones of the upper limb (clavicle, humerus, radius and ulna) with MSM scores (using a Hawkey & Merbs, 1995 methodology) in two populations, Mexican Mayans and medieval Bavarians. Interestingly, they found that the two methods differed clearly in the degree of bilateral asymmetry they identified, in addition to the degree of sexual dimorphism, leading the authors to state that the two approaches supported different conclusions regarding the nature of asymmetry and sexual dimorphism in these samples. The authors therefore support the use of an inclusive approach to asymmetry research, incorporating both methods of analysis.

Further studies have investigated various aspects of this relationship and appear to support the conclusions of Maggiano and colleagues. Stirland (1998) compared cross-sectional properties of the humerus from her samples of medieval male skeletons from a Norwich cemetery and the *Mary Rose* with MSM scores for the *latissimus dorsi*, *pectoralis major*, *teres major* and *deltoid*. Stirland found a complex relationship between the expressions of these traits. For older adults in her study, there were no statistically significant relationships identified between MSM scores and cross-sectional dimensions. However a number of statistically significant relationships were found for the younger adult group. Within this younger group, increased cortical area was correlated with higher MSM scores for the *latissimus dorsi* (left- and right-side) but with low MSM scores for the left-side *deltoid* (right-side *deltoid* was not significantly correlated). Such inconsistencies between these methods supports the claim by Maggiano *et al.* (2008a) that a more inclusive approach is required in upper limb asymmetry research. In addition, Stirland (1998) cautions strongly against assessing individual muscle activities in isolation. An alternative view is proposed by Berget & Churchill (1994), namely that there is agreement between humeral hypertrophy (reflected in cross-sectional dimensions) and MSM expression in their sample of robust Aleut Islanders, although the exact quantitative nature of this relationship is not clear.

Weiss (2003) has attempted to further clarify this issue by comparing aggregate scores for muscle markers, humeral metric and geometric properties. The aggregate approach involves combining MSM scores (or humeral dimensions) across a number of sites in order to improve the statistical power of comparison and increasing the chances of identifying significant correlations. Interestingly, Weiss found that while single measures of MSM development or humeral size/shape were not significantly correlated with each other, increasing the number of dimensions compared produced statistically significant relationships between the bone properties (see also Weiss, 2007). Weiss (2003) interprets the negative findings of Stirland (1998) and Bridges (1997) as potentially resulting from not aggregating MSM scores. This adds further support to the notion that MSM research is hampered when muscles are studied as functionally isolated units.

The examples provided in this section clearly indicate the need for further study into the comparability of metric/geometric and MSM techniques. The methodological and statistical incongruence between the studies above serves to increase the necessity for further comparative work.

2.5. Conclusion

Sections 2.2 to 2.4 above highlight the complexities inherent in attempting to quantify a phenomenon which is itself problematic. A number of different approaches, metric, geometric and MSM-based, have been applied to this issue, and while there are clear problems bound up with each of these approaches they remain informative regarding the nature of upper limb bilateral asymmetry. When methodological issues and those regarding bones' functional adaptations to stress are taken into consideration an overall trend towards right-side dominant asymmetry emerges. Within this trend there is plenty of variation suggesting that it remains possible to infer certain behavioural traits from such approaches. However a certain degree of variation appears to be explainable from differences between the methods themselves, which often appear to differ in the magnitude of the asymmetry they are able to quantify. As each of these methods reflect aspects of bones' ability to deal with mechanical stress it may not be appropriate to continue to use these methods to make fine-grained inferences regarding activity patterns. As Stirland has suggested for the use of MSM analysis, "it is, therefore, unacceptable to relate the development of any single muscle to any particular activity or lifestyle; only groups of muscles may be so related" (1998: 361). While reducing the compulsion to over-analyse data for the purposes of inferring behaviours, it is also essential to have as much data as possible available for interpretation. To this end it is important not to rely on limited measurements taken on only one bone, and to include a range of measurements where possible. In particular the bones of the hand have often been neglected from metric and geometric studies, but especially from MSM analyses, and therefore it remains unclear the exact nature of asymmetry in this region. The same is also true for skeletal asymmetry in non-human primates, which is currently poorly understood. Given the controversy surrounding hand preference in live great ape groups, comparative data on skeletal upper limb asymmetries in these species could prove to be particularly informative. Properly applied, a comprehensive, inclusive and systematic approach to the study of upper limb bilateral asymmetries across skeletal regions has the potential to clarify certain issues surrounding the evolution of handedness within the lineage leading to *Homo sapiens*.

2.6. Aims of thesis

Our understanding of how asymmetry and handedness has developed and evolved in humans is, in part, determined by the measures used in its assessment. However, despite a number of methods available by which to quantify asymmetry (and therefore hand preference), there have been few attempts to synthesise an inclusive approach to understanding the complex expression of asymmetry in the upper limb of both humans and non-human primates. Such an approach is crucial if we are to fully understand the evolutionary history and development of handedness, a uniquely modern human phenomenon. This thesis therefore aims to address some of the problems surrounding the assessment of upper limb bilateral asymmetry in skeletal material. This will be done in two ways:

1) Comparing the expression of asymmetry in the bones of the hand with the humerus. With the general absence of the hand from studies of asymmetry and handedness, in both modern humans and non-human primates, the aim is to better understand the relative expression of asymmetry in this region of the upper limb and what it can tell us about handedness. Rather than studying one bone of the hand in isolation (e.g. the 2nd metacarpal), this study will incorporate a range of measurements across the metacarpals and phalanges which will be compared with corresponding measurements from the humerus, to gain as comprehensive a picture of asymmetry distribution as possible.

2) Comparing methods by which asymmetry can be assessed, namely through the analysis of metric and MSM dimensions. Past studies indicate discrepancies between these approaches, which is likely to be in degree rather than kind. However, further clarification of this relationship is necessary if these methods are used to be used interchangeably, rather than in tandem. This comparison will also provide an opportunity to systematically test an MSM

Chapter 3. Materials and Methods

The aims of this thesis are described in more detail in section 2.6 and address two separate, but inter-connected research questions:

1) What is the nature of the expression of asymmetry in the bones of the hand (which have historically been absent from considerations of upper limb bilateral asymmetry)? Asymmetry in the metacarpals and phalanges will be compared with asymmetry in the humeri to explore the extent to which asymmetry in the hands can be used to answer questions regarding human and primate hand use, but also the appropriateness of continuing to use humeral asymmetry as representative of functional asymmetry across the whole upper limb.
2) What is the relationship between the methods used to assess skeletal asymmetry? Bone robusticity and musculoskeletal stress marker (MSM) development are both frequently, and independently, used to assess asymmetry, but with little consideration of whether these methods provide congruent assessments of asymmetry. A comparison of these methods is therefore crucial to our understanding of the nature of upper limb bilateral asymmetry.

The following sections outline the skeletal materials used to answer these questions and the methods by which these data were analysed.

3.1. Materials

Data were collected from a range of skeletal material. Anatomically modern human material were studied from the medieval site of Écija in southern Spain (N = 65), and the Royal Naval Hospital cemetery in Greenwich, London (N = 31). Comparative data were also taken from a sample of great ape skeletons (N = 42; 21 chimpanzees and 21 gorillas) housed at the Powell-Cotton Museum in Birchington, Kent. A final human sample was studied from the Anglo-Saxon cemetery site in Great Chesterford, Essex (N = 24) for the purposes of performing an intra-observer reliability study. In total, 120 human skeletons and 42 non-human primate skeletons were analysed as part of this study.

The site of Écija (section 3.1.1) was chosen as the main site for investigation due to its large size of the collection (over 4500 individuals) and its distinctive cultural identity as a cemetery for the Muslim residents of the town. In addition, this site is distinguished by the large numbers of well-preserved hand bones, making it particularly suitable for inclusion in this study. The Naval Hospital cemetery site at Greenwich (section 3.1.2) provides a unique collection for investigation. As the name suggests, the site comprises almost exclusively of former military personnel, with documentation providing information regarding the sex, age, occupation, and often, cause of death for many of the individuals. With the current study aiming to explore variation in expression of MSM across and between the upper limbs, a sample in which data pertaining to the main confounding variables of MSM analysis can be known (e.g. sex, age, occupation) is particularly important. Material from the Anglo-Saxon cemetery at Great Chesterford in Essex (section 3.1.4), and curated at the University of Southampton, provided an opportunity to assess intra-observer reliability in this study. The relatively small sample size and often fragmentary nature of the collection meant that it was not suitable for inclusion in the main portion of the current study. However, skeletons from this site were initially measured in 2005 in order for the author to gain data collection experience and for the purposes of practising the osteological methods used in this study. The collection was re-measured in late 2007, after the main body of data collection was completed, and the data used for the purposes of intra-observer comparison.

Comparative data were collected on a sample of chimpanzees and gorillas from the Powell-Cotton Museum in Birchington, Kent (section 3.1.3), which houses an extensive collection of wild-caught African mammals. The large sample sizes (relative to other non-human primate collections), good preservation and cataloguing of the non-human primate material (i.e. all hand bones labelled and sorted by side) makes this collection particularly suitable for inclusion in the current study. While the expression of asymmetry in the upper limb of modern humans is expected to be pronounced and variable due to the nature of mechanical loading in the arm and shoulder, the converse is expected in non-human primates (Drapeau, 2008). With the upper limb of modern humans free from locomotor constraints, robusticity of the limb (and consequently the expression of asymmetry) is primarily influenced by functional recruitment in daily activities. In non-human primates, the upper limb is still strongly involved in locomotor behaviours and, therefore, it is expected that the arms and hands of chimpanzees and gorillas will exhibit a much lower degree of bilateral asymmetry as both limbs will be equally stressed by the requirements of locomotion. Following this assumption, chimpanzee and gorilla material was included in this study to serve as a ‘control’ group. If the non-human primate groups are found to highly asymmetric then this will call into question the representation of hand preference in skeletal populations. These data can also address more general questions regarding upper limb bilateral asymmetry in great ape samples, a topic that is relatively unexplored compared with that in humans (Sarringhaus *et al.*, 2005; Hopkins, 2008).

Sections 3.1.1 to 3.1.4, below, provide contextual information about each of the skeletal collections included in this study.

3.1.1. Écija

The town of Écija is situated approximately 80km east of Seville in Andalucía, southern Spain. The town occupies a strategically important spot on the Genil River in the Guadalquiver valley and the fertile land in this region, combined with the minerals found in the area have made it an important agricultural and mining town (Keay, 1988; Curchin, 1991). Although this region of Spain bears evidence of occupation dating back to the Lower Palaeolithic (Keay, 1998), there is little evidence of settlement at the site of Écija prior to the arrival of the Romans and the foundation of the town as a *Colonia Augusta Firma* by Augustus around the 1st century BC (Curchin, 1991). Under Roman governance, Astigi (as the town was known at the time) was an important centre for the production and distribution of olive oil, in addition to being an important judicial centre in the region (it was the capital of a *conventus*) and also a *colonia* (a settlement for retired legionaries) (Keay, 1988).

By the medieval period, the region and the town had passed into Visigothic control, until 711AD, when an invasion of Arabs and North African Berbers brought much of the Iberian Peninsula under the rule of the Umayyad caliphate in Damascus, and the region became known as al-Andalus (Reilly, 1993). During this time, Écija was a key town in the caliphate (and a site of one of the major battles in 711AD), until the abolition of the caliphate in 1031AD. After this time al-Andalus was ruled by the Almoravid Empire (in the 11th century) and subsequently the Almohad Empire (in the 12th century). By the middle of the 13th century, the Reconquista had returned most of the region to Christian rule and the Muslim population was expelled (Kennedy, 1996). Within al-Andalus, the majority of the population was Muslim, but this population was comprised of a diverse mix of peoples, including the invading Arabs and Berbers, Christians who adopted aspects of Muslim culture (known as Mozarabs), plus male slaves brought in from northern Europe (Reilly, 1993; Collins, 1995; Kennedy, 1996).

Excavation of Écija's Plaza de España between 1997 and 2002 uncovered the extensive Muslim cemetery (or *makbara*) directly on top of Roman ruins, which appears to have been in constant use from the first post-Visigothic settlement in the early 8th century until the region began to return to Christian rule in the 11th century (Jiménez n.d, Ortega n.d., Román n.d.). In osteological terms, Écija is of interest due to the size of the collection, the preservation of the material and the clear cultural identity of the sample. Clear rules regarding burial in Islamic society state that all individuals are equal in death. Bodies of the deceased must be wrapped or dressed in simple cloth and placed in graves without coffins, on their right side, facing Mecca. The depositing of grave goods is not permitted (Insoll, 1999). With the exception of the location of the *makbara* being inside the city walls rather than outside (Jiménez n.d, Ortega n.d., Román n.d.), it appears that many of these burial rules were closely followed. Therefore, the site of Écija provides an opportunity to study the influences of shared cultural practices on the morphology of a population likely to exhibit more diverse geographical origins. Within the context of the current study, this collection offers a large number of well-preserved hand bones for examination.

In total, over 4500 skeletons were excavated from the Écija site. Although the general preservation of individuals across the site was very good, a number of skeletons exhibited crushing due to the numerous grave layers deposited on the site. Therefore, not all individuals were suitable for study. From the site, 65 adults (35 male, 30 female) were included in the present study. These skeletons were selected primarily on the basis of good preservation of the hand bones, with good preservation of the humerus preferred where possible. Further selection criteria applied to this sample are described in section 3.2.

3.1.2. Greenwich Naval Hospital

The area of Greenwich, London is located in an important spot on the River Thames and there is evidence for almost continual habitation of the area, dating back to the Mesolithic period *(Boston et al., 2008)*. In 1692, Christopher Wren was commissioned to convert an uncompleted royal palace into a naval hospital and retirement home, to address a long-standing need for such facilities for the Royal Navy's disabled and elderly seamen and marines, veterans of Britain's conflicts with the Spanish, Dutch, French and Americans (*ibid*). The hospital was completed in 1703 and it was initially intended to house 100 men, but increasing demand saw the hospital reach an eventual maximum capacity of 2710 inpatients. The hospital was busiest during the period of 1815 to 1830 following the Napoleonic Wars (1803 – 1815), but as the veterans of these conflicts began to die, demand for places steadily decreased and the hospital finally closed in 1869. After this time the hospital buildings became the premises of the Royal Navy College, where the college can still be found today (*ibid*). The residents of the Greenwich Naval Hospital were comprised of the "rank and file of the Navy" (Boston *et al.*, 2008: 12), such as landmen, ordinary seamen, able seamen, marines, gunners, cooks, carpenters and other skilled workmen. Landmen (i.e. those with no experience of working at sea) were likely to be engaged in 'unskilled' tasks such as hoisting and lowering sails, rigging tackle, swabbing desks and moving loads around the ship. Ordinary seamen and able seamen were more experienced in sailing and would also be involved in tasks such as reefing and steering. Marines were not involved in sailing the ship, but were employed as soldiers and onboard 'policemen' (*ibid*). Overall, the daily tasks engaged in by the majority of these men can be considered strenuous, and are likely to have placed significant stress on both the arms and the hands. These are also activities that are likely to have recruited both upper limbs to the same extent.

Excavations between 1999 and 2001 as part of a redevelopment of the area recovered a total of 107 skeletons from the cemetery grounds. It is estimated that the grounds originally held up to 20,000 burials, but development and earlier excavations of the area have greatly reduced the numbers of remaining bodies (Boston *et al.,* 2008). The vast majority of these individuals from this most recent excavation were adult (N = 105), although two sub-adults were also identified. While most of the adult skeletons were male (N = 97), seven of the individuals were identified as female. One individual could not be sexed. The general elderly age profile of the Greenwich sample was known from the associated Royal Navy historical records. The advanced age of the individuals, however, made exact age at death difficult to determine (*ibid.*). A number of methods for assessing age were therefore applied to improve the accuracy of estimations (see section 3.2, below). All of the adults considered for study in the current analysis were considered to be approximately 30 years of age and above, although the majority were assessed to be greater than 40 years old. One of the most interesting features of this collection is the vast range of medical conditions reflected in skeletal modifications. The aetiologies of these modifications encompass trauma, infection, metabolic disorders, joint disease, and congenital abnormalities and are distributed across the postcranial and cranial skeleton. Unsurprisingly, there was also evidence of medical interventions such as amputations and craniotomies. The degree of pathology is extensive, with approximately 85% of individuals exhibiting at least one fracture and 100% of individuals exhibiting symptoms of degenerative joint disease in the spine (*ibid.*). This prevalence of pathological changes to the skeleton clearly reflects the arduous physical conditions under which these seamen worked. Interestingly, injuries to the hand were also found to be particularly common in this sample and may have been a result of boxing and interpersonal violence aboard ship. The location of the majority of these injuries in the right hand has led Boston *et al.* (2008) to suggest a right-hand dominance in this sample.

This collection therefore provides a unique opportunity to study bilateral asymmetry in a sample for which age, sex and occupation are well-documented. Due to the extensive range of pathological conditions identified in the skeletons of the Greenwich inpatients, much of the material was not suitable for study. This was due to the presence of skeletal modification which is likely to have impeded normal function of the upper limb. This is discussed further in section 3.2. From this collection, 31 skeletons were selected for inclusion in the current study. Further selection criteria applied to this sample are described in section 3.2.

3.1.3. Non-human primate material

The Powell-Cotton Museum at Quex House near Canterbury, Kent houses an extensive collection of African mammals including approximately 1800 African primates, comprising mostly *Gorilla*, *Pan*, *Papio*, *Colobus*, *Cercopithecus*, *Cercocebus*, *Galago* and *Perodicticus* species. Major Percy Horace Gordon Powell-Cotton was a well-known hunter and naturalist, and established the collection in his museum at Quex House as a result of his hunting expeditions in Africa carried out between the late 1800s and his death in 1940. Major Powell-Cotton observed the destruction of African habitats, environments and traditional ways of life and saw his collection of African animals and ethnographic material as a way of preserving these species and cultural traditions for future generations. Rather than being simply a trophy hunter, Major Powell-Cotton understood the need for conservation and research. He therefore collected specimens for the purpose of facilitating ongoing scientific study (Merfield, 1957). A large proportion of the specimens in the Powell-Cotton Museum were caught by Fred Merfield, a long-time colleague of the Major (see Merfield [1957] for a lively autobiographical account of Mr Merfield's time in Africa).

Of the 199 chimpanzees in the Powell-Cotton collection, 21 adult individuals (9 male, 12 female) were selected for inclusion in the present study. All the chimpanzees in the sample are *Pan troglodytes schweinfurthii* and the majority were caught by Fred Merfield in the Batouri region of Cameroon, western Africa (formerly the French Cameroons) between 1932 and 1939. The remaining 4 chimpanzees were also caught in Cameroon between 1929 and 1935 by Kurt Zenkerman, local hunters and Major Powell-Cotton himself. Of the 242 gorillas in the Powell-Cotton collection, 21 adult individuals (10 male, 11 female) make up the sample used in this study. The sample is comprised exclusively of Western Lowland Gorillas, *Gorilla gorilla gorilla*. Once again, the large majority of the sample was caught by Fred Merfield in the Batourie region of Cameroon between 1932 and 1935. An additional three individuals were bought from local hunters in the Yaoundie region, although no date was noted for the purchases. Further selection criteria applied to this sample are described in section 3.2.

3.1.4. Great Chesterford

Great Chesterfield is the site of a Roman town on the River Cam, south of Cambridge, Essex. Commercial gravel digging in 1952 revealed the presence of Anglo-Saxon burials close to the known location of a Roman cemetery. Excavations were subsequently carried out on the site between 1953 and 1955, initially by FK Annable, on behalf of the Inspectorate of Ancient Monuments, and continued by Vera Evison (Evison, 1994). The excavations uncovered a total of 161 inhumation graves and 33 cremations, in addition to 2 horse graves and 2 dog graves. It is believed that this only represents a fraction of the number of burials likely to have been present at the site, as many were destroyed through gravel digging, ploughing of the area and the later construction of part of the M11 motorway in 1977 (*ibid.*). From the datable material found at the site, the cemetery is thought to span the period between 450 – 600AD, although it is likely that graves from the early 5th and 7th centuries were destroyed before they could be excavated (*ibid.*).

The presence and distribution of grave goods at the site suggest that Great Chesterford was of a comparable economic standard to other Anglo-Saxon sites in the surrounding area (Evison, 1994). Some questions were raised about the identity of a number of males at the site who were buried without weapons, and some who were buried without any grave goods at all. It has been suggested by

Evison (1994) that these graves may represent the burials of non-local merchants (in the case of the weaponless graves) and slaves (in the case of the findless graves). What is perhaps most interesting about the Great Chesterford site is the high proportion of juveniles identified compared with other known Anglo-Saxon burial grounds. Of the 167 individuals represented at the site, 78 (46.7%) were less than 15 years old, including 5 foetuses less than 40 weeks old, 12 ‘stillborn’ infants and 26 neonates less than 2 months old (Waldron, 1994). These figures reflect the high child mortality rate within this Anglo-Saxon population, but also calls into question the discrepancy between these figures and those from other Anglo-Saxon sites. As Evison (1994) points out, the percentage of juveniles at Great Chesterford may be a more accurate representation of Anglo-Saxon mortality rates and the reasons for the apparent under-representation at other sites should be investigated further.

From the Great Chesterford collection, twenty-four adult skeletons, comprising twelve males and twelve females, were selected for study. Further selection criteria applied to this sample are described in section 3.2.

3.2. Methods

For the samples described above, a number of selection criteria were applied to identify skeletons suitable for inclusion in the present study. Only individuals classed as ‘adult’ were selected. Although the definition of ‘adult’ has been debated (e.g. Smith & Jungers, 1997), in this study it is taken to mean those individuals who exhibit epiphyseal fusion of the long bones and therefore have reached their full height and skeletal maturity. While the long bones are still growing there will be continual migration of MSM and change in the size and shape of the bones, making sub-adults unsuitable for study (Hawkey & Merbs, 1995). In addition, identification of the eruption of the M3 and fusion of the spheno-occipital synchondrosis were used to confirm adult status where appropriate. These criteria were applied to both the modern human and the non-human primate material.

Sexing and ageing of the material was undertaken using standard osteological techniques. To assign sex, features of the pelvis and cranium were used. Epiphyseal fusion, pelvic morphology and cranial suture fusion was used to assign skeletons to an age category. The methods by which the skeletons were sexed and aged are outlined in Todd (1920, 1921), Ferembach *et al.* (1980), Brothwell (1981), Lovejoy *et al.* (1985), Krogman & İşcan (1986), Brooks & Suchey (1990), Buikstra & Ubelaker (1994), Schwartz (1995) and O’Connell (2004).

The state of preservation of the skeletal material was also an important selection criterion. Accurate assessment of bilateral asymmetry was reliant on paired left and right side bones being available for study. In addition, reasonable preservation of the cortical surface of the bone was necessary to facilitate accurate assessment of MSM development (particularly for the smaller bones and MSM sites). In order to maximise the number of hand bones available for study, more fragmentary humeral material was included if its accompanying hand bones were more complete. For this reason, humerus sample sizes may be lower than hand bone sample sizes in certain instances. This is particularly true for the Écija sample, in which many of the humeri have suffered post-mortem crushing.

Skeletal material was checked for the presence of pathology before selection. Individuals were excluded if they exhibited pathology which would have been likely to inhibit the normal functioning of the upper limb (and therefore influence the expression of asymmetry) over the course of their adult life, such as, for example, fractures or amputation. In the case of osteoarthritis (OA), while the preferred situation was to exclude all individuals exhibiting arthritic characteristics, it was decided to only exclude those individuals displaying more serious symptoms, i.e. showing evidence of joint surface remodelling (e.g. severe lipping), pitting and eburnation. Those individuals showing only mild lipping were included as mild OA is a common finding in older individuals and therefore likely to be age-related (Mann & Murphy, 1990). While mild OA may be present skeletally or radiographically, it is often not symptomatic in the effected individual and is unlikely to significantly compromise joint mobility (Haslett *et al.*, 2002; Kumar & Clark, 2002). In the Greenwich Naval Hospital sample, almost all the individuals exhibited at least mild OA symptoms. This was particularly common in the elbows, wrists, and hands, and so it was impossible to exclude all individuals displaying slight OA symptoms while maintaining a statistically useful sample size.

In order to make confident assessments of asymmetry in the skeletal samples studied, accurate siding of bones was necessary. This is particularly an issue for excavated hand bone material, where the bones are often stored as one commingled unit. For the humerus and metacarpal material in this study, siding was straightforward and carried out using the methods described in White & Folkens (2000) and Matshes *et al.* (2005). Siding of the phalanges, however, is much more difficult due to the subtle differences in the morphology of these bones. The majority of the phalanx material in this study was sorted by side immediately post-excavation. However, a proportion of individuals (mostly from the Écija site) had hands bagged together, thus requiring siding of the phalanges. Until recently, the only available methodology for siding phalanges existed in an unpublished doctoral dissertation (Ricklan, 1988), meaning that it has not been widely applied and tested on different collections. Case & Heilman (2006) have proposed a method for siding phalanx bones, based on study of articulated hands (where correct side was known) from the Terry Collection and incorporating aspects of Ricklan's (1988) methodology. The Case & Heilman study found that in general, phalanx siding accuracy was high, although there was clear variation in accuracy between the phalanx rows. Proximal phalanges were sided most accurately (100% accuracy for proximal phalanx 1, down to 88% accuracy for proximal phalanx 5), followed by the intermediate phalanges (98% accuracy for intermediate phalanx 5, down to 78% accuracy for intermediate phalanx 4). Distal phalanx siding proved to be the least accurate (94% accuracy for distal phalanx 1, down to 52% accuracy for distal phalanx 2). The results of this test suggest that care must be taken when endeavouring to side phalanges. However, further testing and refinement of phalanx siding methods must be attempted in order to increase the availability of phalanx data for research. The current study provides an opportunity to apply the methods proposed by Case & Heilman (2006) on a 'real world' sample from a different temporal and cultural context. However, as it is not possible to know the 'true' siding of excavated phalanges, caution needs to be exercised when interpreting these results.

The following sections will describe the methods by which metric and MSM data were collected in more detail.

3.2.1. Metric analysis

Standard metric data were collected on the bones of the hand and upper arm in all of the skeletal collections selected for study. Although the trend in studies of upper limb morphology and robusticity studies has favoured cross-sectional, geometric data (e.g. Ruff *et al.*, 2006), only external metric properties were analysed in the current study. Computer tomographic (CT) and radiographic imaging facilities were not available for this study, therefore the collection of metric data was favoured. This approach was relatively quick and inexpensive and allowed a larger quantity of hand bone data to be collected. No specialist equipment (other than callipers) was required and the method was non-destructive. Although geometric methods dominate robusticity and asymmetry research (see section 2.2.2 for further discussion of this approach), recent research has identified a correlation between external metric and cross-sectional geometric bone properties (Pearson *et al.*, 2006; Stock & Shaw, 2007). While a relationship might be expected between inter-connected bone properties, little experimental research has been carried out to confirm this association (Stock & Shaw, 2007). Stock & Shaw (2007) investigated the statistical relationship between measures of diaphyseal robusticity (circumference, maximum and minimum diameter, total subperiosteal area) and cross-sectional properties pertaining to bone strength (second moment of area, $I_{\max/\min}$, and polar second moment of area, J) in the long bones and clavicle. They found relatively strong correlations between diaphyseal properties and polar second moment of area, particularly for humeral measurements (with r^2 ranging from 0.964 to 0.992). Substantial prediction error was often identified for these correlations, although the authors found that deriving external diaphyseal properties from periosteal contour moulding (see Stock, 2002 for further description of the technique) increased the strength of the correlations and reduced prediction error. This method was not available for use in the current study, but provides an interesting alternative to the more commonly used data collection techniques. Pearson *et al.* (2006)

compared diaphyseal shape indices (based on midshaft diameters) and robusticity indices (based on the ratio of midshaft diameter to articular breadth) with cross-sectional properties ($I_{max/min}$ and J) in the humerus, femur and tibia. They once again found strong correlations between humeral indices and J ($r^2 = 0.81$) and $I_{max/min}$ ($r^2 = 0.88$). When humerus external dimensions were used to predict J, the r^2 value was found to be high ($r^2 = 0.90$). A further study by Pearson *et al.* (n.d.) has also found a reasonably strong correlation between external long bone dimensions and cross-sectional properties, with prediction error lower than that found by Stock & Shaw (2007). In contrast to the other studies described here, lower limb external dimensions (particularly for the tibia) showed stronger correlations with cross-sectional properties than upper limb dimensions. Together, the findings of these studies suggest that in the absence of more sophisticated imaging equipment, external diaphyseal properties can predict cross-sectional bone properties with a reasonable degree of accuracy. In the context of the current study the findings add support to the collection of metric data on the hands and humeri included in this study.

Section 3.2.1.1 (below) details the metric data collected on the hand bones and section 3.2.1.2 (below) details the humerus measurements taken. Measurements were selected to represent a range of shaft and articular surface measurements, with the aim being to gain as much information as possible pertaining to asymmetry expression in the upper limb. Most measurements were taken with a standard set of plastic vernier dial callipers with a 0.1mm scale. Humerus length measurements were taken on an osteometric board. Humerus midshaft and head circumference measurements were taken with a tape measure. The same methods were applied to both the human and the non-human primate material.

3.2.1.1. Hand bone measurements

In total, 39 measurements were taken on each hand, 5 on each metacarpal (25 in total), and one on each phalanx (14 in total). Table 3.1, below, describes the measurements taken in more detail. All metacarpal and phalanx measurements were taken according to Braüer (1988). Due to the relative lack of observable MSM, the carpal bones were not included in the current study.

Figure 3.1, below, provides a visual representation of the location of these measurements on the metacarpals. Phalanx length was taken in the same way as metacarpal length and is not shown here.

Table 3.1. Metric properties of the metacarpals and phalanges measured in the current study, as outlined in Braüer (1988).

Braüer code	Code used in study	Metacarpal and phalanx measurement	Description of measurement
2	mc*L	Length	Straight distance from the middle point of the surface of the base to the topmost point of the head
6	mc*RU	Radio-ulnar midshaft diameter	Maximum distance from the radial to the ulnar side of the shaft at its midpoint, perpendicular to the long axis of the bone
7	mc*DP	Dorso-palmar midshaft diameter	Same as measurement 6 (above) but taken parallel to the long axis of the bone
8	mc*PB	Maximum proximal breadth	Maximum breadth of the proximal end of the bone, measured perpendicular to the long axis of the bone
9	mc*DB	Maximum distal breadth	Maximum breadth of the distal end of the bone, measured perpendicular to the long axis of the bone
3	pp*L	Length of proximal phalanx	Straight distance from the middle point of the surface of the base to the topmost point of the head
3	ip*L	Length of intermediate phalanx	Same as above
3	dp*L	Length of distal phalanx	Same as above

Asterisk (*) denotes metacarpal or phalanx number, e.g. mc1L, mc2L, etc.

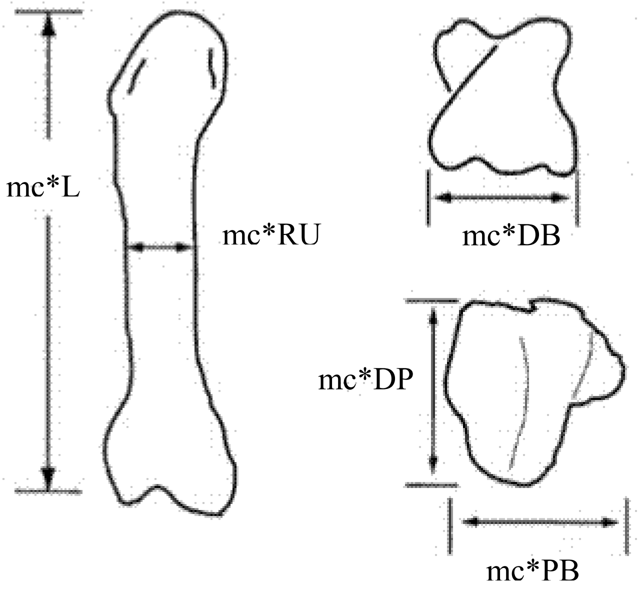


Figure 3.1. Measurements taken on the metacarpals, as defined in Table 3.1. Mc*L = metacarpal length, mc*RU = radio-ulnar midshaft diameter, mc*DP = dorso-palmar midshaft diameter (as measured at midshaft), mc*DB = maximum distal breadth, mc*PB = maximum proximal breadth. Asterisk (*) denotes the metacarpal number, e.g. mc1L, mc2L. After Lazenby (2002b).

3.2.1.2. Humerus measurements

For the purposes of comparison with the metacarpals and phalanges, asymmetry was also assessed in the associated humeri for each of the skeletal samples. A total of nine measurements were taken on the humerus, representing a range of shaft and articular surface dimensions. Measurements were taken following Martin & Saller (1957) and are described in detail in Table 3.2, below. The humerus was selected for comparison with the metacarpals and phalanges as it is commonly included in skeletal studies of upper limb bilateral asymmetry and hand preference, thus providing a body of literature with which to compare the result of the current study.

Figure 3.2, below, provides a visual representation of the location of these measurements on the humerus.

Table 3.2. Metric properties of the humerus measured in the current study, as outlined in Martin & Saller (1957).

Martin & Saller code	Code used in study	Humerus measurement	Description of measurement
1	MxL	Maximum length	Straight distance from the highest point on the humeral head to the deepest point of the trochlea
5	MxDm	Maximum diameter at midshaft	Greatest diameter at the midshaft, regardless of the sagittal or transverse plane
6	MnDm	Minimum diameter at midshaft	Smallest diameter at the midshaft, regardless of the edge or location of the maximum diameter
7	MnCir	Minimum circumference of shaft	Thinnest point on the shaft, usually slightly below the deltoid tuberosity
8	CirHd	Circumference of head	Circumference of the head, measured around the outer edge (cartilage boundary)
9	MxTDm	Maximum transverse diameter of head	Straight distance between the two most protruding points of the edge of the head in the horizontal plane (if the humerus is in the vertical position)
10	MxSDm	Maximum sagittal diameter of head	Straight distance from the highest to the deepest point of the edge of the head, perpendicular to the transverse diameter
4	EpBr	Epiphyseal diameter	Distance from the highest projecting point on the lateral epicondyle to the corresponding point on the medial epicondyle
12a	TCBr	Trochlea-Capitulum breadth	Distance from the middle point of the outer edge of the trochlea to the middle point of the outer edge of the capitulum.

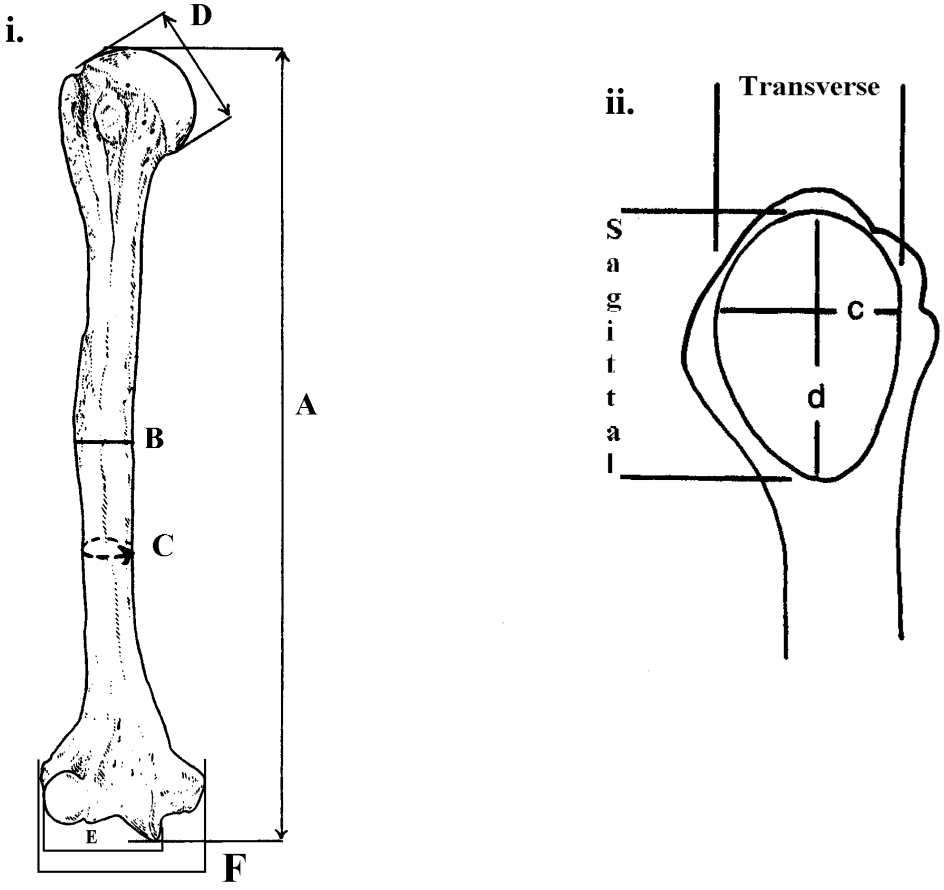


Figure 3.2. i) Measurements taken on the humerus, as defined in Table 3.2. A = maximum diameter, B = maximum and minimum diameter of midshaft, C = minimum circumference of shaft, D = diameter measurements of head, E = trochlea-capitulum breadth, F = epiphyseal diameter. ii) Measurements taken on the humerus head in more detail, c = transverse diameter, and d = sagittal diameter. After Bass (1995).

3.2.2. Musculoskeletal stress marker (MSM) analysis

Assessment of MSM development has also been used to ascertain the degree of upper limb bilateral asymmetry in skeletal samples, although perhaps not to the same extent as metric and geometric methods. Traditionally, the assessment of MSM development has been qualitative in nature, commonly using the ordinal scaling system proposed by Hawkey & Merbs (1995). In their scheme, the development of muscle attachment sites is graded in three categories: robusticity, stress lesion and ossification exostosis, and is rated on an ordinal scale, where 0 = no development, 1 = faint development, 2 = moderate development and 3 = strong development. The qualitative nature of this method has been criticised by some authors (e.g. Robb, 1998; Wilczak, 1998), although more quantitative approaches to studying MSM development have met with limited success (Stirland, 1993; Wilczak, 1998). One alternative approach, proposed by al-Oumaoui *et al.* (2004), employs a simple presence/absence method, scoring MSM as either ‘present’ or ‘absent’ (Figure 3.3., below). This approach can potentially remove some of the ‘subjectivity’ of the Hawkey & Merbs (1995) method, by having MSM exist in a binary state.

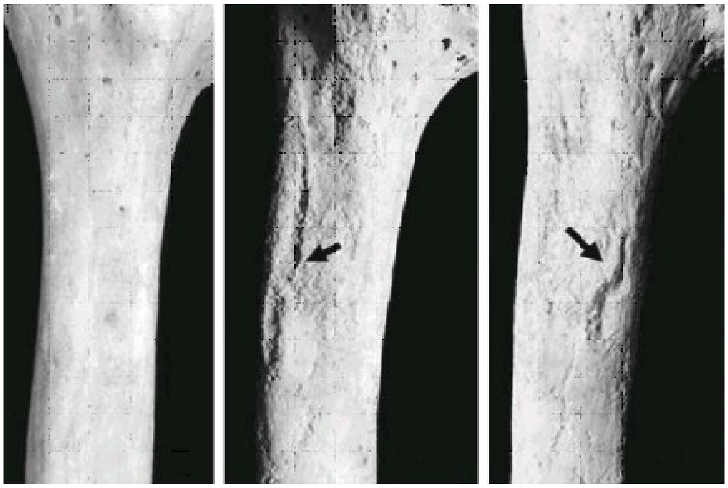


Figure 3.3. Criteria by which ‘presence’ and ‘absence’ of MSM in the humerus is judged, as defined by al-Oumaoui *et al.* (2004). From L-R: Absence of *pectoralis* and *teres major* markers; presence of *pectoralis* marker; presence of *teres major* marker.

While a certain amount of information regarding MSM development may be lost using a presence/absence technique such as that proposed by al-Oumaoui *et al.* (2004), this technique has the potential to allow analysis of MSM smaller in size or perhaps exhibiting less variation than those more commonly studied, such as those in the hand. It is for these reasons that Robb (1998) stated that the MSM of the hand were not suitable for analysis using a Hawkey & Merbs (1995) type method. The paucity of MSM studies in the region of the hand make it unclear the extent to which hand MSM reflect laterality of hand use in past populations, and how this compares with more commonly studied regions of the upper limb. It is also unclear how suitable MSM analysis is for reflecting occupational laterality. Applying the presence/absence method to analyses of MSM in the hand provides an opportunity to address these questions.

The following sections outline how MSM development in the hands and humerus was assessed using a presence/absence approach such as that advocated by al-Oumaoui *et al.* (2004). By applying this methodology to both the hands and the humerus, it was possible to compare asymmetry in MSM expression across the upper limb, irrespective of the size differences between the bones.

3.2.2.1. MSM analysis in the hand

To date, no systematic assessment of MSM development in the hand has been attempted and therefore there were no available guidelines as to which MSM would be most suitable for study. Research led by Mary Marzke (Marzke *et al.,* 1998) which measured, using electromyography (EMG), the activation of muscles recruited during experimental Oldowan tool manufacture identified a group of ten muscles that were most frequently active during this process (Table 3.3). The majority of these muscles (8/10) were intrinsic to the hand (i.e. originating from and inserting onto bones of the hand), suggesting that the bones and MSM of the hand have the potential to provide considerable information regarding the asymmetric use of the hands in past populations, information that is being missed by studies focusing only on extrinsic muscles and those of the arm. It was therefore decided to use these ten muscles as a starting point for the identification and assessment of MSM development in the hand.

Table 3.3. Ten muscles identified by Marzke *et al.* (1998) through EMG analysis as most commonly recruited during the experimental Oldowan tool manufacture.

Muscles in the thenar (thumb/index finger) region of the hand	Muscles in the hypothenar (5th finger) region of the hand
Flexor pollicis brevis Dorsal interosseous 1 Flexor digitorum profundus 2 Oppenens pollicis Adductor pollicis (transverse) Palmar interosseous 1	Flexor carpi ulnaris Flexor digitorum profundus 5 Abductor digiti minimi Flexor digiti minimi

A pilot study was undertaken on skeletal material from the University of Southampton osteological collection (including the Great Chesterford collection, see section 3.1.4) to practise the osteological methods used in the current study and to test the validity of the presence/absence methodology. During the course of this study, it was noted that a number of the muscle attachment sites highlighted in Table 3.3 could not be reliably identified on the skeletal material, due either to a general lack of any discernible development of the attachment area, or because multiple muscles were attaching to the bone in the same area, making identification of individual MSM impossible. It was therefore decided to expand the analysis to include all muscle attachment sites that could be readily and repeatedly identified on the bones of the hand. Five of the MSM outlined in Table 3.3 were deemed suitable for inclusion in the current study, with a further seven MSM identified during the pilot study. The complete list of hand MSM included in this study, plus their anatomical location and muscle function, is outlined in Table 3.4 (below). All the MSM described in Table 3.4 originate from or insert onto the metacarpals and phalanges. No carpal MSM were included due to problems with reliably identifying MSM in this region.

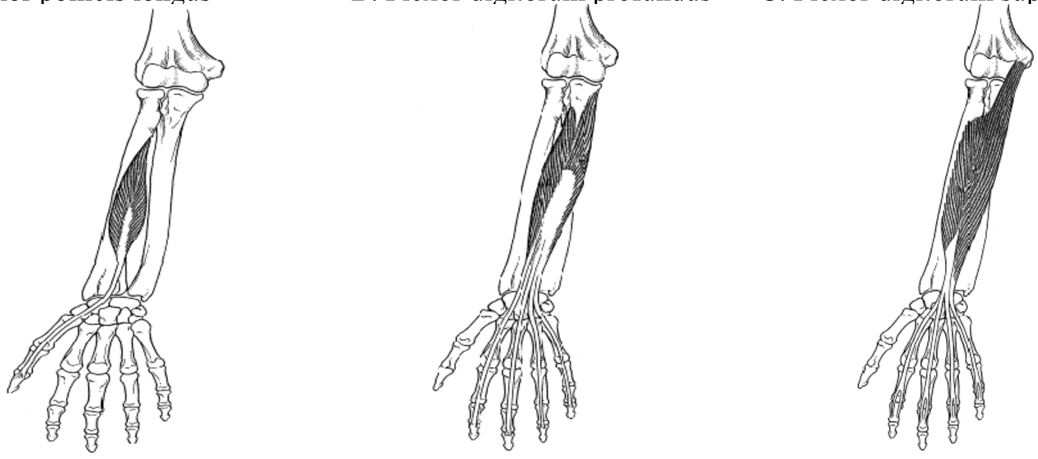
Figure 3.4 (below) provides a diagrammatic representation of each of the hand muscles whose MSM are included in the present study, outlining both the area of origin and insertion.

Table 3.4. Description of the location and function of the MSM of the hands included in present study.

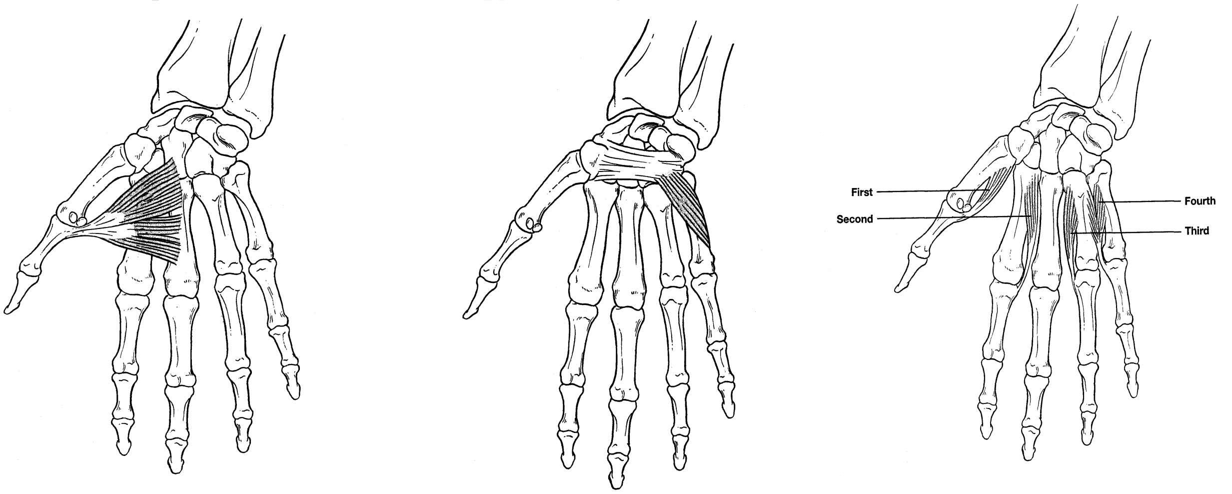
Code used in study	Hand MSM	Location of MSM	Action of muscle
FPL	Flexor pollicis longus (I)	Palmar surface of base of distal pollical phalanx	Flexion of thumb
APT	Adductor pollicis (transverse) (O)	Palmar surface of third metacarpal	Adduction and flexion of thumb
ODM	Oppenens digiti minimi (I)	Medial edge of fifth metacarpal	Rotation of mc5 into opposition with thumb, draw mc5 forward, assists in flexion of 5th carpometacarpal joint
FDP	Flexor digitorum profundus 2,3,4 +5 (I)	Palmar surface of base of distal phalanges 2,3,4 +5	Flexion of distal interphalangeal joints of digits 2 - 5. Assists in adduction of 2nd, 4th and 5th digits and in flexion at wrist
FDS	Flexor digitorum superficialis 2,3,4 +5 (I)	Both sides of the palmar surface of intermediate phalanges 2,3,4 +5	Flexion of intermediate phalanges of digits 2 – 5, plus flexion of wrist
PI2	Palmar interosseous 2 (O)	Palmar surface of second metacarpal	Adduction of digits towards centre of 3rd digit, at metacarpophalangeal joints.
PI3	Palmar interosseous 3 (O)	Palmar surface of fourth metacarpal	Assist in flexion of digits at these joints
PI4	Palmar interosseous 4 (O)	Palmar surface of fifth metacarpal	
DI1	Dorsal interosseous 1 (O)	Medial edge of mc1 & lateral edge of mc2	Abduction of 2nd, 3rd and 4th digits from the midline of the hand
DI2	Dorsal interosseous 2 (O)	Medial edge of mc2 & lateral edge of mc3	
DI3	Dorsal interosseous 3 (O)	Medial edge of mc3 & lateral edge of mc4	
DI4	Dorsal interosseous 4 (O)	Medial edge of mc4 & lateral edge of mc5	

After Bowden & Bowden (2005). O = origin of muscle, I = insertion of muscle.

A. Flexor pollicis longus B. Flexor digitorum profundus C. Flexor digitorum superficialis



D. Adductor pollicis (transverse) E. Opponens digiti minimi F. Palmar interossei



G. Dorsal interossei

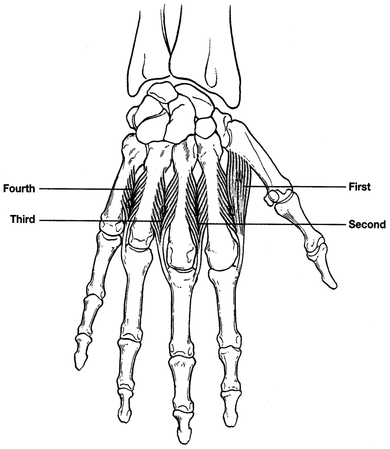


Figure 3.4. Origin and insertion sites of hand muscles whose MSM are included in current study: (a) flexor pollicis longus, (b) flexor digitorum profundus 2-5, (c) flexor digitorum superficialis 2-5, (d) adductor pollicis (transverse), (e) oppenens digiti minimi, (f) palmar interossei, (g) dorsal interossei. The flexor digitorum superficialis originates from the common flexor origin on the medial epicondyle of the distal humerus, described in section 3.2.2.2. After Bowden & Bowden (2005).

For the purposes of comparison, Figure 3.5 provides the relative positions of all muscle origin and insertion sites in the hand, in both palmar and dorsal aspects.

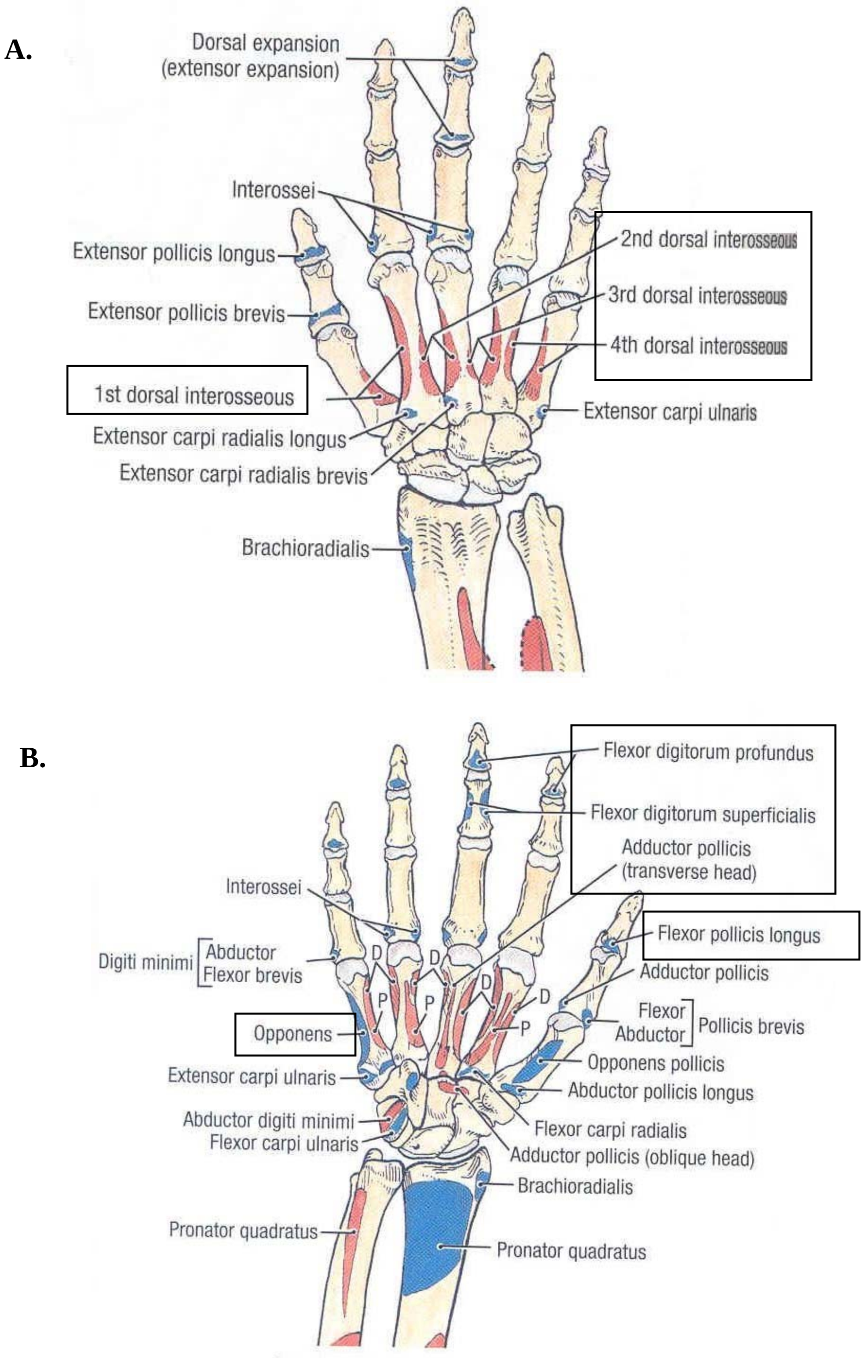


Figure 3.5. The relative positions of all sites of muscle origin (red) and insertion (blue) in the hands: A) dorsal aspect of the right hand, B) palmar aspect of the right hand. Muscle attachment sites included in the current study highlighted in boxes. After Agur & Dalley (2005).

The early pilot study established a set of diagnostic criteria for the identification of ‘present’ and ‘absent’ MSM. As MSM were being scored on a binary scale, it was important to establish the boundary between a MSM being ‘absent’ or ‘present’. Determination of a ‘present’ MSM was primarily based on visual identification of pronounced development of an attachment site with the naked eye. This 'development' was taken to mean the presence of bone deposition and/or bone resorption, thus combining aspects of the Hawkey & Merbs (1995) robusticity and stress lesion categories. It does not rely on the presence of cortical defects as is the case for the presence/absence method as applied to the MSM of the humerus by al-Oumaoui *et al.* (2004). Such an approach therefore maximises the MSM data available for the hands. Due to the small size of many of the MSM sites, the presence of dirt, plus the taphonomic damage suffered by many of the specimens, tactile confirmation of the presence or absence of MSM was also employed. This was done simply by rubbing the index finger along the bone. Figure 3.6 (below), provides an example of the visual criteria used for scoring the *opponens digiti minimi* as present or absent. Visual identification criteria for the remaining hand MSM can be found in Appendix A.1.

Figure 3.6. Visual criteria used to determine (A) absence, and (B) presence of the *opponens digiti minimi* MSM on the medial side of the 5th metacarpal. Area of muscle attachment site highlighted within the circle.

This presence/absence method for identifying MSM was applied in the same manner to the MSM of both the human and non-human primate samples. With the exception of the *flexor pollicis longus* muscle, all the muscles identified in the human samples are also present in the chimpanzee and gorilla samples. The location of hand MSM is broadly similar between humans and chimpanzees (Swindler & Wood, 1973). Data pertaining to upper limb musculature in *Gorilla* is limited (Aiello & Dean, 1990), but the pattern of MSM in the gorilla skeletal material was considered to be the same as that seen in chimpanzees. A recent study of gorilla and chimpanzee MSM development in the humerus (Drapeau, 2008), incorporating the same MSM as the current study, provides a statistical basis for the assumption that MSM development follows similar trajectories in modern humans, gorillas and chimpanzees. This therefore supports the application of the MSM technique across the three species included in the current study.

3.2.2.2. MSM analysis in the humerus

For the purposes of comparison with the hand, and to assess the efficacy of the presence/absence method on a more commonly studied region of the appendicular skeleton, MSM development was scored for all nine muscle insertion sites on the humerus. Insertion sites were selected rather than origin sites in this analysis as sites of muscle insertion are likely to exhibit more observable variation than sites of muscle origin, being most influenced by differing muscle activity during the life of an individual (Marieb, 2004). The common flexor origin and the common extensor origin sites were also included in the analysis due to the relative ease of identification of the MSM, and for the common flexor origin, as a point of comparison with the flexor insertion sites in the hands. Table 3.5 (below) provides the complete list of humerus MSM included in this study, plus their anatomical location and muscle function.

Figure 3.7 (below) provides a diagrammatic representation of each of the humerus muscles whose MSM are included in the present study, outlining both the area of origin and insertion.

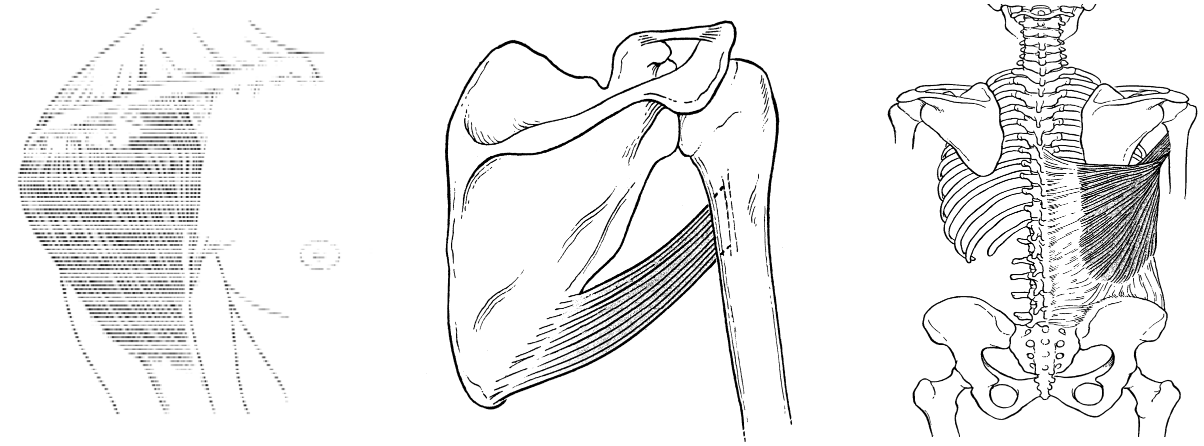
Figure 3.8 (below) gives the relative positions of all muscle origin and insertion sites on the humerus, in both anterior and posterior aspects.

Visual identification criteria for the presence and absence in the humerus MSM can be found in Appendix A.2.

Table 3.5. Description of the location and function of the MSM of the humerus included in present study.

Code used in study	Humerus MSM	Location of MSM	Action of muscle
Delt	Deltoideus	Deltoid tuberosity	*Anterior portion* – flexion and medial rotation of arm *Middle portion* – abduction of arm *Posterior portion* – extension and lateral rotation of arm
TMj	Teres major	Medial lip of intertubercular groove	Medial rotation and adduction of arm
LD	Latissimus dorsi	Floor of intertubercular groove	Extension, adduction and medial rotation of the arm. Draws shoulder downwards and backwards
PM	Pectoralis major	Lateral lip of the intertubercular groove	Adduction and medial rotation of arm. Clavicular head flexes humerus, sternal head extends humerus, and with insertion fixed it assists in elevation of thorax
CB	Coracobrachialis	Antero-medial surface of midshaft, opposite deltoid tuberosity	Flexion and adduction of humerus
IS	Infraspinatus	Middle part of greater tubercle and shoulder joint capsule	Lateral rotation of humerus. Stabilises humeral head in glenoid cavity. “Rotator cuff” muscle
SSp	Supraspinatus	Superior part of greater tubercle and shoulder joint capsule	Abducts arm and stabilisation of humeral head in glenoid cavity. “Rotator cuff” muscle
TMn	Teres minor	Inferior part of greater tubercle and shoulder joint capsule	Lateral rotation of arm. Draws humerus towards glenoid cavity
SSc	Subscapularis	Lesser tubercle and ventral part of the capsule of shoulder joint	Medial rotation of humerus and stabilisation of humeral head in glenoid cavity
CFO	Common flexor origin	Medial epicondyle of distal humerus	Various muscles involved in flexion of the hand and wrist
CEO	Common extensor origin	Lateral epicondyle of distal humerus	Various muscles involved in extension of the hand and wrist

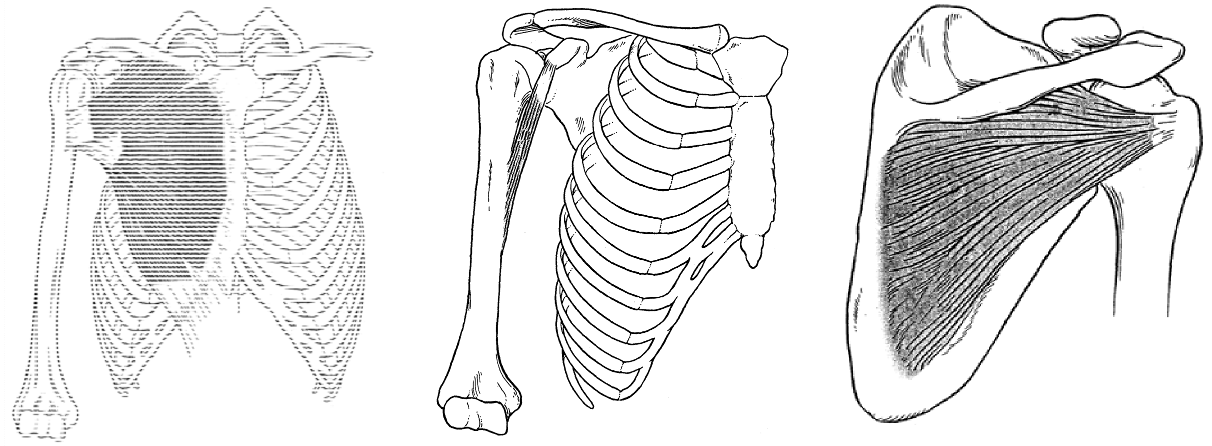
After Bowden & Bowden (2005).



A. Deltoideus

B. Teres major

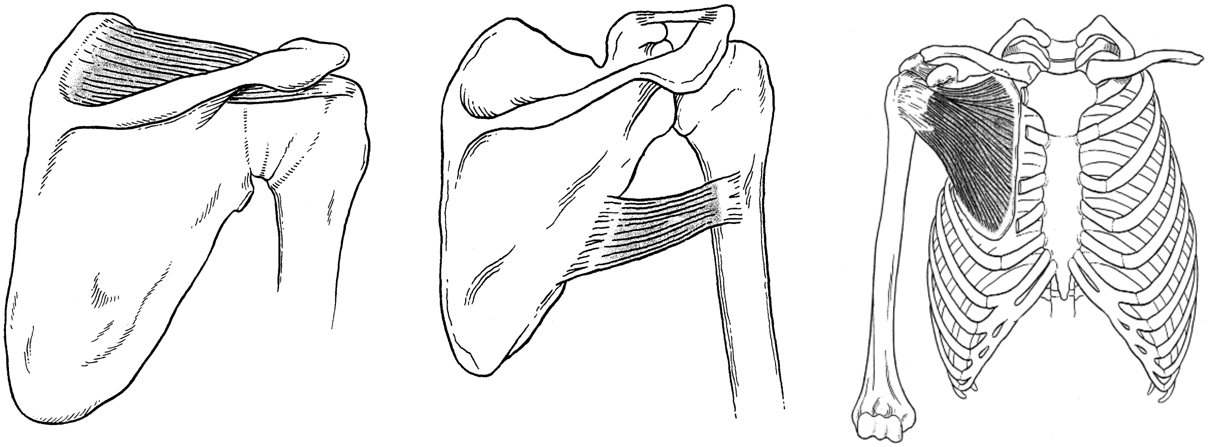
C. Latissimus dorsi



D. Pectoralis major

E. Coracobrachialis

F. Infraspinatus



G. Supraspinatus

H. Teres major

I. Subscapularis

Figure 3.7. Origin and insertion sites of humerus muscles whose MSM are included in current study (not including common flexor and common extensor origins): (a) deltoideus, (b) teres major, (c) latissimus dorsi, (d) pectoralis major, (e) coracobrachialis, (f) infraspinatus, (g) supraspinatus, (h) teres minor, (i) subscapularis. After Bowden & Bowden (2005).

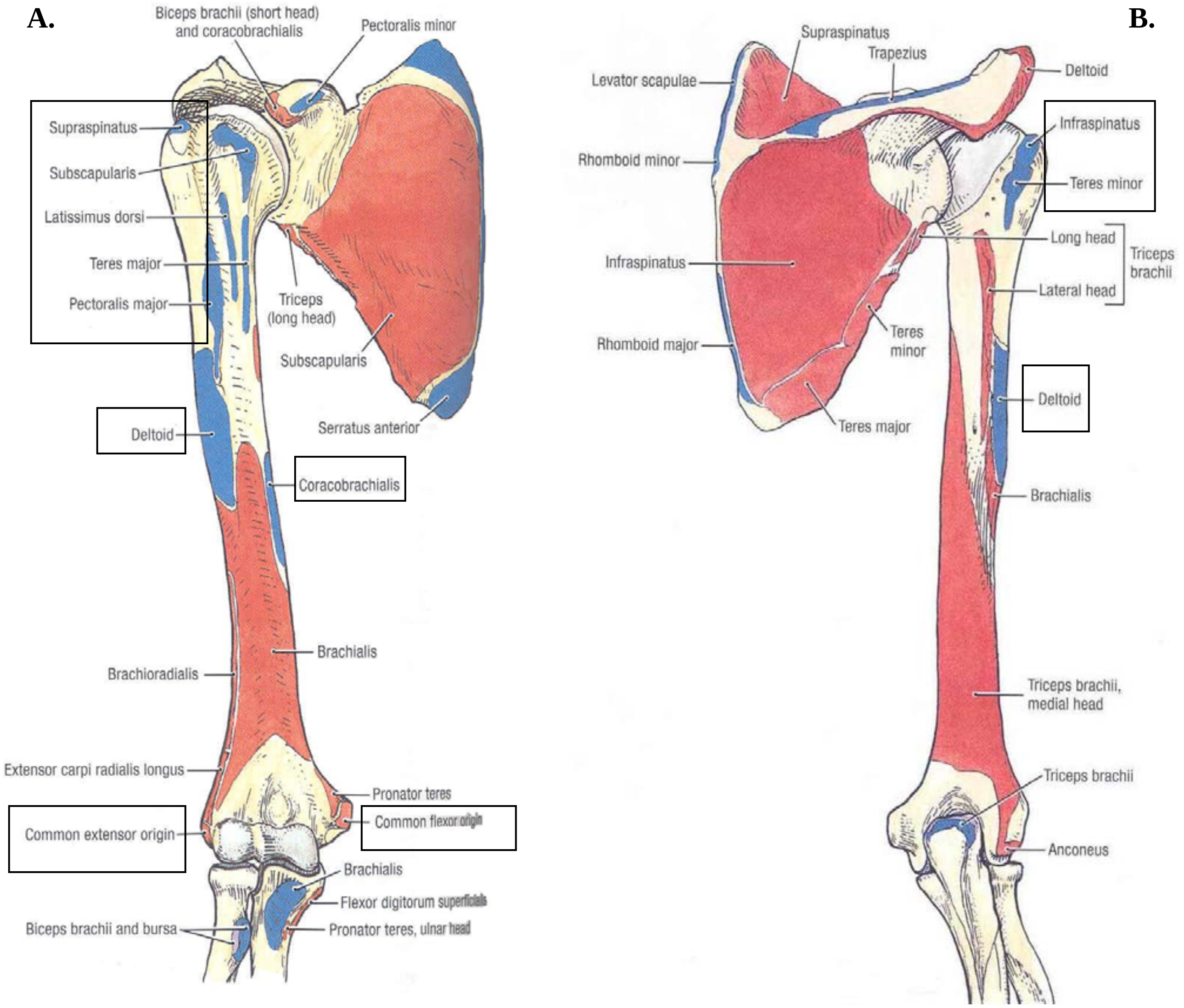


Figure 3.8. The position of all sites of muscle origin (red) and insertion (blue) in the humerus and shoulder: A) anterior aspect of the right humerus and shoulder, B) posterior aspect of the right humerus and shoulder. Muscle attachment sites included in the current study highlighted in boxes. After Agur & Dalley (2005).

The following chapters will discuss the application of metric and MSM methods described above to the analysis of upper limb bilateral asymmetry in both human material from the sites of Écija (Chapter 5) and Greenwich (Chapter 6) and the non-human primate material from the Powell-Cotton Museum (Chapter 7). These chapters will be preceded by a chapter exploring the inter- and intra-observer reliability for both methods and for both regions of the upper limb, using material from Écija and the site of Great Chesterford (Chapter 4).

The data analyses in these chapters will involve statistical comparisons of the differences between left-side and right-side metric measurements, in terms of both absolute asymmetry between the sides and the relative direction and strength of that asymmetry. Asymmetry will be determined for the metric sample as a whole, and also for each individual. Asymmetry in MSM development will be ascertained through statistical comparisons of the relative frequencies of scores between the MSM. The effects of sex and age on asymmetry will be calculated for both metric and MSM data.

Chapter 4. Analysis of Observer Reliability

When collecting data on skeletal material, it is important to be confident that data were collected without significant error, as this affects the reliability of results and impedes the repeatability of the study. To that end, many quantitative studies of bone properties have included analyses of intra-observer and/or intra-observer reliability, i.e. the difference between measurements taken by different researchers on the same material (inter-observer), or the difference between measurements taken by the same researcher on a particular data set on two separate occasions (intra-observer). With the methodological focus of the current study, an analysis of inter- and intra-observer reliability was necessary to ascertain the level of error potentially present in the data. This was particularly pertinent in the current study, due to the relative inexperience of the author in osteological data collection prior to the start of the study. Also, with the inclusion of musculoskeletal stress marker (MSM) analysis, often criticised for its subjective nature (Robb, 1998; Stirland, 1998; Wilczak, 1998), an analysis of observer error was essential. Inter-observer reliability was assessed by comparison of humeral material from the medieval cemetery of Écija (section 3.1.1). Intra-observer error was assessed using material from the site of Great Chesterford (section 3.1.4), which did not form part of the main data analyses in this study.

4.1. Inter-observer reliability

Inter-observer reliability was tested using humeral material from the medieval Islamic cemetery site of Écija in Andalucía, Spain. This site is described in more detail in section 3.1.1 and analysed in Chapter 5. For the inter-observer analysis, humeral metric data collected by the author was compared to metric data collected on the same individuals, by another researcher (referred to in the text as ‘EP’, the author being referred to as ‘LC’). The measurements taken by EP follow Martin & Saller (1957) and were therefore directly comparable with the measurements taken by LC (see Table 3.2 for a description of the humeral measurements taken in the current study). This comparison was only possible for the Écija humeri as no other comparable metric data were available for the Écija hand bones. There was also no comparable musculoskeletal stress marker (MSM) data available for either the Écija hands or humeri.

Inter-observer reliability was quantified simply by calculating the absolute difference between two corresponding measurements, following Sarringhaus *et al.* (2005). Measurements taken by EP were subtracted from the corresponding measurements taken by LC. Any negative values were converted to positive values. Table 4.1 (below) provides, for each left and right measurement, the range of the differences (i.e. the difference between the maximum and minimum difference value for each variable), the average of the difference between measurements for each variable, and percentage error. Percentage error was calculated taking each average difference as a percentage of the average measurement value of EP and LC measurements combined. Trochlea-capitulum breadth was not measured by EP, and therefore it was not possible to make inter-observer comparisons for this variable. For ease of comparison, data were analysed as a combined-sex, combined-age sample.

Table 4.1. Inter-observer differences in humerus measurements taken on the Écija sample.

Measurement	Side	N	Range (mm)	Average (mm)	Percentage (%)
MxL	L	28	3.0	0.8	0.25
	R	41	4.0	1.0	0.31
MxDm	L	30	0.7	0.3	1.28
	R	40	0.8	0.3	1.56
MnDm	L	31	4.0	0.4	2.31
	R	40	0.9	0.3	1.72
MnCir	L	33	4.0	1.2	1.83
	R	34	4.0	1.1	1.71
CirHd	L	22	5.0	2.2	1.71
	R	31	7.0	2.0	1.51
MxTDm	L	34	3.7	0.5	1.34
	R	36	0.8	0.3	0.75
MxSDm	L	34	1.2	0.4	1.01
	R	43	5.6	0.5	1.18
EpBr	L	38	2.0	0.2	0.30
	R	39	1.9	0.3	0.49

Inter-observer differences represented in terms of range of difference (in mm), average difference (in mm) and the average difference as a percentage of the average measurement value, for each variable. Trochlea-capitulum breadth was not included in this comparison. Abbreviations used: MxL = maximum length, MxDm = maximum midshaft diameter, MnDm = minimum midshaft diameter, MnCir = minimum shaft circumference, CirHd = circumference of head, MxTDm = maximum transverse diameter of head, MxSDm = maximum sagittal diameter of head, EpBr = epicondylar breadth.

From Table 4.1 it can be seen that there is a low degree of difference between the LC and EP measurements, with average differences ranging from 0.2mm (for left EpBr) to 2.2mm (for left CirHd). Only two measurements show an average difference of 2mm or greater, left and right CirHd. The next largest average differences are for left MnCir (1.2mm) and right MnCir (1.1mm). CirHd and MnCir are the only measurements taken with a tape measure (rather than callipers), suggesting that these measurements are more difficult to accurately replicate. Data were collected by LC using plastic dial callipers and by EP using metal digital callipers, which may explain some of the difference between each observer’s measurements. However, when these differences are viewed as a percentage of the average measurement value (LC and EP combined), the low level of difference between LC and EP measurements is further confirmed. The differences between measurements represent less than 2% of the overall measurement value, with the exception of left MnDm (2.31%). Although the average difference for this measurement is small (0.4mm), MnDm is the smallest measurement taken, which may explain its slightly larger percentage value. Overall, the level of inter-observer error is within acceptable limits (e.g. Auerbach & Ruff, 2006; Auerbach & Raxter, 2008).

4.2. Intra-observer reliability

Further comparisons were undertaken to assess intra-observer reliability in data collection. Due to time constraints, it was not possible to remeasure any of the material used in the main body of data analysis (Chapters 5 to 7). Therefore, for the purposes of the intra-observer comparison, 24 individuals from the site of Great Chesterford were used (see section 3.1.4 for further description of this site). This collection was measured in 2005 as part of a pilot study (unreported), to trial the metric and MSM methods used in subsequent analyses and in order to gain experience of osteological data collection techniques. Due to the collection's rather fragmentary nature and the relatively small number of suitable individuals, data from Great Chesterford was not included in the main skeletal analysis. However, it was considered suitable for the purposes of assessing intra-observer reliability. The collection was therefore remeasured in late 2007 after all other data collection was complete. This provided a unique opportunity to compare the measurements of a 'novice' with those of a more experienced skeletal data collector. This was particularly necessary for the MSM method, which had not previously been systematically applied to the muscles of the hand.

4.2.1. Metric data

Reliability for the comparative metric data (referred to as '2005' and '2007') was quantified for humeral, metacarpal and phalangeal material. This was undertaken using the method outlined in section 4.1 to provide values of the absolute difference between the measurements taken in 2005 versus those taken in 2007. Table 4.2, below, provides the results of this analysis for the Great Chesterford humeral data. As with the inter-observer comparison, data were analysed as a combined-sex, combined age sample.

In general, the average difference between humerus measurements taken in 2005 and those taken in 2007 is low, with the majority of measurements (12/18) showing an average difference of less than 1mm. Only two measurements show an average difference greater than 2mm: left CirHd (5.2mm) and right CirHd (4.9mm). Interestingly, CirHd was also found to have the largest average difference between measurements in the Écija humerus sample (Table 4.1). This supports the earlier observation that measurements taken with a tape measure are prone to more error than those taken with callipers. This error may have been inflated by the lack of experience of taking osteological measurements in the 2005 data collection. Viewing the average of the difference as a percentage of the overall measurement size, it can be seen that the majority of percentage errors (12/18) are less than 2%. As might be expected, the larger percentages are for CirHd and MnCir, which are both measured with a tape measure. Left and right MxDm also have percentage errors slighter greater than 2%, although the reason for this is unclear. Overall, the intra-observer error for the Great Chesterford humeri data is slightly higher than the inter-observer error found for the Écija humeri, but still considered acceptable (i.e. less than 5%). Some of the error is likely to be due to the author's lack of experience. Practice at taking osteological measurements is therefore important, and this experience appears to have reduced measurement error, as evidenced in the Écija humerus comparison. This suggests that variation in subsequent humeral measurements will reflect primarily functional and osteological differences within the sample, rather than measurement error.

Table 4.2. Intra-observer differences in humerus measurements taken on the Great Chesterford sample in 2005 and 2007.

Measurement	Side	N	Range (mm)	Average (mm)	Percentage (%)
MxL	L	16	2.0	1.1	0.33
	R	16	6.0	1.3	0.39
MxDm	L	18	2.1	0.7	2.96
	R	18	2.0	0.7	2.95
MnDm	L	19	0.9	0.3	1.77
	R	18	1.4	0.3	1.84
MnCir	L	19	5.0	1.9	3.07
	R	18	4.0	2.0	3.04
CirHd	L	13	11.0	5.2	3.62
	R	9	10.0	4.9	3.36
MxTDm	L	17	1.3	0.4	0.92
	R	9	0.7	0.2	0.54
MxSDm	L	17	1.0	0.4	0.81
	R	15	1.2	0.5	1.07
EpBr	L	14	1.1	0.3	0.50
	R	15	0.9	0.2	0.40
TCBr	L	14	2.7	0.8	1.77
	R	15	3.1	0.7	1.64

Intra-observer differences represented in terms of range of difference (in mm), average difference (in mm) and the average difference as a percentage of the average measurement value, for each variable. Abbreviations used: MxL = maximum length, MxDm = maximum midshaft diameter, MnDm = minimum midshaft diameter, MnCir = minimum shaft circumference, CirHd = circumference of head, MxTDm = maximum transverse diameter of head, MxSDm = maximum sagittal diameter of head, EpBr = epicondylar breadth, TCBr = trochlea-capitulum breadth.

Table 4.3, below, shows the results of the intra-observer reliability analysis on the Great Chesterford metacarpal data. Upon first inspection, the degree of error in the metacarpal sample appears to be very low, with no average differences greater than 1mm, and only 5/50 measurements showing an average difference greater than 0.5mm. These differences are for proximal metacarpal breadth (four measurements) and distal metacarpal breadth (one measurement). This suggests that there was a slight modification to the way in which metacarpal base breadth was measured between 2005 and 2007. This may have been a result of unfamiliarity with the irregular morphology of the metacarpal bases during the 2005 data collection period.

Table 4.3. Intra-observer differences in metacarpal measurements taken on the Great Chesterford sample in 2005 and 2007.

Measurement	Side	N	Range (mm)	Average (mm)	Percentage (%)
mc1L	L	19	3.6	0.5	1.13
	R	17	1.1	0.3	0.77
mc2L	L	20	0.9	0.3	0.48
	R	21	2.7	0.5	0.69
mc3L	L	18	0.9	0.4	0.58
	R	23	0.8	0.3	0.41
mc4L	L	16	0.7	0.2	0.41
	R	20	4.0	0.5	0.86
mc5L	L	14	0.7	0.3	0.49
	R	19	0.7	0.3	0.53
mc1RU	L	18	0.6	0.3	2.64
	R	18	0.4	0.2	1.92
mc2RU	L	22	1.0	0.4	4.25
	R	21	1.1	0.3	4.12
mc3RU	L	20	0.4	0.1	1.58
	R	24	0.7	0.2	2.17
mc4RU	L	21	0.8	0.2	3.37
	R	21	0.7	0.2	3.45
mc5RU	L	17	1.2	0.5	6.25
	R	20	1.5	0.4	5.52
mc1DP	L	18	0.8	0.2	2.44
	R	18	0.6	0.2	2.22
mc2DP	L	22	1.1	0.2	2.76
	R	21	0.7	0.3	3.45
mc3DP	L	19	0.7	0.2	2.31
	R	24	0.6	0.2	2.28
mc4DP	L	21	1.5	0.3	4.27
	R	21	0.6	0.2	3.09
mc5DP	L	17	1.2	0.4	6.26
	R	20	1.4	0.5	6.86
mc1PB	L	19	1.2	0.4	2.70
	R	17	0.7	0.3	1.90
mc2PB	L	20	2.7	0.5	3.16
	R	21	2.0	0.7	4.22
mc3PB	L	17	2.4	0.6	4.26
	R	23	1.6	0.5	3.79
mc4PB	L	18	1.4	0.4	3.63
	R	20	1.1	0.3	2.71
mc5PB	L	12	2.9	1.0	8.33
	R	21	4.1	1.0	7.93
mc1DB	L	18	1.3	0.4	3.04
	R	18	1.3	0.5	3.18
mc2DB	L	19	1.7	0.7	4.97
	R	19	1.2	0.3	2.19

Measurement	Side	N	Range (mm)	Average (mm)	Percentage (%)
mc3DB	L	17	2.0	0.3	2.46
	R	22	1.4	0.5	3.29
mc4DB	L	19	1.7	0.3	2.35
	R	19	1.2	0.3	2.75
mc5DB	L	15	1.0	0.2	1.95
	R	18	0.6	0.2	1.31

Intra-observer differences represented in terms of range of difference (in mm), average difference (in mm) and the average difference as a percentage of the average measurement value, for each variable. Abbreviations used: mc*L = metacarpal length, mc*RU = radio-ulnar midshaft diameter, mc*DP = dorso-palmar midshaft diameter, mc*PB = proximal breadth, mc*DB = distal breadth. Asterisk (*) denotes metacarpal number.

These differences appear much larger, however, when considered as a percentage of the overall measurement size. This is most likely due to the general small size of the metacarpal measurements. This is evident when metacarpal length percentages are compared with the other metacarpal dimensions. Length is the largest of the metacarpal measurements and has the smallest corresponding percentage values. While the majority of percentage errors are below 5%, 6 out of 50 percentage errors are over 5% (but less than 10%). With the small size of the metacarpal measurements, it is worth noting that the dial callipers used in this study measure at 0.1mm increments. Therefore, a systematic bias of 0.05mm is present across all measurements. Finally, the small sample sizes available for comparison in the Great Chesterford sample may also compound the error identified. The results in Table 4.3 suggest that metacarpal data can, on the whole, be reliably collected. However, observer reliability studies are important, as this analysis suggests that researcher inexperience can introduce error in smaller measurements. As the data presented in the subsequent chapters were collected after the author had gained experience of osteological methods, it is not considered that substantial measurement error would be present in any of the hand bone analyses.

Table 4.4, below, presents the results for the intra-observer reliability study of the Great Chesterford phalanx data. Although the number of available comparisons for the phalanx data was small, it can be seen that the average difference between the 2005 and the 2007 measurements was small, with only two measurements (out of 28) showing a difference greater than 0.5mm. Of these two measurements, one (left dp4L) is greater than 1mm, although only two comparisons were available for these measurements. Given the small size of the phalanx measurements, it is interesting to note that only two measurements (left and right dp4L) have percentage errors over 2%. The sample sizes for these analyses were less than 5 in both cases and therefore it is likely that these errors would be significantly reduced with an increased number of comparisons. Overall, these results show high intra-observer reliability between the 2005 and 2007 Great Chesterford phalanx data.

Table 4.4. Intra-observer differences in phalanx measurements taken on the Great Chesterford sample in 2005 and 2007.

Measurement	Side	N	Range (mm)	Average (mm)	Percentage (%)
pp1L	L	19	2.0	0.4	1.52
	R	19	0.9	0.4	1.32
pp2L	L	16	1.9	0.5	1.38
	R	18	0.9	0.3	0.79
pp3L	L	16	1.4	0.4	1.00
	R	20	0.8	0.4	0.83
pp4L	L	17	2.2	0.6	1.41
	R	20	2.4	0.5	1.19
pp5L	L	16	1.6	0.4	1.34
	R	17	0.6	0.2	0.60
ip2L	L	11	3.6	0.4	1.79
	R	10	0.5	0.2	0.96
ip3L	L	13	1.6	0.3	0.92
	R	14	1.9	0.5	1.79
ip4L	L	10	2.1	0.3	1.21
	R	12	1.4	0.4	1.31
ip5L	L	10	0.3	0.2	0.92
	R	15	0.4	0.1	0.64
dp1L	L	9	1.0	0.3	1.40
	R	9	0.4	0.3	1.14
dp2L	L	5	0.9	0.3	1.55
	R	2	0.2	0.1	0.58
dp3L	L	6	0.7	0.3	1.34
	R	9	0.4	0.3	1.63
dp4L	L	2	1.8	1.2	6.67
	R	4	0.5	0.4	2.12
dp5L	L	5	0.5	0.3	1.85
	R	6	0.1	0.2	1.03

Intra-observer differences represented in terms of range of difference (in mm), average difference (in mm) and the average difference as a percentage of the average measurement value, for each variable. Abbreviations used: pp*L = proximal phalanx length, ip*L = intermediate phalanx length, dp*L = distal phalanx length. Asterisk (*) denotes phalanx number.

4.2.2. MSM data

Intra-observer reliability was also assessed for the MSM data from the Great Chesterford sample. This was done primarily on a visual assessment of comparable data. In line with subsequent MSM analyses, the percentage of individuals with a MSM scored as ‘present’ was plotted for each muscle attachment site. Data were analysed as a combined-sex, combined-age sample. Figure 4.1 provides the results of the intra-observer comparison for the 2005 and 2007 humerus MSM data. For ease of comparison, the 2005 and 2007 data for each MSM are plotted side-by-side. Data from this analysis can be found in Table B.1, Appendix B.

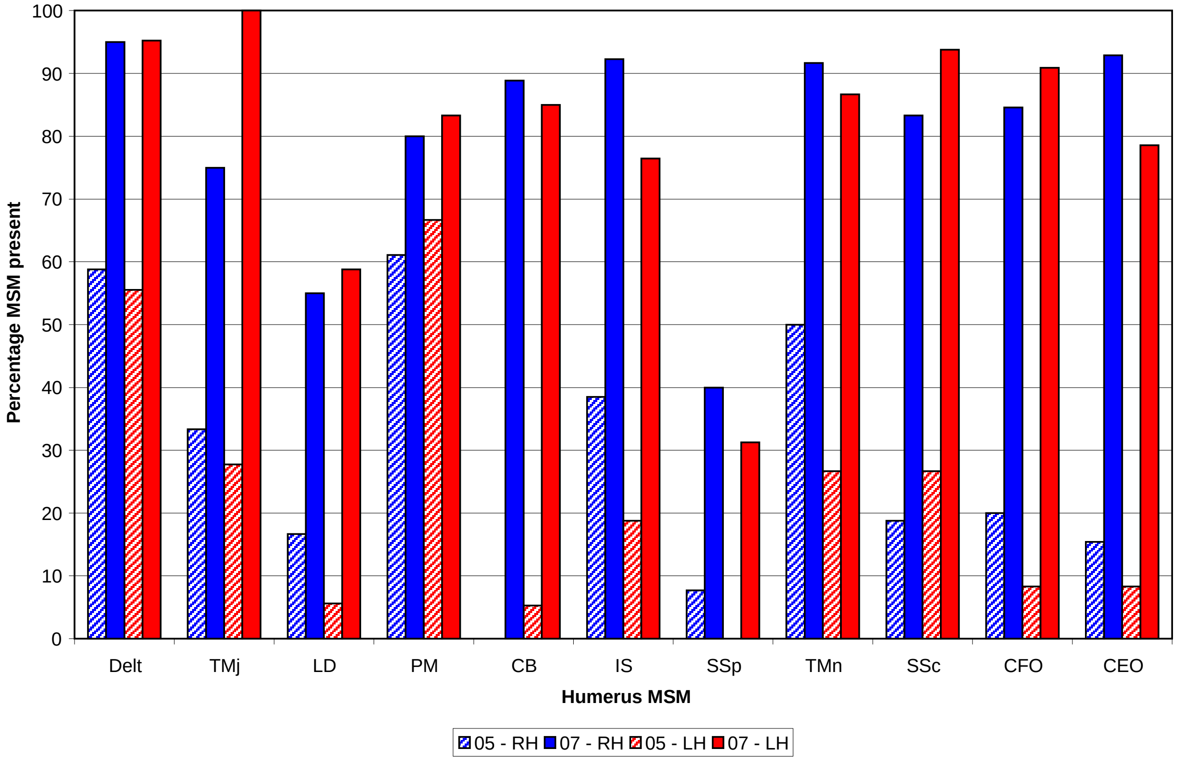


Figure 4.1. For both the Great Chesterford 2005 and 2007 data, the percentage of ‘present’ MSM for the left humerus (red) and the right humerus (blue), for each of the 11 MSM studied. Block colour columns represent 2007 data, diagonal line columns represent 2005 data. Abbreviations used: Delt = deltoid, TMj = teres major, LD = latissimus dorsi, PM = pectoralis major, CB = coracobrachialis, IS = infraspinatus, SSp = supraspinatus, TMn = teres minor, SSc = subscapularis, CFO = common flexor origin, CEO = common extensor origin.

It is immediately clear from Figure 4.1 that there is a marked discrepancy between the percentage of MSM scored as ‘present’ in 2005 compared with 2007, with MSM much more likely to be scored as ‘present’ in the 2007 sample. The difference between 2005 scoring and 2007 scoring varies between MSM. The PM MSM shows the least difference between 2005 and 2007 (less than 20% for left and right), which is likely to be a result of the large size and ease of identification of this MSM. These differences certainly result, in part, from a lack of experience of MSM scoring during the 2005 data collection. This is reflected in the scoring of the CB MSM. In 2005, the left CB was rated as ‘present’ on only approximately 5% of humeri, with the right CB never being rated as ‘present’. In 2007, and with more experience, these percentages increase to 85% and 89% for the left and right CB, respectively. As the 2005 study of the Great Chesterford material was a pilot study undertaken with no prior experience of MSM scoring, it is to be expected that some discrepancies would be present. However, the magnitude of the difference between the 2005 and 2007 MSM data highlights problems with the qualitative nature of the approach. What is interesting to note in Figure 4.1 are changes in the direction of asymmetry in MSM scoring between 2005 and 2007. For five of the MSM, the direction of asymmetry (i.e. right MSM scored as ‘present’ more frequently than left MSM, or vice versa) changed between 2005 and 2007, with the general trend being towards more left-side dominant scores in 2007.

Together, these findings raise important questions about the ability of MSM analysis to accurately assess bilateral asymmetry and therefore the results of this analysis highlight the caution that must be taken when interpreting such data.

Figure 4.2 presents the results of the intra-observer comparison of the Great Chesterford hand MSM data. Further data from this analysis can be found in Table B.2, Appendix B.

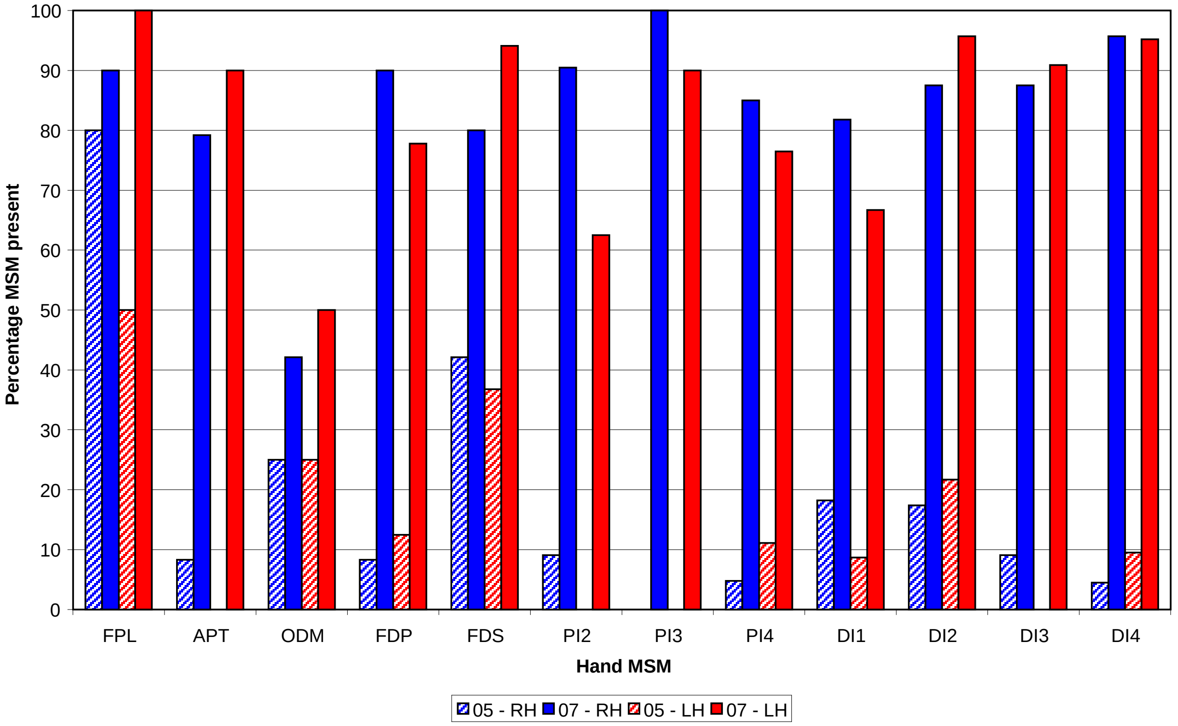


Figure 4.2. For both the Great Chesterford 2005 and 2007 data, the percentage of 'present' MSM for the left hand (red) and the right hand (blue), for each of the 12 MSM studied. Block colour columns represent 2007 data, diagonal line columns represent 2005 data. Abbreviations used: FPL = flexor pollicis longus, APT = adductor pollicis (transverse head), ODM = oppenens digiti minimi, FDP = flexor digitorum profundus (2-5), FDS = flexor digitorum superficialis (2-5), PI = palmar interosseous, DI = dorsal interosseous.

The results presented in Figure 4.2 support the findings of the previous study of humerus MSM, namely the presence of a large discrepancy between the percentage of MSM scored as 'present' in 2005 compared with 2007. In general, these differences are greater for the hand MSM than those found for the humerus MSM. This observation is not unexpected, given the small size of the hand MSM and initial difficulties in identifying certain MSM sites (for example, the PI). It is worth noting that, between 2005 and 2007, the Great Chesterford collection underwent extensive cleaning, and it is possible that this increased the success of MSM identification in 2007, for both the hand and humerus MSM. As with the humerus MSM, the larger and more distinctive MSM in the hand, such as the FPL, ODM and FDS show the smallest difference between 2005 and 2007. Changes in the direction of asymmetry were once again identified, with 7 out of 12 MSM showing a change. A move towards left-side asymmetry was found for 4 MSM, with 3 MSM moving towards right-side asymmetry. Again, this highlights a particular issue in using MSM to specifically assess bilateral asymmetry.

To address the issue of the extent to which experience improves MSM scoring reliability, MSM development in the Great Chesterford hand bones was scored for a third time, in 2008. This was for the purposes of comparison with the 2007 data, to compare two episodes of data collection carried out by a more experienced researcher. The MSM of the hands were chosen for this intra-observer analysis as they had shown the largest degree of error in the previous analysis (Fig. 4.2) and would possibly continue to be more prone to replicability error due to their small size. Figure 4.3 provides the results of the comparison between the 2007 and 2008 Great Chesterford hand MSM data. Further data from this analysis is provided in Table B.3, Appendix B.

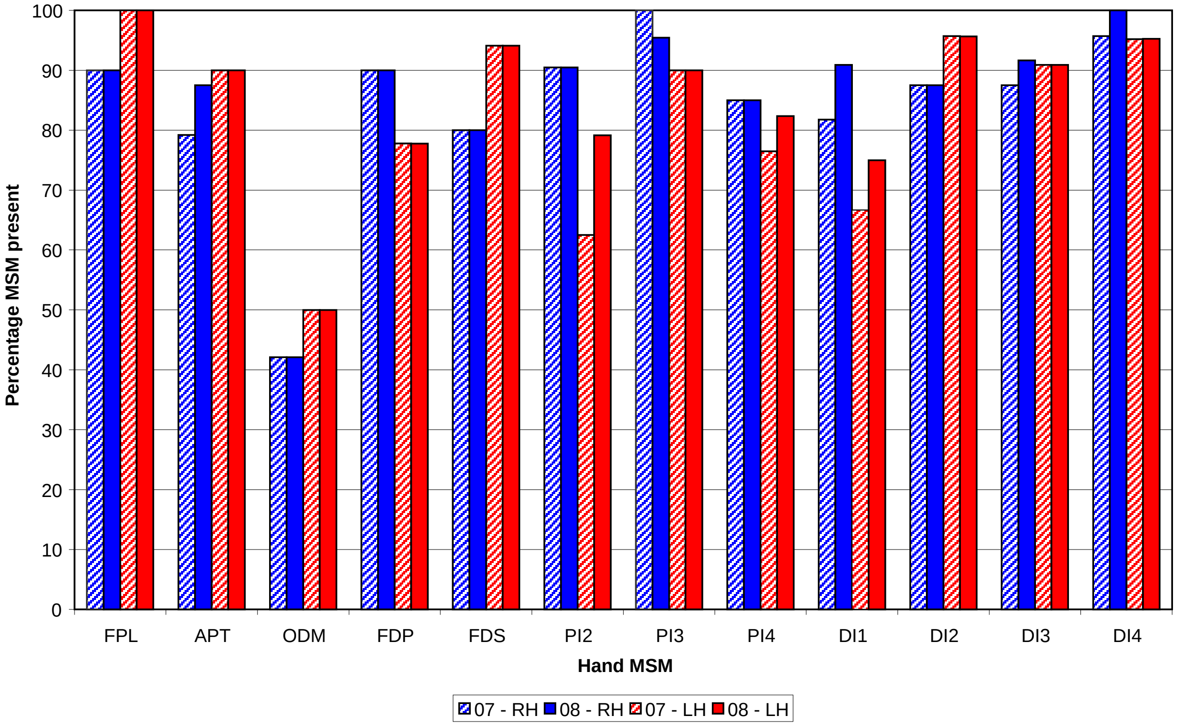


Figure 4.3. For both the Great Chesterford 2007 and 2008 data, the percentage of 'present' MSM for the left hand (red) and the right hand (blue), for each of the 12 MSM studied. Block colour columns represent 2008 data, diagonal line columns represent 2007 data. Abbreviations used: FPL = flexor pollicis longus, APT = adductor pollicis (transverse head), ODM = oppenens digiti minimi, FDP = flexor digitorum profundus (2-5), FDS = flexor digitorum superficialis (2-5), PI = palmar interosseous, DI = dorsal interosseous.

In contrast to both Figures 4.1 and 4.2, it is immediately evident from Figure 4.3 that there is very little difference between 2007 and 2008 Great Chesterford hand MSM scoring for both the left and right hands. Of the 12 left hand and 12 right hand MSM scored, only 8 MSM (3 left, 5 right) show a difference in the percentage of individuals scored as 'present' between the 2007 and 2008 data collection periods. These differences were less than 10% for all MSM, with the exception of left PI2 (16.7%). A chi-squared test performed on left PI2 scores from 2007 and 2008 found that there was a strong, statistically significant association between the variables (χ^2 [1] = 10.53, $p < 0.01$). This clearly indicates that increased experience of MSM data collection methods improves the repeatability of the data. These findings support the notion that the discrepancies found between 2005 and 2007 MSM data in Figures 4.1 and 4.2 primarily resulted from a lack of MSM scoring experience during the 2005 data collection period. This analysis once again highlights the problems inherent in using such a qualitative methodology in asymmetry analyses.

Within the Écija MSM sample, there were data collected in 2006 and 2007 and therefore it is possible that there could be variation in MSM scoring between the years. Unfortunately, due to the nature of the data set, no individuals were measured in both 2006 and 2007 and therefore it was not possible to compare scoring methods across this time period. The results from Figure 4.3, however, indicate a high level of intra-observer accuracy between 2007 and 2008 data, suggesting that once experience in MSM scoring has been obtained (as was the case in 2006 and 2007), the application of the MSM technique can be considered to be accurate.

4.3. Summary

Overall, the results of the inter-observer analysis indicate a high level of reliability between observers, suggesting an acceptably low level of error present in the current study. Although it was only possible to test inter-observer reliability for humeral data, it is assumed that a low level of error would have also been found for measurements of the metacarpals and phalanges. Results of the intra-observer comparisons suggest a higher level of error present, particularly prominent for the 2005 vs 2007 MSM analyses. For the metric analyses, measurement error was generally low and within acceptable limits. For a small number of metacarpal measurements, percentage error was greater than 5% (but less than 10%). In part, this is a result of the small size of metacarpal measurements, although it was observed that percentage error was generally lower for the phalanges than the metacarpals. Comparing the inter- and intra-observer analyses of metric properties suggests that osteological experience improves the reliability of measurements and therefore the experience of the researcher must be borne in mind during data collection and analysis.

Intra-observer analysis of MSM scoring reliability emphasises the importance of observer experience, particularly when using a qualitative method, as evidenced by the 2007 vs 2008 hand MSM analysis. The size of the differences found between the 2005 and 2007 MSM data highlights the need to account for observer effects in all analyses of MSM development. This should particularly be the case for bilateral asymmetry, where this analysis suggests changes in assessment of the direction of asymmetry can occur. It is interesting to note the systematic nature of the error across the humerus and hand MSM data. This suggests that any problems with the method of assessing MSM are found across all MSM and not just those of the hand. Therefore this should not prejudice the analysis of hand MSM.

Chapter 5. Écija Data Analysis

The site of Écija, east of Seville in Andalucía, Spain is described in section 3.1.1. Of the sixty-five individuals measured from Écija, 35 were male and 30 were female. All subjects were assigned to one of three age categories: young adult (approx. 17 – 30 years), middle adult (approx. 30 – 45 years) and old adult (approx. 45 years and above) (see section 3.2 for description of sexing and ageing methods). This resulted in 35 subjects being classified as young adult, 25 subjects classified as middle adult and 5 subjects being classified as old adult. Due to the very small size of the old adult sample, this group was excluded from analysis where necessary. Data from the hands and the humeri were collected following the methods outlined in section 3.2 and analysed independently. Metric and musculoskeletal stress marker (MSM) data were also considered separately. Metric data is described in sections 5.1 and 5.2 and MSM data in sections 5.3 and 5.4. This facilitated comparisons between the hands and humeri, and the methods used to study them. Table 5.1 outlines the age and sex profile for the Écija sample.

Table 5.1. Age and sex profile of Écija sample

	Young adult	**Middle adult**	**Old adult**	**Total**
Male	18	15	2	**35**
Female	17	10	3	**30**
Total	**35**	**25**	**5**	Total sample: **65**

5.1. Metacarpal and phalanx metric analysis

Descriptive statistics for the metacarpals and phalanges in the age-combined sample, split by sex are provided in Table C.1, Appendix C. Box-and-whisker plots were used to identify outliers within the data. Any outlying values were compared with the original data to confirm that they had been recorded and processed correctly. Data collection notes were also checked to identify any possible reasons for extreme measurements (i.e. damage to the area of measurement, presence of muscle markers). If such causes were identified then the measurements were excluded from further analysis. If no obvious reason for exclusion was identified then the value was left in the data set and appropriate measures taken during analysis (i.e. adoption of non-parametric methods). Although a small number of outliers were identified, histograms and p-p plots confirmed the overall normal distribution of the data. The following sections will first analyse absolute size differences between left and right measurements and the effects of sex and age on these differences. The relative direction and magnitude of any observable asymmetry will then be analysed, plus the effects of sex and age on such asymmetry. The asymmetry for each individual subject will also be considered.

5.1.1. Significance testing

Statistical testing was required to identify the presence of any significant left/right differences between the measurements. Although the distribution of the data points was normal, the presence of outliers in the sample supported the use of a non-parametric test to compare left and right metacarpal measurements. A Wilcoxon test was therefore performed on the data (Table 5.2, below). The Wilcoxon test is the non-parametric equivalent of the paired-samples t-test and compares median values rather than mean values of related samples of scale data (i.e. each individual is recorded in two related categories), as is the case in the t-test. While the Wilcoxon test assumes that the samples come from a population with the same distribution shape, it does not assume that they have a normal distribution or homogeneity of variance. This makes the Wilcoxon test more robust to the presence of outliers than the t-test (Kinnear & Gray, 2006).

Table 5.2. Wilcoxon test results for the combined-sex and combined-age Écija metacarpal sample.

Measurement	Side	N	Mean	Std dev.	Sig. (2-tailed)
mc1L	L	55	42.97	3.18	**$p < 0.01$**
	R	56	43.77	3.08	
mc2L	L	54	64.95	4.02	**$p = 0.01$**
	R	53	65.22	3.99	
mc3L	L	57	62.60	4.16	$p = 0.49$
	R	59	62.66	4.17	
mc4L	L	52	55.77	3.78	**$p = 0.03$**
	R	62	55.84	3.61	
mc5L	L	58	51.74	4.02	$p = 0.15$
	R	61	51.96	3.44	
mc1RU	L	57	11.55	1.12	**$p < 0.01$**
	R	58	12.00	1.05	
mc2RU	L	62	8.09	0.77	**$p < 0.01$**
	R	64	8.28	0.82	
mc3RU	L	62	8.27	0.72	**$p < 0.01$**
	R	62	8.42	0.73	
mc4RU	L	60	6.65	0.62	**$p < 0.01$**
	R	65	6.98	0.71	
mc5RU	L	61	7.56	0.77	**$p < 0.01$**
	R	64	8.02	0.95	
mc1DP	L	57	8.40	1.16	**$p < 0.01$**
	R	58	8.53	0.96	
mc2DP	L	62	8.72	0.87	**$p < 0.01$**
	R	64	9.00	0.85	
mc3DP	L	62	8.84	0.91	**$p < 0.01$**
	R	62	9.28	0.80	
mc4DP	L	60	7.32	0.82	**$p < 0.01$**
	R	65	7.63	0.85	
mc5DP	L	61	6.80	0.86	**$p < 0.01$**
	R	63	7.28	0.89	

Measurement	Side	N	Mean	Std dev.	Sig. (2-tailed)
mc1PB	L	56	14.85	1.59	**p = 0.02**
	R	58	15.10	1.43	
mc2PB	L	55	16.53	1.54	p = 0.51
	R	56	16.37	1.63	
mc3PB	L	61	13.50	1.19	p = 0.36
	R	60	13.57	1.08	
mc4PB	L	58	11.81	0.99	**p < 0.01**
	R	63	12.04	0.99	
mc5PB	L	60	11.18	1.14	**p < 0.01**
	R	63	11.74	1.09	
mc1DB	L	57	13.71	1.34	**p < 0.01**
	R	58	14.01	1.21	
mc2DB	L	58	13.42	1.12	**p < 0.01**
	R	58	13.64	1.19	
mc3DB	L	58	13.26	1.09	**p < 0.01**
	R	59	13.60	1.07	
mc4DB	L	55	11.39	0.89	**p < 0.01**
	R	61	11.74	0.91	
mc5DB	L	58	11.06	0.73	**p < 0.01**
	R	61	11.25	0.84	

Mean and standard deviation values rounded to two decimal places. Significant p-values highlighted in bold. P-values approaching significance (between 0.055 and 0.1) highlighted in italics. Abbreviations used: mc*L = metacarpal length, mc*RU = radio-ulnar midshaft diameter, mc*DP = dorso-palmar midshaft diameter, mc*PB = proximal breadth, mc*DB = distal breadth. Asterisk (*) denotes metacarpal number.

Table 5.2 details the results of the Wilcoxon test, carried out on the combined-age and combined-sex sample. Significance was calculated at the two-tailed level (one-tailed levels are not reported). These levels can be considered to reflect the difference between directional (one-tailed) and non-directional (two-tailed) hypotheses. If a hypothesis can reasonably predict the direction of the effect that is being measured then a one-tailed test can be used. This makes it twice as easy to reject the null hypothesis as the ‘test statistic’ will fall into the top .05 of the distribution. In comparison, a directionless or two-tailed test assumes that the ‘test statistic’ will fall in the top .025 at either end (or ‘tail’) of the distribution (Kinnear & Gray, 2006). In this study it was decided to only use two-tailed significance values to improve the strength of the conclusions drawn.

The results of the Wilcoxon test in Table 5.2 identify a clear, statistically significant difference between left side and right side measurements in this sample, with the right-side measurements generally being larger than those on the left. The only exceptions to this are mc3L, mc5L, mc2PB and mc3PB, suggesting less size asymmetry in these variables. Why these variables do not show significant left/right differences is unclear, but could potentially reflect functional influences on these bones. Section 5.1.2 will explore the effects of sex and age on this sample.

Table 5.3. Wilcoxon test results for the combined-sex and combined-age Écija phalanx sample.

Measurement	Side	N	Mean	Std dev.	Sig. (2-tailed)
pp1L	L	53	28.53	2.30	p = 0.23
	R	53	28.64	2.31	
pp2L	L	53	38.48	2.55	**p = 0.05**
	R	54	38.38	2.56	
pp3L	L	57	42.52	2.94	**p = 0.01**
	R	59	42.81	2.77	
pp4L	L	52	40.25	2.63	*p = 0.07*
	R	58	40.10	2.84	
pp5L	L	52	31.51	2.09	*p = 0.08*
	R	52	31.89	1.96	
ip2L	L	45	22.77	1.83	**p = 0.03**
	R	49	23.00	1.76	
ip3L	L	50	27.59	2.67	p = 0.18
	R	53	27.80	2.58	
ip4L	L	41	26.27	1.93	p = 0.47
	R	48	26.19	1.80	
ip5L	L	41	18.54	1.64	p = 0.20
	R	51	18.38	1.60	
dp1L	L	42	21.52	1.76	p = 0.33
	R	46	21.84	1.82	
dp2L	L	11	17.01	1.19	p = 1.00
	R	14	16.49	1.15	
dp3L	L	18	18.09	1.30	p = 0.68
	R	26	18.22	1.34	
dp4L	L	17	17.63	1.52	p = 0.63
	R	16	17.61	1.17	
dp5L	L	10	16.42	1.90	p = 0.50
	R	17	16.14	1.60	

Mean and standard deviation values rounded to two decimal places. Significant p-values highlighted in bold. P-values approaching significance (between 0.055 and 0.1) highlighted in italics. Abbreviations used: pp*L = proximal phalanx length, ip*L = intermediate phalanx length, dp*L = distal phalanx length. Asterisk (*) denotes phalanx number.

Table 5.3 provides the results of the Wilcoxon test on phalanx measurements and shows that the size difference between the left and right phalanx measurements is reduced compared to that seen in the metacarpals, with only three of the phalanx measurements showing a significant left/right difference: pp2L (p = 0.05), pp3L (p = 0.01), and ip2L (p = 0.03). There is no clear asymmetry trend in this sample, with equal numbers of measurements larger on the left side compared to the right, and vice versa. It is interesting to note that significant differences are found for the second and third fingers, compared to the metacarpal analysis where second and third metacarpal variables did not exhibit significant side differences. This reduced level of phalanx asymmetry may reflect functional congruency between the fingers in this sample. However, it is also possible that there are methodological factors at play. The small size of the phalanx bones may increase the effect of measurement error on this sample. Alternatively, any problems in the siding of the phalanges could mask potential asymmetry in the sample.

5.1.2 Analysis of Variance

An Analysis of Variance (ANOVA) was performed to determine the effects of age and sex on the metric properties of the metacarpals. The ANOVA is similar to the t-test in that it compares group means but unlike the t-test, has the ability to compare three or more groups (Kinnear & Gray, 2006). Despite the presence of a small number of outliers in the data set, the sample has a normal distribution and therefore an ANOVA analysis was considered appropriate. This test is generally robust to some violations of the assumptions underpinning the analysis (Kinnear & Gray, 2006). Table 5.4 (below) gives the results of the univariate General Linear Model (GLM) ANOVA performed on the data. Due to the small number of 'old adults', these data were excluded from this analysis.

The strong main effect of sex on the metacarpal sample is evident (Table 5.4). Sex has a strong statistically significant effect on all variables, with the exception of right mc5PB ($p = 0.82$), right mc2L and left mc5PB (although these are both approaching significance: $p = 0.07$ and $p = 0.08$, respectively). Alongside the Wilcoxon analysis (Table 5.2), these results suggest a degree of homogeneity in the metacarpal length and proximal breadth properties, both in terms of left/right differences and male/female differences. Overall, these results are as expected, confirming that males generally have larger metacarpal dimensions than females (see Table C.1, Appendix C for mean values). In contrast, there is virtually no effect of age on any of the variables in the sample suggesting that there is no difference between young adults and middle adults in terms of the size of the measurements. An exception to this is left mc5DB ($p = 0.05$), with right mc1DB having a p-value approaching significance ($p = 0.09$). While this lack of a strong main effect of age may represent difficulties in accurately assessing skeletal age, it more likely reflects an absence of age differences in the metacarpals measurements as these dimensions would not be expected to change in size over the course of a lifetime. On the whole there was no statistically significant interaction between sex and age suggesting that the effect of each variable is the same at each level of the other, i.e. sex has the same effect on 'young' adults, 'middle' adults and 'old' adults, and vice versa. The exceptions to this are right mc5L and right mc1PB, which show significant interactions between sex and age. Why there should be a significant interaction for these measurements is unclear.

Table 5.5 (below) outlines the results of the GLM ANOVA analysis of the effects of sex and age on phalanx measurements.

Table 5.4. Univariate GLM ANOVA for the effects of sex and age on each of the metacarpal metric variables, plus the interaction between sex and age.

Measurement	Side	N	Mean	Sex		Age		Sex*Age	
				F	Sig.	F	Sig.	F	Sig.
mc1L	L	55	42.97	37.10	**p < 0.01**	0.17	p = 0.85	0.72	p = 0.49
	R	56	43.77	10.86	**p < 0.01**	0.92	p = 0.41	0.14	p = 0.84
mc2L	L	54	64.95	10.94	**p < 0.01**	0.37	p = 0.69	0.98	p = 0.38
	R	53	65.22	3.45	*p = 0.07*	1.28	p = 0.29	0.59	p = 0.56
mc3L	L	57	62.60	22.68	**p < 0.01**	0.60	p = 0.56	1.44	p = 0.25
	R	59	62.66	18.42	**p < 0.01**	1.51	p = 0.23	1.36	p = 0.27
mc4L	L	52	55.77	22.42	**p < 0.01**	0.77	p = 0.47	2.72	*p = 0.08*
	R	62	55.84	20.85	**p < 0.01**	0.39	p = 0.68	1.86	p = 0.17
mc5L	L	58	51.74	26.02	**p < 0.01**	0.71	p = 0.50	2.27	p = 0.11
	R	61	51.96	25.43	**p < 0.01**	0.14	p = 0.87	4.10	**p = 0.02**
mc1RU	L	57	11.55	10.42	**p < 0.01**	0.47	p = 0.63	0.13	p = 0.88
	R	58	12.00	12.42	**p < 0.01**	1.56	p = 0.22	0.28	p = 0.75
mc2RU	L	62	8.09	21.80	**p < 0.01**	0.25	p = 0.78	0.23	p = 0.79
	R	64	8.28	11.47	**p < 0.01**	0.82	p = 0.45	0.63	p = 0.54
mc3RU	L	62	8.27	11.16	**p < 0.01**	0.39	p = 0.68	0.66	p = 0.52
	R	62	8.42	9.29	**p < 0.01**	0.85	p = 0.44	0.19	p = 0.83
mc4RU	L	60	6.65	9.95	**p < 0.01**	0.70	p = 0.50	0.24	p = 0.79
	R	65	6.98	6.64	**p = 0.01**	0.56	p = 0.58	0.44	p = 0.65
mc5RU	L	61	7.56	9.38	**p < 0.01**	0.20	p = 0.82	0.53	p = 0.60
	R	64	8.02	8.57	**p < 0.01**	1.24	p = 0.30	0.22	p = 0.80
mc1DP	L	57	8.40	14.57	**p < 0.01**	0.02	p = 0.98	0.14	p = 0.87
	R	58	8.53	12.97	**p < 0.01**	0.05	p = 0.95	0.95	p = 0.39
mc2DP	L	62	8.72	7.65	**p < 0.01**	0.63	p = 0.53	0.49	p = 0.61
	R	64	9.00	8.50	**p < 0.01**	0.22	p = 0.81	0.09	p = 0.91
mc3DP	L	62	8.84	8.34	**p < 0.01**	0.15	p = 0.86	0.25	p = 0.78
	R	62	9.28	6.82	**p = 0.01**	0.53	p = 0.59	0.81	p = 0.45

Measurement	**Side**	**N**	**Mean**	**Sex**		**Age**		**Sex*Age**	
				F	**Sig.**	**F**	**Sig.**	**F**	**Sig.**
mc4DP	L	60	7.32	11.26	**p < 0.01**	0.65	p = 0.52	0.65	p = 0.53
	R	65	7.63	9.70	**p < 0.01**	0.30	p = 0.74	0.40	p = 0.67
mc5DP	L	61	6.80	7.18	**p = 0.01**	0.05	p = 0.95	0.05	p = 0.95
	R	63	7.28	4.99	**p = 0.03**	0.08	p = 0.92	0.07	p = 0.94
mc1PB	L	56	14.85	15.47	**p < 0.01**	1.72	p = 0.19	1.49	p = 0.24
	R	58	15.10	14.19	**p < 0.01**	2.09	p = 0.13	3.64	**p = 0.03**
mc2PB	L	55	16.53	8.27	**p < 0.01**	1.50	p = 0.23	0.81	p = 0.45
	R	56	16.37	5.32	**p < 0.01**	0.05	p = 0.95	1.83	p = 0.17
mc3PB	L	61	13.50	16.23	**p < 0.01**	0.14	p = 0.87	2.42	*p = 0.10*
	R	60	13.57	1.59	**p < 0.01**	0.42	p = 0.66	1.96	p = 0.15
mc4PB	L	58	11.81	13.81	**p < 0.01**	0.10	p = 0.90	0.77	p = 0.47
	R	63	12.04	6.78	**p = 0.01**	0.50	p = 0.61	0.70	p = 0.50
mc5PB	L	60	11.18	3.28	*p = 0.08*	0.87	p = 0.42	0.39	p = 0.68
	R	63	11.74	0.05	p = 0.82	0.92	p = 0.41	0.43	p = 0.65
mc1DB	L	57	13.71	33.17	**p < 0.01**	0.66	p = 0.52	1.07	p = 0.35
	R	58	14.01	21.03	**p < 0.01**	2.56	*p = 0.09*	2.08	p = 0.14
mc2DB	L	58	13.42	21.40	**p < 0.01**	0.68	p = 0.51	1.56	p = 0.29
	R	58	13.64	13.14	**p < 0.01**	0.79	p = 0.46	1.08	p = 0.35
mc3DB	L	58	13.26	21.63	**p < 0.01**	0.31	p = 0.73	1.13	p = 0.33
	R	59	13.60	15.43	**p < 0.01**	0.07	p = 0.93	0.53	p = 0.59
mc4DB	L	55	11.39	11.69	**p < 0.01**	0.26	p = 0.77	0.59	p = 0.56
	R	61	11.74	13.46	**p < 0.01**	1.14	p = 0.33	0.68	p = 0.51
mc5DB	L	58	11.06	10.47	**p < 0.01**	3.09	**p = 0.05**	0.63	p = 0.54
	R	61	11.25	16.01	**p < 0.01**	0.95	p = 0.39	2.35	p = 0.11

Mean and F values rounded to two decimal places. Significant p-values highlighted in bold. P-values approaching significance (between 0.055 and 0.1) highlighted in italics. Abbreviations used: mc*L = metacarpal length, mc*RU = radio-ulnar midshaft diameter, mc*DP = dorso-palmar midshaft diameter, mc*PB = proximal breadth, mc*DB = distal breadth. Asterisk (*) denotes metacarpal number.

Table 5.5. Univariate GLM ANOVA for the effects of sex and age on each of the phalanx metric variables, plus the interaction between sex and age.

Measurement	Side	N	Mean	Sex		Age		Sex*Age	
				F	Sig.	F	Sig.	F	Sig.
pp1L	L	53	28.53	9.57	**p < 0.01**	0.58	p = 0.56	0.17	p = 0.84
	R	53	28.64	16.76	**p < 0.01**	0.20	p = 0.82	0.72	p = 0.49
pp2L	L	53	38.48	27.94	**p < 0.01**	0.43	p = 0.66	0.75	p = 0.48
	R	54	38.38	24.48	**p < 0.01**	0.20	p = 0.82	1.10	p = 0.34
pp3L	L	57	42.52	32.47	**p < 0.01**	0.03	p = 0.97	1.94	p = 0.15
	R	59	42.81	28.95	**p < 0.01**	0.21	p = 0.81	1.83	p = 0.17
pp4L	L	52	40.25	26.24	**p < 0.01**	0.06	p = 0.94	1.05	p = 0.36
	R	58	40.10	14.44	**p < 0.01**	0.26	p = 0.77	1.21	p = 0.31
pp5L	L	52	31.51	19.86	**p < 0.01**	0.20	p = 0.82	1.17	p = 0.32
	R	52	31.89	9.48	**p < 0.01**	1.93	p = 0.16	0.17	p = 0.84
ip2L	L	45	22.77	18.23	**p < 0.01**	0.38	p = 0.69	0.72	p = 0.49
	R	49	23.00	9.36	**p < 0.01**	0.80	p = 0.45	0.09	p = 0.91
ip3L	L	50	27.59	8.84	**p < 0.01**	0.22	p = 0.81	0.38	p = 0.68
	R	53	27.80	7.03	**p = 0.01**	0.13	p = 0.88	0.05	p = 0.95
ip4L	L	41	26.27	3.89	*p = 0.06*	0.76	p = 0.47	0.02	p = 0.98
	R	48	26.19	4.24	**p = 0.05**	0.43	p = 0.65	0.002	p = 0.99
ip5L	L	41	18.54	9.03	**p < 0.01**	0.04	p = 0.96	0.99	p = 0.38
	R	51	18.38	2.11	p = 0.15	0.54	p = 0.58	0.09	p = 0.91
dp1L	L	42	21.52	3.62	*p = 0.07*	1.21	p = 0.31	0.14	p = 0.87
	R	46	21.84	1.61	p = 0.21	0.13	p = 0.88	0.91	p = 0.41
dp2L	L	11	17.01	0.82	p = 0.40	0.23	p = 0.80	0.46	p = 0.52
	R	14	16.49	0.53	p = 0.48	0.39	p = 0.69	1.52	p = 0.25
dp3L	L	18	18.09	1.45	p = 0.25	0.98	p = 0.40	5.12	**p = 0.04**
	R	26	18.22	9.51	**p < 0.01**	0.74	p = 0.49	3.88	**p = 0.04**
dp4L	L	17	17.63	7.05	**p = 0.02**	0.33	p = 0.73	2.16	p = 0.17
	R	16	17.61	8.43	**p = 0.01**	0.05	p = 0.95	2.39	p = 0.15
dp5L	L	10	16.42	2.94	p = 0.13	0.52	p = 0.50	-	-
	R	17	16.14	0.99	p = 0.34	1.03	p = 0.39	0.20	p = 0.66

Mean and F values round to two decimal places. Significant p-values highlighted in bold. P-values approaching significance (between 0.055 and 0.1) highlighted in italics. Abbreviations used: pp*L = proximal phalanx length, ip*L = intermediate phalanx length, dp*L = distal phalanx length. Asterisk (*) denotes phalanx number.

The results of the ANOVA on phalanx measurements (Table 5.5) are consistent with those of the metacarpals. As might be expected there was a strong main effect of sex on phalanx length, with males being larger than females for all measurements (see Table C.1, Appendix C). The distal phalanges provide an exception however as most show no significant sex effect. This may be due to similarities in distal phalanx size between males and females. Alternatively, as with the Wilcoxon analysis (Table 5.3) it may be a consequence of small sample sizes, measurement error or issues with accurate phalanx siding. As with the metacarpal ANOVA, there was no significant main effect of age on any of the phalanx variables. Left and right dp3L were the only variables where an interaction was found between sex and age.

5.1.3. Asymmetry in the metacarpals and phalanges

The analyses above have identified the presence of significant asymmetry in the Écija hand bones in terms of size (right larger than left) and sex (males larger than females). However, to quantify the extent of this asymmetry and to explore its distribution through the Écija sample as a whole further analysis is needed. The degree of asymmetry between each individual's left and right measurements was quantified using the equation outlined by Trinkaus *et al.* (1994):

$$\frac{(\text{max. value} - \text{min. value})}{\text{min. value}} * 100 = \text{\% difference between left and right}$$

This equation benefits from maximising the perceived asymmetry between the sides, particularly in cases where the variation is small and stochastic in nature (*ibid.*), making it particularly suitable for analysis of metacarpal and phalanx asymmetry. This equation gives a value for absolute asymmetry between left and right, i.e. the amount of difference between the sides. The equation results in positive values and therefore does not inform regarding the direction of the asymmetry, i.e. whether the value is left-side or right-side dominant. The direction of the asymmetry was calculated using an equation such as that found in Steele & Mays (1995):

$$\frac{\text{Right} - \text{Left}}{(\text{Right} + \text{Left})/2} *100$$

A positive value indicates a right-side dominant asymmetry and a negative value indicates left-side dominant asymmetry. The absolute asymmetry equation of Trinkaus *et al.* (1994) and the directional asymmetry equation of Steele & Mays (1995) provide similar results (with any differences occurring only at the second decimal place); therefore the information from these equations was combined to give an asymmetry score that encompassed both absolute and directional aspects.

For each of the 65 subjects in the Écija sample, the percentage of metacarpal measurements that were right-side dominant (right-side measurement bigger than the left-side measurement), left-side dominant (left-side bigger than right) and symmetrical (both measurements equal) were calculated and plotted in Figures 5.1 to 5.5 (below). Each metacarpal variable is displayed in a separate graph: length (Fig. 5.1), radio-ulnar diameter (Fig. 5.2), dorso-palmar diameter (Fig. 5.3), proximal breadth (Fig. 5.4), and distal breadth (Fig. 5.5). For the purposes of brevity and clarity the data from the metacarpal asymmetry equations are presented in Table C.2, Appendix C. Sex and age effects on asymmetry are assessed in sections 5.1.4 and 5.1.5, respectively.

Figures 5.1 to 5.5 show a clear right-side dominant asymmetry across all metacarpal variables. The extent of the right-side dominance is reasonably strong with 11 out of the 25 variables exhibiting right-side dominance greater than 70% (i.e. at least 70% of individuals were right-side dominant), although overall asymmetry varies from 51% (mc3L) to 91.5% (mc5DP). If we assume a strong right-hand preference in the living Écija population (typical of that found in modern living populations) then these values are lower and more variable than expected. The percentage of symmetrical subjects stays constant across all measurements. Although the results of the asymmetry equation are size-independent they confirm the right-side dominance identified in the Wilcoxon analysis (Table 5.2).

A number of patterns can be identified in the distribution of asymmetry. For metacarpal length (Fig. 5.1), there is a decrease in the degree of asymmetry moving medially across the metacarpal row (from mc1 to mc5), with an obvious dip at mc3, which is approaching symmetry. For the other metacarpals this pattern is reversed, with asymmetry increasing medially across the metacarpal row (Figs 5.2 to 5.5). The magnitude of asymmetry also appears to vary across the metacarpal properties. For example, asymmetry is greatest for dorso-palmar breadth (Fig. 5.3), relative to other variables. Proximal breadth (Fig. 5.4) shows the lowest levels of asymmetry, with mc2PB in particular approaching symmetry. Generally, the metacarpal shaft (mcRU and mcDP) exhibit stronger right-side asymmetry than head or base measurements (mcDB and mcPB). This pattern supports the observation that, in the long bones diaphyses tend to be more asymmetric than articular surfaces due to continuing remodelling of the bone shaft relative to the articular surfaces after epiphyseal fusion (Ruff, 2000).

Why metacarpal length should show a lateral to medial decrease in asymmetry, when the other variables show a corresponding *increase* in asymmetry is unclear. Potential issues with assessing asymmetry between small metacarpal bones may influence the expression of this asymmetry as seen in the Figures below. Metacarpal length is the largest variable and has a different pattern of asymmetry. To help determine the cause of this trend, the results from this analysis need to be compared with those of other metacarpal samples.

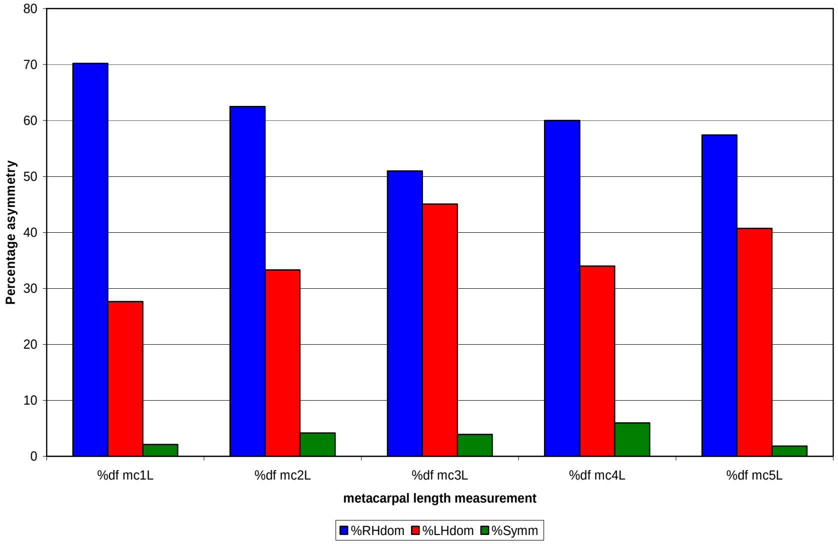


Figure 5.1.Percentage of right- and left-side dominant and symmetric individuals for metacarpal length (mc*L).

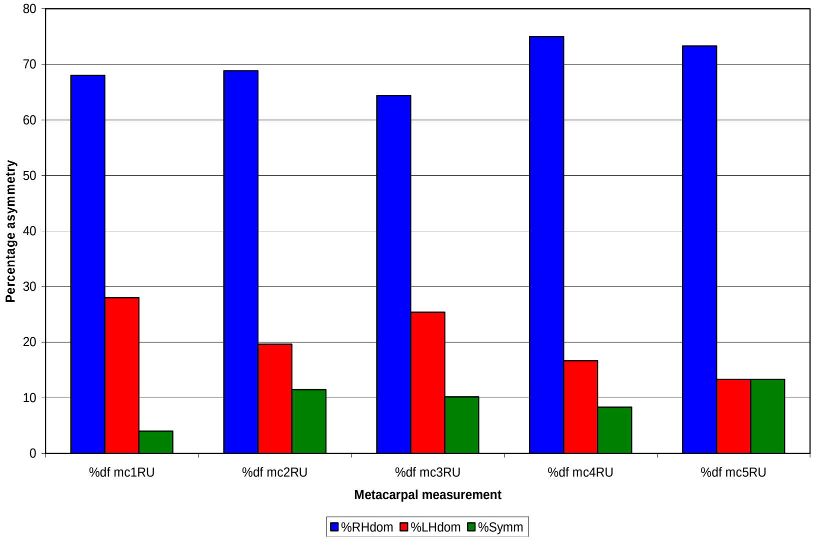


Figure 5.2.Percentage of right- and left-side dominant and symmetric individuals for metacarpal radio-ulnar diameter (mc*RU).

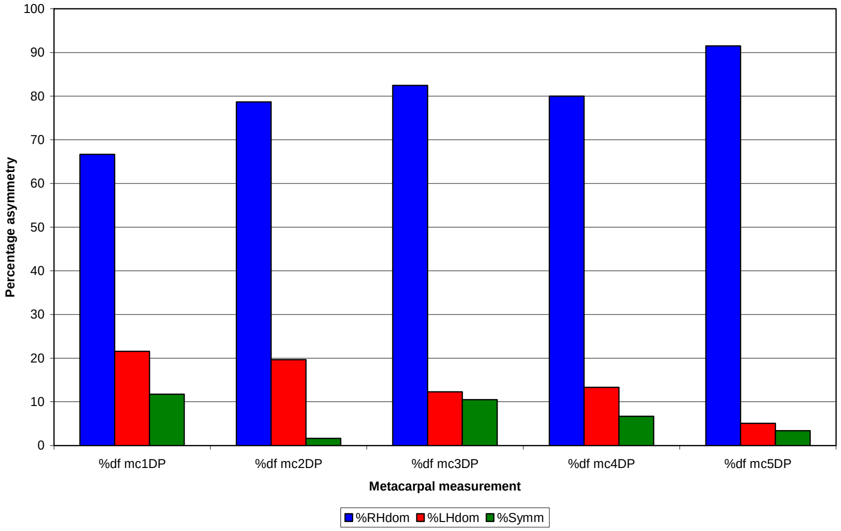


Figure 5.3. Percentage of right- and left-side dominant and symmetric individuals for metacarpal dorso-palmar diameter (mc*DP).

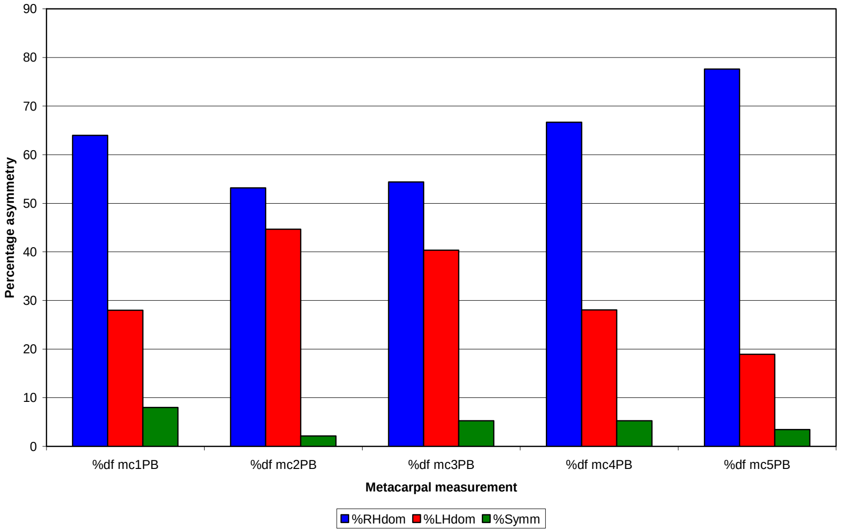


Figure 5.4. Percentage of right- and left-side dominant and symmetric individuals for metacarpal proximal breadth (mc*PB).

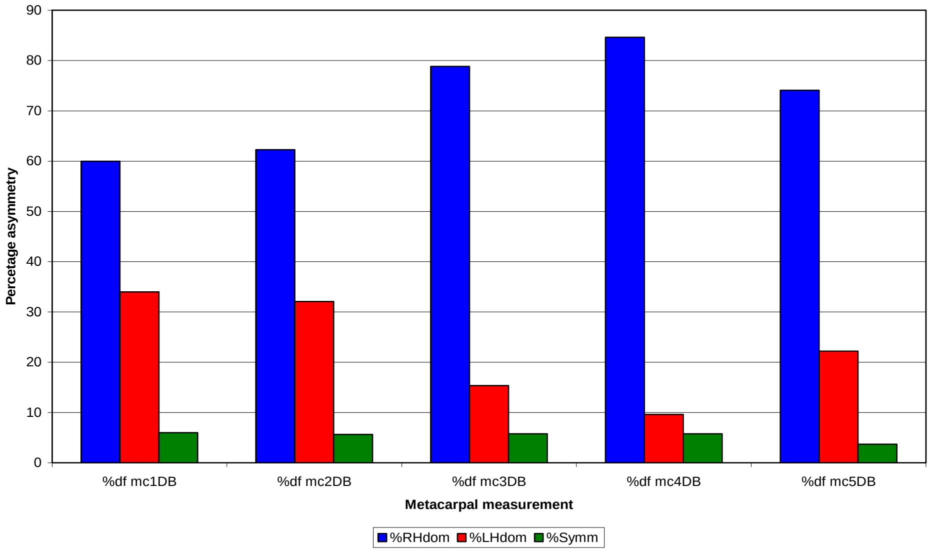


Figure 5.5. Percentage of right- and left-side dominant and symmetric individuals for metacarpal distal breadth (mc*DB). Further data for asymmetry analysis available in Table C.2, Appendix C.

To further explore patterns in the metacarpal data, the asymmetry values in Figures 5.1 to 5.5 were re-plotted to produce graphs representing the asymmetry data for each metacarpal separately. Figures 5.6 to 5.10 (below) provide the results of this re-plotted asymmetry data.

When the asymmetry profile of each metacarpal is examined separately, further patterns emerge. Asymmetry in metacarpal 1 (Fig. 5.6) shows a similar trend to metacarpal length, i.e. a decreasing degree of right-side dominance across the measurements (from mc length to distal breadth). Interestingly, the other metacarpals show a different pattern of asymmetry to mc1 but one that is consistent across mc2 to mc5. This trend is for length to show a low degree of right-side dominant asymmetry but for this asymmetry to increase across subsequent measurements, peaking at dorso-palmar diameter. There is a decrease in proximal breadth asymmetry before it increases again for distal breadth (with the exception of mc5DB). This broadly consistent pattern of asymmetry across the metacarpals, which shows variation in the degree of asymmetry *between* the variables, suggests that care must be taken when assessing metacarpal asymmetry. To gain the most accurate picture of metacarpal asymmetry as many measurements of each bone should be taken as possible, as the current results suggest that studying one measurement in isolation may over- or under-estimate the degree of asymmetry present. The different pattern of asymmetry identified in mc1 is may be related to the unique functional role of this bone in the human hand compared to other metacarpals (e.g. Aiello, 1994; Susman, 1994; Marzke, 1997).

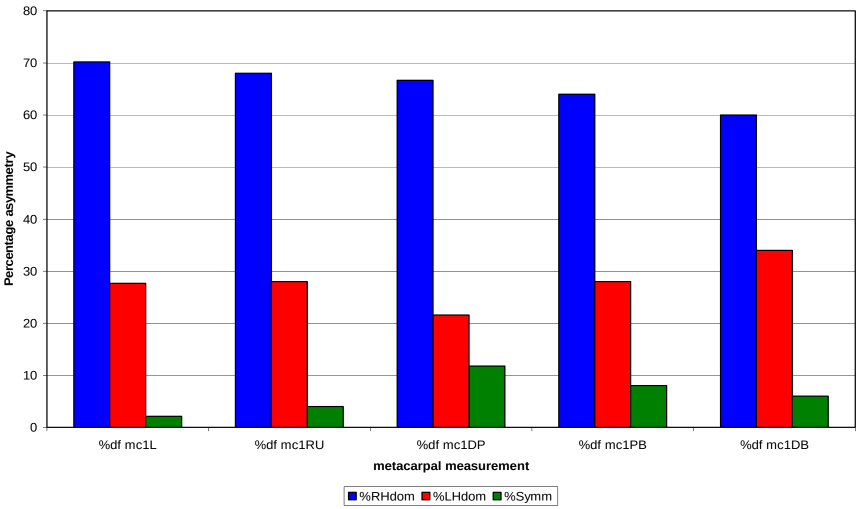


Figure 5.6. Asymmetry values for each metacarpal 1 measurement (length, radio-ulnar diameter, dorso-palmar diameter, proximal breadth and distal breadth).

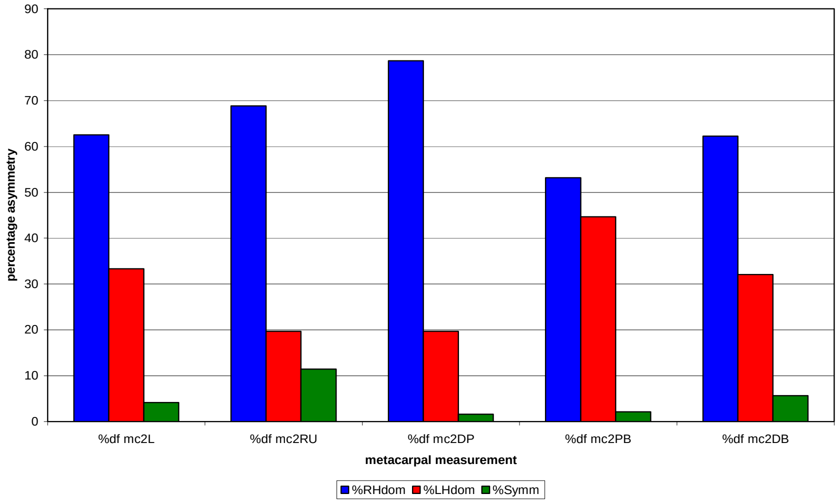


Figure 5.7. Asymmetry values for each metacarpal 2 measurement (length, radio-ulnar diameter, dorso-palmar diameter, proximal breadth and distal breadth).

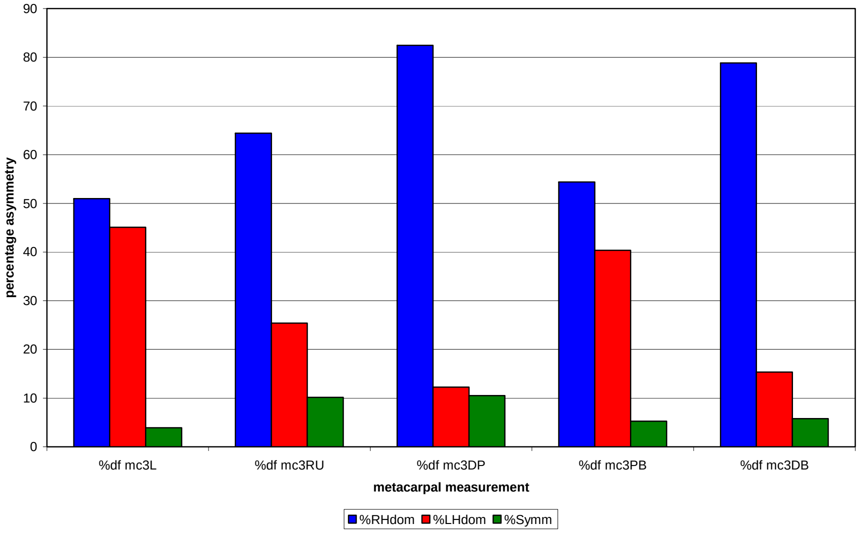


Figure 5.8. Asymmetry values for each metacarpal 3 measurement (length, radio-ulnar diameter, dorso-palmar diameter, proximal breadth and distal breadth).

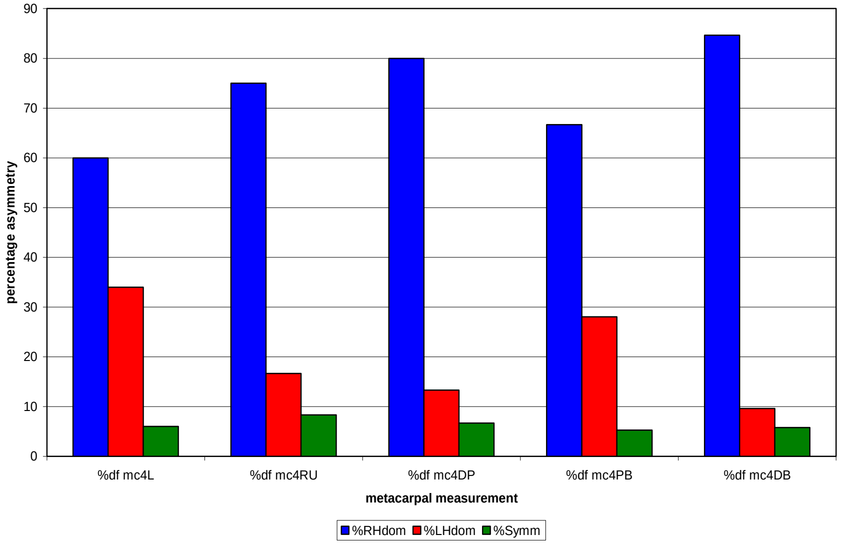


Figure 5.9. Asymmetry values for each metacarpal 4 measurement (length, radio-ulnar diameter, dorso-palmar diameter, proximal breadth and distal breadth).

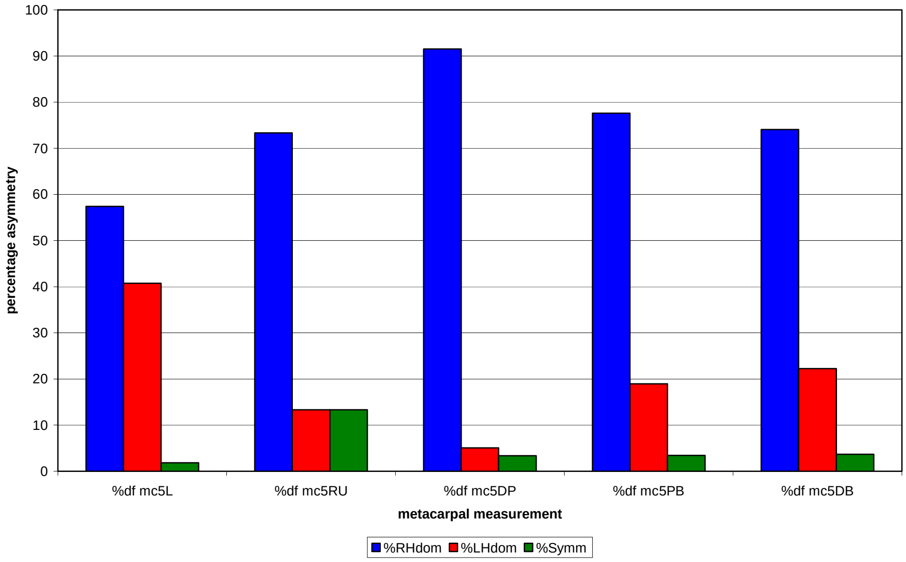


Figure 5.10. Asymmetry values for each metacarpal 5 measurement (length, radio-ulnar diameter, dorso-palmar diameter, proximal breadth and distal breadth). Further data for asymmetry analysis available in Table C.2, Appendix C.

Percentage asymmetry values for the Écija phalanx length data were calculated using the equations outlined above. Figure 5.11 provides the results of this analysis. Due to small sample sizes, data for distal phalanges 2 to 5 were not included. The data from this analysis can be found in Table C.3, Appendix C.

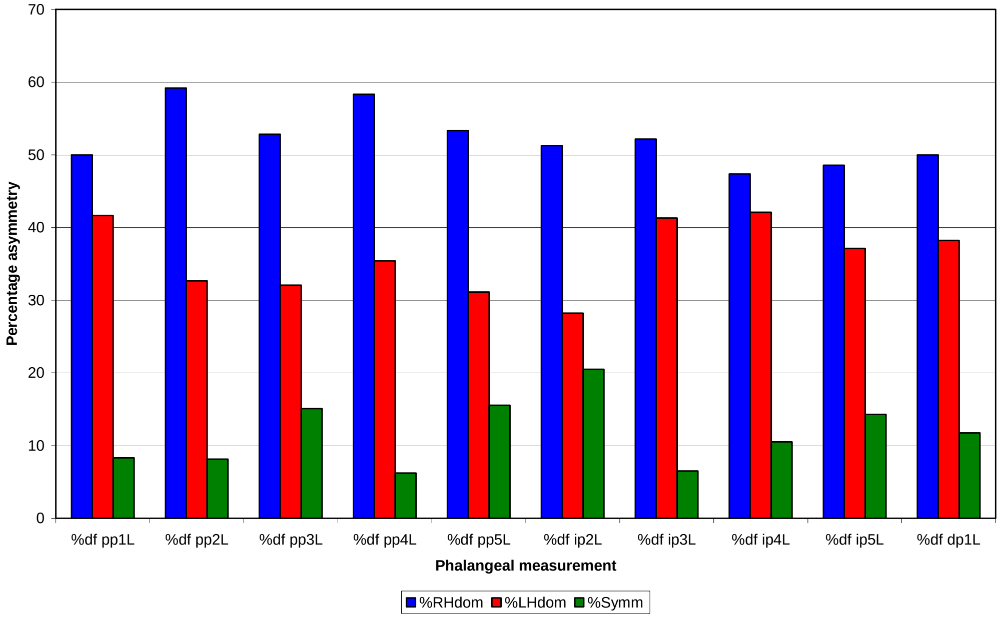


Figure 5.11. Asymmetry values for each phalanx measurement (pp*L, ip*L). Data for distal phalanges 2 to 5 not included due to small sample sizes. Further data available in Table C.3, Appendix C.

It can be seen from Figure 5.11 that while all phalanx length measurements are right-side dominant the level of asymmetry is greatly reduced compared to that of the metacarpals. Right-side dominance in the phalanges ranges from 47.4% (ip4L) to 59.2% (pp2L), in comparison to the metacarpals where only 4 variables (out of 25) had a right-side asymmetry value of less than 60% (mc3L, mc5L, mc2PB, mc3PB). This indicates a more uniform distribution in asymmetry in the finger bones, with no clear patterns emerging. This may be a reflection of functional differences in the utilisation of the fingers compared to the metacarpals. However as highlighted previously, methodological issues must also be considered when discussing phalanx results (section 5.1.1).

5.1.4. Sex effects on asymmetry in the metacarpals and phalanges

The earlier ANOVA analyses (section 5.1.2) showed that while metacarpal and phalanx measurement size were clearly sexually dimorphic, there was very little age difference in variable size. The asymmetry values reported in section 5.1.3 are independent of the effects of size and therefore left/right differences between the sexes or age categories may reflect differences in activity patterns. To assess the effects of sex and age on asymmetry data, Mann-Whitney U tests were performed. The Mann-Whitney U test is the non-parametric equivalent of the independent-samples t-test and tests the null hypothesis that two populations will have the same median value (Kinnear & Gray, 2006).

This analysis also provided the opportunity to explore differences between absolute and directional asymmetry. As discussed in section 5.1.3 the asymmetry equation proposed by Trinkaus *et al.* (1994) is a measure of absolute asymmetry. Subtracting the minimum value from the maximum value always results in a positive number, which represents the magnitude of the asymmetry but not the direction. The equation used by Steele & Mays (1995) subtracts the left value from the right and provides a measure of the direction of the asymmetry, for left-side dominant measurements will give a negative asymmetry value and right-side dominant measurements a positive value. It is therefore possible to examine whether males and females, plus subjects in different age categories differ in terms of the direction of their asymmetry (right- or left-side dominant), or in the magnitude of the asymmetry (absolute asymmetry).

A Mann-Whitney U test was performed on both the directional and absolute asymmetry data for the metacarpals from section 5.1.3 to identify any differences between males and females in the nature of their asymmetry. The results of this analysis are presented in Table 5.6 (below) and it can be seen that males and females differ only slightly in terms of their directional and absolute asymmetry values. For directional asymmetry sex is found to only have a statistically significant effect on mc3DP and mc5PB. This suggests that males and females do not differ significantly in the direction of their asymmetry (i.e. males are not significantly more left-side or right-side dominant for instance). The rank data for the

Mann-Whitney U test (not shown – see Table C.4, Appendix C) shows a trend for females to have a larger rank value than males (for 19 of 25 variables, including mc3DP and mc5PB), suggesting that females are more likely to be right-side dominant than male (left-side dominant scores are minus values, therefore the mean rank value is likely to be smaller the more left-side asymmetry there is).

Table 5.6. A Mann-Whitney U test of the effects of sex on directional asymmetry and absolute asymmetry values for each metacarpal measurement.

Measurement	**N**	**Directional asymmetry (cf. Steele & Mays, 1995)**				**Absolute asymmetry (cf. Trinkaus *et al.*, 1994)**			
		mean	**std dev.**	**U**	**Sig. (2-tailed)**	**mean**	**std dev.**	**U**	**Sig. (2-tailed)**
mc1L	47	0.79	1.59	237.5	p = 0.49	1.37	1.13	213.0	p = 0.22
mc2L	48	0.52	1.20	255.5	p = 0.62	0.93	0.91	250.0	p = 0.54
mc3L	51	0.16	1.36	257.0	p = 0.22	1.11	0.81	318.5	p = 0.95
mc4L	50	0.53	1.50	209.5	*p = 0.06*	1.25	0.98	265.5	p = 0.45
mc5L	54	3.30	1.57	271.5	p = 0.14	1.24	1.02	340.5	p = 0.79
mc1RU	50	2.61	4.47	222.5	p = 0.11	4.33	3.47	229.5	p = 0.14
mc2RU	61	1.72	6.28	414.5	p = 0.56	5.52	4.50	306.5	**p = 0.03**
mc3RU	59	4.94	4.69	367.5	p = 0.33	3.98	3.15	263.0	**p < 0.01**
mc4RU	60	5.86	5.87	417.5	p = 0.68	6.29	4.40	436.5	p = 0.90
mc5RU	60	1.96	6.96	335.0	*p = 0.10*	6.85	6.01	340.0	p = 0.12
mc1DP	51	3.63	4.76	265.0	p = 0.31	3.94	3.62	233.0	*p = 0.10*
mc2DP	61	4.53	4.70	352.5	p = 0.14	4.91	3.35	413.0	p = 0.55
mc3DP	59	4.43	5.67	274.0	**p = 0.02**	5.73	4.42	313.0	**p = 0.05**
mc4DP	60	7.46	4.32	426.0	p = 0.78	5.07	3.54	431.0	p = 0.83
mc5DP	59	1.78	6.74	420.0	p = 0.86	8.23	5.84	418.0	p = 0.84
mc1PB	50	0.35	4.84	241.5	p = 0.22	4.22	3.11	249.0	p = 0.28
mc2PB	47	0.40	5.35	200.5	p = 0.19	4.32	3.54	257.5	p = 0.94
mc3PB	57	0.78	3.90	334.0	p = 0.25	3.18	2.44	358.0	p = 0.45
mc4PB	57	2.58	4.74	293.5	*p = 0.10*	4.45	3.19	247.5	**p = 0.02**
mc5PB	58	5.38	6.32	264.5	**p = 0.02**	6.47	5.19	311.5	*p = 0.10*
mc1DB	50	1.47	3.11	253.0	p = 0.29	2.78	2.03	297.5	p = 0.84
mc2DB	53	1.80	3.66	306.0	p = 0.49	3.23	2.51	279.0	p = 0.24
mc3DB	52	2.89	3.72	315.5	p = 0.75	4.01	2.49	321.5	p = 0.83
mc4DB	52	3.66	3.15	326.5	p = 0.90	4.06	2.61	299.5	p = 0.54
mc5DB	54	2.22	3.72	280.5	p = 0.17	3.64	2.42	296.5	p = 0.27

Mean and standard deviation values rounded to two decimal places. Significant p-values highlighted in bold. P-values approaching significance (between 0.055 and 0.1) highlighted in italics. Abbreviations used: mc*L = metacarpal length, mc*RU = radio-ulnar midshaft diameter, mc*DP = dorso-palmar midshaft diameter, mc*PB = proximal breadth, mc*DB = distal breadth. Asterisk (*) denotes metacarpal number.

For absolute metacarpal asymmetry, four measurements showed a significant sex effect: mc2RU, mc3RU, mc3DP, mc4PB. For these variables, male and females are statistically different in the size of their asymmetry scores. As with the directional asymmetry, the mean rank values for females is larger than that for males in 19 out of 25 variables and for the four significant variables (see Table C.5,

Appendix C). Although the overall effect of sex on metacarpal asymmetry can be considered weak, there is a general trend for females to be more often right-side dominant than males, and for the size of this asymmetry to be larger for females.

A second Mann-Whitney U test was performed to determine the effect of sex on phalanx length asymmetry. Table 5.7 provides the results of this analysis.

Table 5.7. A Mann-Whitney U test of the effects of sex on directional asymmetry and absolute asymmetry values for each of the phalanx measurements.

Measurement	**N**	**Directional asymmetry (cf. Steele & Mays, 1995)**				**Absolute asymmetry (cf. Trinkaus *et al.*, 1994)**			
		mean	**std dev.**	**U**	**Sig. (2-tailed)**	**mean**	**std dev.**	**U**	**Sig. (2-tailed)**
pp1L	48	0.15	1.95	250.5	p = 0.54	1.47	1.34	195.5	*p = 0.08*
pp2L	49	0.40	1.31	182.5	**p = 0.02**	1.13	0.78	248.5	p = 0.34
pp3L	53	0.55	1.41	290.5	p = 0.41	1.16	0.98	263.0	p = 0.19
pp4L	48	-0.05	3.25	283.0	p = 0.96	1.55	3.64	284.0	p = 0.97
pp5L	45	0.46	1.72	225.0	p = 0.62	1.38	1.13	239.5	p = 0.87
ip2L	39	0.66	1.79	155.0	p = 0.34	1.39	1.31	180.0	p = 0.81
ip3L	46	-0.08	4.13	257.0	p = 0.95	2.19	4.73	223.5	p = 0.43
ip4L	38	0.20	1.87	121.5	p = 0.13	1.51	1.15	138.0	p = 0.31
ip5L	35	0.46	2.24	77.0	**p = 0.01**	1.88	1.31	128.0	p = 0.42
dp1L	34	0.93	3.70	105.5	p = 0.28	2.43	2.93	133.0	p = 0.91
dp2L	5	-0.02	5.17	2.0	p = 0.80	3.94	3.03	2.0	p = 0.80
dp3L	14	0.29	3.04	4.5	**p = 0.01**	2.41	1.85	22.5	p = 1.00
dp4L	10	-0.43	3.48	12.0	p = 1.00	2.42	2.65	2.0	**p = 0.03**
dp5L	6	0.67	2.08	3.0	p = 0.80	1.63	1.31	2.0	p = 0.53

Minus values for directional asymmetry means reflects the equation used to calculate asymmetry, in which left-side dominant individual will have a minus score. Mean and standard deviation values rounded to two decimal places. Significant p-values highlighted in bold. P-values approaching significance (between 0.055 and 0.1) highlighted in italics. Abbreviations used: pp*L = proximal phalanx length, ip*L = intermediate phalanx length, dp*L = distal phalanx length. Asterisk (*) denotes phalanx number.

For phalanx length asymmetry, sex is found to have more of an effect on directional asymmetry than absolute asymmetry, the reverse to that pattern seen in the metacarpals. However, as with the metacarpals, the general effect is limited and there appears to be no pattern in the distribution of significant effects. For directional asymmetry, there was a trend for females to be right-side dominant more often than males, with 8 out of 14 mean rank values (see Table C.6, Appendix C) larger for females than males and 4 out of 14 larger for males (dp4L was tied).

For absolute asymmetry there was almost no difference between males and females in terms of the size of their asymmetric values, with only one statistically significant effect for dp4L. In this instance the male mean rank value was larger than that of females and more generally, 8 out of the 14 measurements had larger male mean rank values than female mean rank values (see Table C.7, Appendix C). While the trend is towards females being more right-side dominant than males the difference between right and left phalanges is greater for males.

5.1.5. Age effects on asymmetry

To assess the effect of age on directional and absolute asymmetry further Mann-Whitney U tests were performed on the Écija metacarpal and phalanx data. Table 5.8 provides the results of the metacarpal analysis. Due to the small number of individuals classified as 'old adult', this category was excluded from the analysis.

Table 5.8. A Mann-Whitney U test of the effects of age on directional asymmetry and absolute asymmetry values for each of the metacarpal measurements.

Measurement	N	Directional asymmetry (cf. Steele & Mays, 1995)				Absolute asymmetry (cf. Trinkaus *et al.*, 1994)			
		mean	std dev.	U	Sig. (2-tailed)	mean	std dev.	U	Sig. (2-tailed)
mc1L	47	0.79	1.59	212.5	p = 0.49	1.37	1.13	204.5	p = 0.38
mc2L	48	0.52	1.20	226.0	p = 0.53	0.93	0.91	254.5	p = 1.00
mc3L	51	0.16	1.36	251.5	p = 0.80	1.11	0.81	225.0	p = 0.41
mc4L	50	0.53	1.50	219.0	p = 0.33	1.25	0.98	252.0	p = 0.80
mc5L	54	3.30	1.57	285.0	p = 0.77	1.24	1.02	255.5	p = 0.38
mc1RU	50	2.61	4.47	264.5	p = 0.98	4.33	3.47	236.5	p = 0.53
mc2RU	61	1.72	6.28	363.5	p = 0.73	5.52	4.50	333.5	p = 0.40
mc3RU	59	4.94	4.69	323.5	p = 0.57	3.98	3.15	352.5	p = 0.94
mc4RU	60	5.86	5.87	363.5	p = 0.74	6.29	4.40	379.5	p = 0.94
mc5RU	60	1.96	6.96	192.5	**p < 0.01**	6.85	6.01	240.5	**p = 0.02**
mc1DP	51	3.63	4.76	268.0	p = 0.80	3.94	3.62	203.5	p = 0.11
mc2DP	61	4.53	4.70	294.5	p = 0.14	4.91	3.35	319.5	p = 0.29
mc3DP	59	4.43	5.67	293.5	p = 0.27	5.73	4.42	364.5	p = 0.96
mc4DP	60	7.46	4.32	288.0	p = 0.11	5.07	3.54	328.5	p = 0.36
mc5DP	59	1.78	6.74	328.5	p = 0.48	8.23	5.84	364.5	p = 0.86
mc1PB	50	0.35	4.84	237.0	p = 0.54	4.22	3.11	173.0	**p = 0.04**
mc2PB	47	0.40	5.35	225.0	p = 0.68	4.32	3.54	186.0	p = 0.19
mc3PB	57	0.78	3.90	319.0	p = 0.76	3.18	2.44	194.5	**p < 0.01**
mc4PB	57	2.58	4.74	335.5	p = 0.83	4.45	3.19	333.0	p = 0.79
mc5PB	58	5.38	6.32	356.0	p = 0.91	6.47	5.19	331.0	p = 0.59
mc1DB	50	1.47	3.11	207.5	p = 0.18	2.78	2.03	203.5	p = 0.16
mc2DB	53	1.80	3.66	265.0	p = 0.37	3.23	2.51	276.0	p = 0.48
mc3DB	52	2.89	3.72	286.0	p = 0.97	4.01	2.49	258.0	p = 0.55
mc4DB	52	3.66	3.15	260.0	p = 0.63	4.06	2.61	248.5	p = 0.47
mc5DB	54	2.22	3.72	274.5	p = 0.62	3.64	2.42	230.5	p = 0.17

Mean and standard deviation values rounded to two decimal places. Significant p-values highlighted in bold. P-values approaching significance (between 0.055 and 0.1) highlighted in italics. Abbreviations used: mc*L = metacarpal length, mc*RU = radio-ulnar midshaft diameter, mc*DP = dorso-palmar midshaft diameter, mc*PB = proximal breadth, mc*DB = distal breadth. Asterisk (*) denotes metacarpal number.

It can be seen from Table 5.8 that there is very little effect of age on metacarpal asymmetry with only one significant effect on directional asymmetry (mc5RU) and three effects on absolute asymmetry (mc5RU, mc1PB, mc3PB). This suggests that the expression of asymmetry in an individual does not change over the course of their adult life and 'young' and 'middle' adults do not differ significantly in terms of their side preference. The general trend in the mean rank values (see Tables C.8 and C.9, Appendix C) is for middle-aged adults to be more right-side dominant than 'young' adults but for both age categories to have asymmetry scores of similar size. These results follow from those of the earlier ANOVA analysis (section 5.1.2) which found very little effect of age on metacarpal size.

Table 5.9 provides the results of the Mann-Whitney U test to assess the effects of age on asymmetry in phalanx length.

Table 5.9. A Mann-Whitney U test of the effects of age on directional asymmetry and absolute asymmetry values for each of the phalanx measurements.

Measurement	**N**	**Directional asymmetry**				**Absolute asymmetry**			
		mean	**std dev.**	**U**	**Sig. (2-tailed)**	**mean**	**std dev.**	**U**	**Sig. (2-tailed)**
pp1L	48	0.15	1.95	216.5	p = 0.43	1.47	1.34	247.0	p = 0.92
pp2L	49	0.40	1.31	124.5	**p = 0.01**	1.13	0.78	157.5	*p = 0.08*
pp3L	53	0.55	1.41	258.0	p = 0.60	1.16	0.98	277.5	p = 0.91
pp4L	48	-0.05	3.25	232.0	p = 0.86	1.55	3.64	207.0	p = 0.44
pp5L	45	0.46	1.72	193.0	p = 0.38	1.38	1.13	192.0	p = 0.36
ip2L	39	0.66	1.79	149.0	p = 0.71	1.39	1.31	107.0	*p = 0.08*
ip3L	46	-0.08	4.13	220.5	p = 0.81	2.19	4.73	228.0	p = 0.95
ip4L	38	0.20	1.87	149.5	p = 0.70	1.51	1.15	113.5	p = 0.13
ip5L	35	0.46	2.24	118.0	p = 0.74	1.88	1.31	103.0	p = 0.37
dp1L	34	0.93	3.70	39.0	**p < 0.01**	2.43	2.93	105.0	p = 0.49
dp2L	5	-0.02	5.17	1.0	p = 1.00	3.94	3.03	1.0	p = 1.00
dp3L	14	0.29	3.04	12.5	p = 0.25	2.41	1.85	14.5	p = 0.39
dp4L	10	-0.43	3.48	6.0	p = 0.50	2.42	2.65	6.0	p = 0.51
dp5L	6	0.67	2.08	2.0	p = 0.53	1.63	1.31	4.0	p = 1.00

Minus values for directional asymmetry means reflects the equation used to calculate asymmetry, in which left-side dominant individual will have a minus score. Mean and standard deviation values rounded to two decimal places. Significant p-values highlighted in bold. P-values approaching significance (between 0.055 and 0.1) highlighted in italics.

In keeping with the results of the metacarpal asymmetry this analysis found that there was almost no relationship between age and either the direction or the magnitude of phalanx asymmetry. However, as with the analysis of sex and phalanx asymmetry, there is more of an effect of age on directional asymmetry than on absolute asymmetry (which is opposite to the pattern seen in metacarpal asymmetry).When mean rank values are compared (see Tables C.10 and C.11, Appendix C), there are no clear trends in age difference for either the direction of asymmetry or the magnitude of the asymmetry. It is interesting to note this further difference between the metacarpals and phalanges following from the asymmetry plots in Figures 5.1 to 5.11, which showed that absolute asymmetry was reduced in the phalanges compared to the metacarpals.

The results of the Mann-Whitney U tests on the Écija sample suggest that while there is some evidence to suggest that the direction and magnitude of bilateral asymmetry in the hands are differentially affected by sex and age, this effect is limited. The effect of sex is slightly stronger on asymmetry size than direction in the metacarpal sample, with this trend reversed in the phalanges. The same is found for age and asymmetry. For both the metacarpals and phalanges females are right-side dominant more frequently than males, with the degree of asymmetry in females also tending to be larger. This could be a consequence of the males in this sample engaging in activities which stressed both hands equally thus reducing bilateral asymmetry. Conversely, females may have been engaged in activities which loaded the right hand preferentially. In the age analysis the general trend is for middle adults to be more frequently right-side dominant than young adults from which it could be tentatively concluded that asymmetry in this sample was increasing over time. However, with few significant effects found it is unwise to draw firm conclusions at this stage.

5.1.6. Individual asymmetry

The nature of asymmetry within the individual was also investigated. To do this, the percentage of each individual's measurements that were right-side dominant, left-side dominant and symmetrical was calculated (in terms of absolute asymmetry) as described in section 5.1.3. The results of this analysis for the Écija metacarpals are plotted in Figure 5.12 (below) which indicates clear variation in individual metacarpal asymmetry. The clear right-side dominance identified in Figures 5.1 to 5.10 remains with only 4 out of 65 individuals exhibiting overall left-side dominance. Right-side dominance ranges between individuals from 42% to 100%, a much larger range than identified in any previous metacarpal analyses. In total, 92.3% of individuals display right-side dominance in metacarpal asymmetry. While this supports a strong right-side dominance in the sample as a whole and is comparable to published figures relating to the distribution of self-reported handedness in modern human populations (Marchant *et al.*, 1995), the variability of the magnitude of the right-side dominance in Figure 5.12 appears to mask the strength of the asymmetry when asymmetry is examined in the sample as a whole.

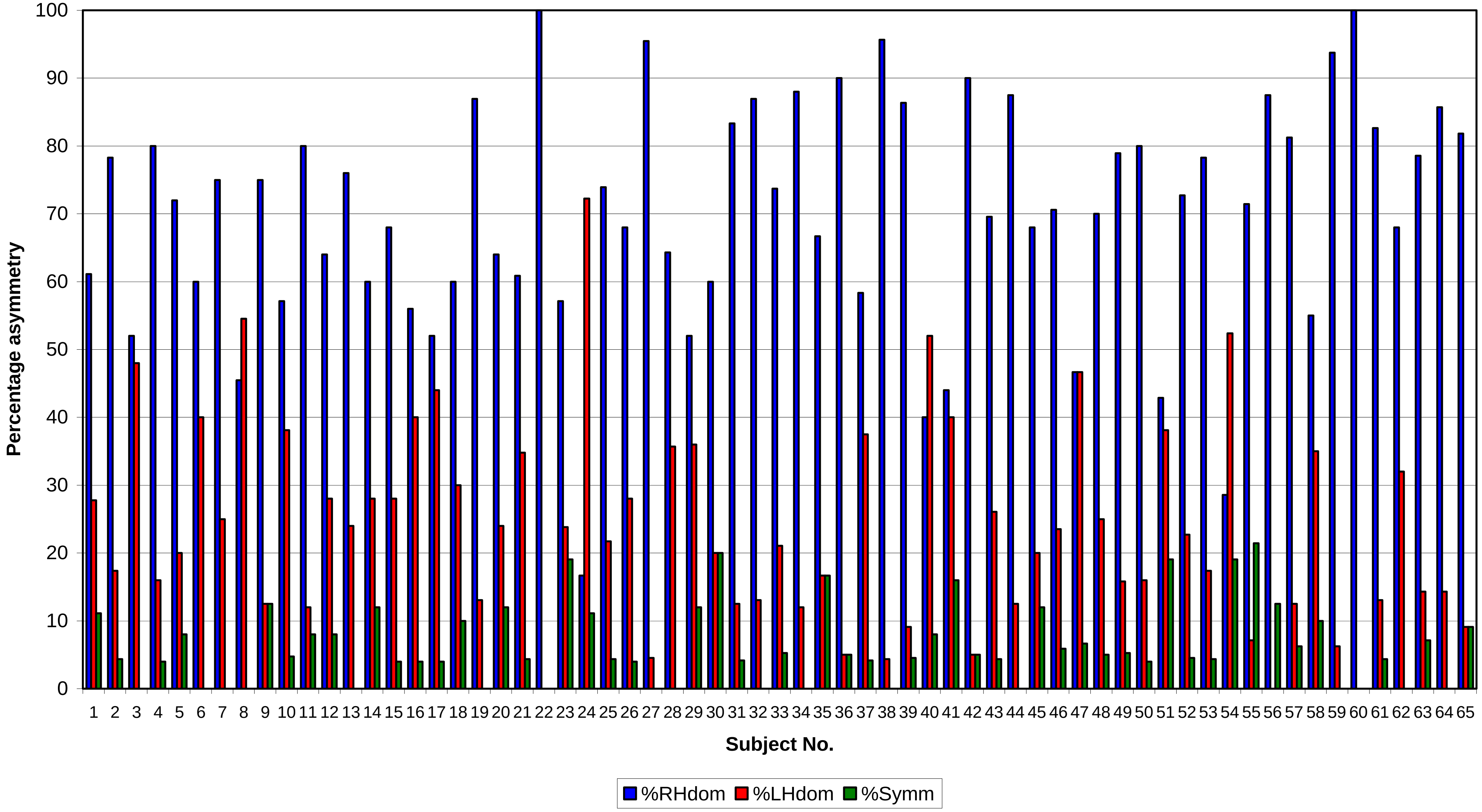


Figure 5.12. For each individual, the percentage of right-side dominant, left-side dominant and symmetric scores for all 25 metacarpal measurements. Each individual is represented by a number along the X axis.

Analysis of individual asymmetry was repeated for the phalanges and reported in Figure 5.13. What is immediately clear from this analysis is that phalanx length asymmetry is highly variable between individuals and to a greater degree than was seen for the metacarpals. Although the general pattern is towards right-side dominance (in 37/61 or 60.7% of individuals) there are a sizeable proportion of individuals that show a left-side dominance (approx. 25%) or equal side dominances (approx. 15%) in phalanx asymmetry. This analysis supports the observation of reduced asymmetry in phalanx length compared to metacarpal properties (Fig. 5.11).

5.1.7. Summary of metacarpal and phalanx metric analysis

The analyses above indicate the presence of a clear right-side dominant asymmetry in the Écija metacarpals, an asymmetry stronger than that found in the phalanges from this sample. Wilcoxon tests showed that left and right metacarpal properties are significantly different in size although far fewer significant size differences were found for the phalanges. ANOVA tests identified a strong main effect of sex on both the metacarpals and phalanges (this effect was stronger for the proximal phalanges than the intermediate and distal phalanges) with males found to be larger than females. In contrast, the ANOVA for age found very few significant effects for either the metacarpals or the phalanges suggesting that the metric properties of these bones are not influenced by increasing age. A small number of significant interaction effects were found for sex on age.

Analysis of asymmetry in the hands found clear variation in the distribution and magnitude of asymmetry across the hand with metacarpal 1 in particular showing reduced levels of asymmetry relative to the other metacarpals. Reduced phalanx asymmetry may represent either functional or methodological influences. Mann-Whitney U tests found limited effects of sex and age on asymmetry. Comparisons of individual asymmetry found that as expected, the majority of individuals display right-side dominance although the magnitude of this asymmetry varies greatly between individuals.

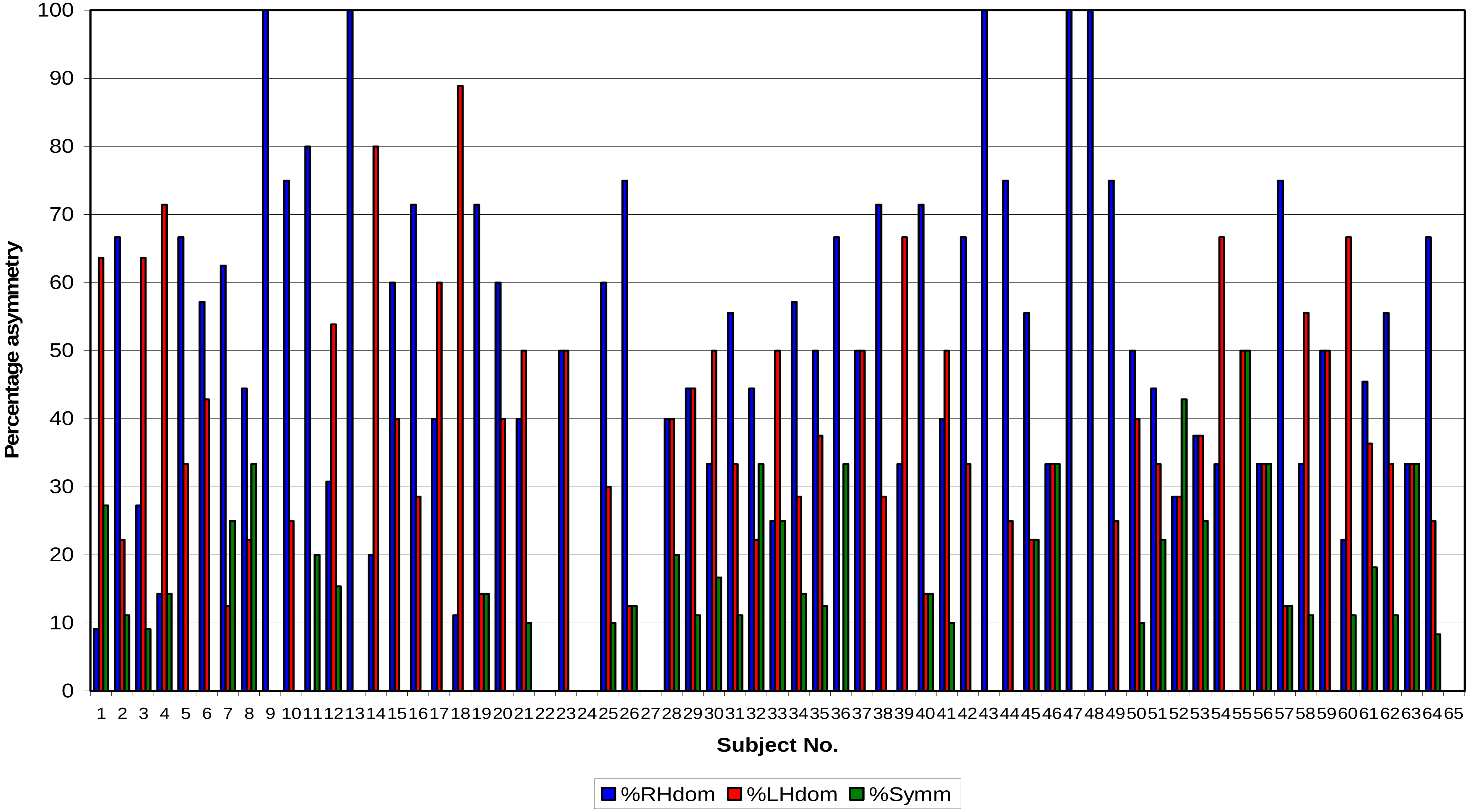


Figure 5.13. For each individual, the percentage of right-side dominant, left-side dominant and symmetric scores for all phalanx measurements. Due to missing data, individual asymmetry could not be calculated for subjects 22, 24, 27 and 65.

5.2. Humerus metric data

Metric variation and asymmetry was also explored in the corresponding humeral material from the Écija sample. As the long bones of the upper limb are more regularly assessed in terms of their asymmetric properties this analysis provides an important comparison to the analysis of the hand bones presented in section 5.1. The descriptive statistics for the humerus sample are provided in Table C.12, Appendix C. Boxplots of each of the variables identified the presence of a number of outliers in the data which were dealt with following the procedures outlined in section 5.1. In addition histograms and p-p plots confirmed the normal distribution of the data. The structure of the data analysis in this section follows that of the hand bones in section 5.1.

5.2.1 Significance testing

A Wilcoxon test was conducted to identify statistically significant differences between the left and right humerus measurements. As it was decided not to exclude any outliers, this non-parametric test was chosen, rather than the paired-samples t-test. Table 5.10 provides the results of this analysis.

Table 5.10. Wilcoxon test results for the combined-sex and combined-age Écija humerus sample.

Measurement	Side	N	Mean	Std dev.	Sig. (2-tailed)
MxL	L	34	301.24	19.72	**$p < 0.01$**
	R	52	309.02	21.14	
MxDm	L	46	21.23	1.70	**$p < 0.01$**
	R	59	22.01	1.87	
MnDm	L	45	16.47	1.76	**$p = 0.03$**
	R	60	16.82	1.99	
MnCir	L	36	59.31	5.59	**$p < 0.01$**
	R	38	60.76	5.66	
CirHd	L	27	129.26	10.34	**$p < 0.01$**
	R	36	132.25	12.32	
MxTDm	L	41	39.89	2.93	**$p < 0.01$**
	R	50	40.77	3.14	
MxSDm	L	43	42.48	3.66	**$p < 0.01$**
	R	52	43.64	3.96	
EpBr	L	50	59.72	5.81	**$p < 0.01$**
	R	57	60.38	5.41	
TCBr	L	51	42.58	3.97	**$p < 0.01$**
	R	58	43.67	3.74	

Mean and standard deviation values rounded to two decimal places. Significant p-values highlighted in bold. Abbreviations used: MxL = maximum length, MxDm = maximum midshaft diameter, MnDm = minimum midshaft diameter, MnCir = minimum shaft circumference, CirHd = circumference of head, MxTDm = maximum transverse diameter of head, MxSDm = maximum sagittal diameter of head, EpBr = epicondylar breadth, TCBr = trochlea-capitulum breadth.

From Table 5.10 it can be clearly seen that left and right values for each measurement are significantly different, indicating significant size differences between the left and right humeri. These left/right differences for the humeri are more extensive than those seen in the metacarpals (and clearly more so than the phalanges). As might be expected, the mean values show that all right humerus variables are larger than left humerus variables in this sample.

5.2.2 Analysis of Variance (ANOVA)

To assess the influence of sex and age on this sample a univariate GLM ANOVA was performed. Table 5.11 (below) provides the results of this analysis. It is immediately clear from the ANOVA that there is a very strong main effect of sex on all of the humerus variables showing once more that males and females differ clearly in humeral dimensions (with males likely to be larger than females – see Table C.12, Appendix C for mean values). It is interesting to compare this finding with that of Pomeroy & Zakrzewski (2009), who did not find significant sexual dimorphism in diaphyseal shape in an analysis of humeri from the Écija site also measured in the current analysis. It is not clear why levels of sexual dimorphism should differ so markedly between external diaphyseal properties and cross-sectional dimensions derived from external properties in this sample.

The effect of age was found to be much more limited with only right-side minimum circumference (MnCir), right maximum transverse diameter (MxTDm), left epicondylar breadth (EpBr) and left trochlea-capitulum breadth (TCBr) showing statistically significant main effects (although a number of variables are approaching significance – generally the corresponding side to the significant measurement). While this shows that young adults, middle adults and old adults differ in size for these measurements, it is unclear why this should be the case as it would not be expected for individuals to significantly change in size over the course of adulthood. All young adults had fully fused epiphyses so further growth would not have occurred. Therefore these results could reflect difficulties in accurately assigning individuals to age categories. It may also be the case that the 'arbitrary' nature of these age categories masks other age-related trends in the data. There is only one significant interaction between sex and age, for left TCBr.

5.2.3. Asymmetry in the humerus

The distribution and magnitude of size-independent asymmetry in the Écija humeri was examined using the equations described in section 5.1.3. Figure 5.14 (below) presents the results of this asymmetry analysis where the percentage right-side dominant, left-side dominant and symmetrical measurements for each of the humerus variables was calculated. The data from this analysis can be found in Table C.13, Appendix C.

Table 5.11. Univariate GLM ANOVA for the effects of sex and age on each of the humeral metric variables, plus the interaction between sex and age.

Measurement	Side	N	Mean	Sex		Age		Sex*Age	
				F	Sig.	F	Sig.	F	Sig.
MxL	L	34	301.24	20.46	**p < 0.01**	2.26	p = 0.12	3.11	*p = 0.06*
	R	52	309.02	38.58	**p < 0.01**	1.38	p = 0.26	2.16	p = 0.13
MxDm	L	46	21.23	20.68	**p < 0.01**	2.76	*p = 0.08*	0.33	p = 0.72
	R	59	22.01	11.03	**p < 0.01**	0.99	p = 0.38	0.34	p = 0.72
MnDm	L	45	16.47	17.36	**p < 0.01**	2.33	p = 0.11	0.73	p = 0.49
	R	60	16.82	21.43	**p < 0.01**	1.31	p = 0.28	0.08	p = 0.93
MnCir	L	36	59.31	57.84	**p < 0.01**	3.17	*p = 0.06*	0.03	p = 0.87
	R	38	60.76	65.38	**p < 0.01**	3.43	**p = 0.04**	1.38	p = 0.25
CirHd	L	27	129.26	35.51	**p < 0.01**	1.59	p = 0.23	0.16	p = 0.69
	R	36	132.25	54.43	**p < 0.01**	1.43	p = 0.26	0.10	p = 0.75
MxTDm	L	41	39.89	29.49	**p < 0.01**	1.91	p = 0.16	1.48	p = 0.24
	R	50	40.77	34.65	**p < 0.01**	4.17	**p = 0.02**	0.50	p = 0.61
MxSDm	L	43	42.48	19.93	**p < 0.01**	0.29	p = 0.75	0.58	p = 0.56
	R	52	43.64	25.85	**p < 0.01**	2.39	*p = 0.10*	0.24	p = 0.78
EpBr	L	50	59.72	48.73	**p < 0.01**	4.58	**p = 0.02**	2.08	p = 0.14
	R	57	60.38	36.43	**p < 0.01**	2.71	*p = 0.08*	0.84	p = 0.44
TCBr	L	51	42.58	66.10	**p < 0.01**	7.84	**p < 0.01**	4.93	**p = 0.01**
	R	58	43.67	53.29	**p < 0.01**	2.74	*p = 0.07*	1.89	p = 0.16

Mean and F values rounded to two decimal places. Significant p-values highlighted in bold. P-values approaching significance (between 0.055 and 0.1) highlighted in italics. Abbreviations used: MxL = maximum length, MxDm = maximum midshaft diameter, MnDm = minimum midshaft diameter, MnCir = minimum shaft circumference, CirHd = circumference of head, MxTDm = maximum transverse diameter of head, MxSDm = maximum sagittal diameter of head, EpBr = epicondylar breadth, TCBr = trochlea-capitulum breadth.

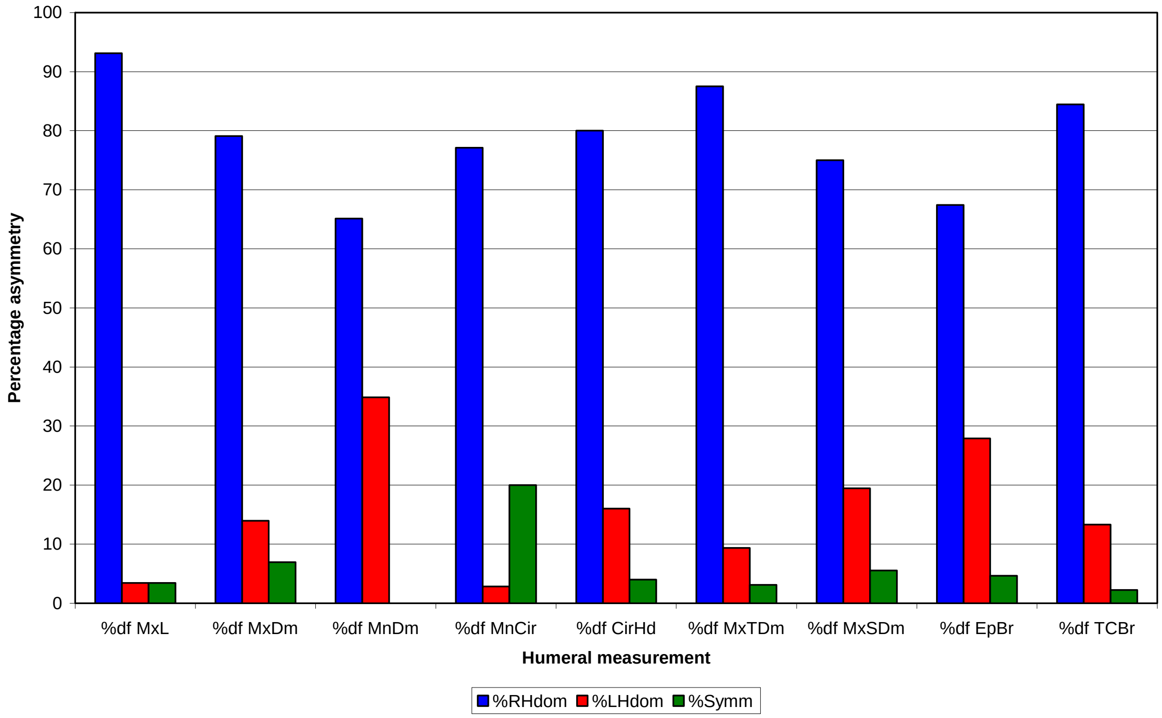


Figure 5.14. Percentage of right and left side dominant and symmetric individuals for humerus measurements. Further data available in Table C.13, Appendix C.

Figure 5.14 shows that all humeral metric measurements display strong right-side dominance with the magnitude of asymmetry ranging from 65% (MnDm) to 93% (MxL). The magnitude of right-side dominance is larger than seen in either the metacarpals or phalanges. There appears to be no clear pattern in the right-side asymmetry between the measurements. There is variation between the measurements although this does not seem to be related to any particular humeral properties. Measurements related to features of the humeral shaft (MxDm, MnDm, MnCir), humeral head (CirHd, MxTDm, MxSDm) and distal articular surface (EpBr, TCBr), do not share any distinct patterns of asymmetry.

5.2.4. Sex effects on asymmetry in the humerus

The analysis in section 5.1.4 and section 5.1.5 indicated that sex and age had a very limited effect on both the direction and magnitude of asymmetry in the hand. With the increased asymmetry identified in the humeral measurements (Fig. 5.14) it is interesting to now investigate whether increased effects of sex and age will also be found in the humerus. To assess whether or not this was the case a Mann-Whitney U test was performed on the Écija humerus data, as described in section 5.1.4. Table 5.12 provides the results of the Mann-Whitney U test for these data.

Table 5.12. A Mann-Whitney U test of the effects of sex on directional asymmetry and absolute asymmetry values for each of the humerus measurements.

Measurement	N	Directional asymmetry (cf. Steele & Mays, 1995)				Absolute asymmetry (cf. Trinkaus *et al.*, 1994)			
		Mean	**std dev.**	**U**	**Sig. (2-tailed)**	**Mean**	**std dev.**	**U**	**Sig. (2-tailed)**
MxL	29	1.28	0.96	84.5	p = 0.38	1.39	0.77	73.5	p = 0.18
MxDm	43	2.30	3.13	206.5	p = 0.58	2.90	2.59	204.5	p = 0.54
MnDm	43	1.63	4.58	109.5	**p < 0.01**	3.81	3.05	208.5	p = 0.61
MnCir	35	2.37	2.21	147.0	p = 0.85	2.47	2.10	149.0	p = 0.90
CirHd	25	1.84	2.07	30.0	**p < 0.01**	2.38	1.40	40.0	**p = 0.04**
MxTDm	32	1.87	2.31	92.0	p = 0.18	2.47	1.66	89.0	p = 0.15
MxSDm	36	1.48	1.80	133.5	p = 0.38	1.86	1.39	139.5	p = 0.49
EpBr	43	0.88	4.27	151.5	*p = 0.06*	2.34	4.04	175.5	p = 0.19
TCBr	45	2.65	2.69	248.5	p = 0.98	3.12	2.14	247.5	p = 0.96

Mean and standard deviation values rounded to two decimal places. Significant p-values highlighted in bold. P-values approaching significance (between 0.055 and 0.1) highlighted in italics. Abbreviations used: MxL = maximum length, MxDm = maximum midshaft diameter, MnDm = minimum midshaft diameter, MnCir = minimum shaft circumference, CirHd = circumference of head, MxTDm = maximum transverse diameter of head, MxSDm = maximum sagittal diameter of head, EpBr = epicondylar breadth, TCBr = trochlea-capitulum breadth.

From Table 5.12 it can be seen that sex has a weak effect on both directional asymmetry and absolute asymmetry in the humerus. There are only two statistically significant sex effects for directional asymmetry (MnDm, CirHd) and one for absolute asymmetry (CirHd). This is in keeping with the analysis of Pomeroy & Zakrzewski (2009) who also failed to identify statistically significant sexual dimorphism in asymmetry in the Écija humeri. In contrast to asymmetry in the hand males had a larger mean rank value than females in 6 of 9 humerus variables for directional asymmetry (see Table C.14, Appendix C) suggesting that in the humerus males are right-side dominant more frequently than females. However, for absolute asymmetry the trend is for females to have a larger mean rank value than males in 5 of 9 cases which suggests that females generally have larger asymmetry scores than males in this sample (see Table C.15, Appendix C). This supports in part the findings of Auerbach & Ruff (2006) who found males to be more asymmetric than females for humerus diaphyseal properties and head breadth. However they found females to be more asymmetric for humerus length, a trend supported by the mean rank values in this analysis.

5.2.5. Age effects on humerus asymmetry

A further Mann-Whitney U test was performed to assess the effect of age on directional and absolute asymmetry in the humerus. As in section 5.1.5 older adults were not included in the analysis. The results of this analysis are presented in Table 5.13 (below). As with previous analyses age was found to have a weak effect on directional asymmetry (with significant effects found only for MxDm and MnDm) and no effect at all on absolute asymmetry. However, the trend for a greater directional asymmetry effect than absolute asymmetry effect is similar to the pattern found in the phalanges although contrary to the metacarpals. Despite the lack of significant results there is a trend towards middle-aged adults being right-side dominant more frequently than young adults (in 7 of 9 instances for directional asymmetry) and also having larger asymmetry scores than young adults (8 of 9 cases for absolute asymmetry) (see Tables C.16 and C.17, Appendix C).

Table 5.13. A Mann-Whitney U test of the effects of age on directional asymmetry and absolute asymmetry values for each of the humerus measurements.

Measurement	N	Directional asymmetry (cf. Steele & Mays, 1995)				Absolute asymmetry (cf. Trinkaus *et al.*, 1994)			
		mean	std dev.	U	Sig. (2-tailed)	mean	std dev.	U	Sig. (2-tailed)
MxL	29	1.28	0.96	79.0	p = 0.57	1.39	0.77	87.0	p = 0.86
MxDm	43	2.30	3.13	127.0	**p = 0.05**	2.90	2.59	146.0	p = 0.16
MnDm	43	1.63	4.58	109.5	**p = 0.02**	3.81	3.05	173.0	p = 0.55
MnCir	35	2.37	2.21	105.5	p = 0.19	2.47	2.10	112.5	p = 0.28
CirHd	25	1.84	2.07	46.5	p = 0.30	2.38	1.40	58.5	p = 0.75
MxTDm	32	1.87	2.31	103.0	p = 0.95	2.47	1.66	72.0	p = 0.17
MxSDm	36	1.48	1.80	101.5	p = 0.28	1.86	1.39	124.5	p = 0.80
EpBr	43	0.88	4.27	189.5	p = 0.95	2.34	4.04	189.0	p = 0.94
TCBr	45	2.65	2.69	146.0	p = 0.19	3.12	2.14	164.5	p = 0.42

Mean and standard deviation values rounded to two decimal places. Significant p-values highlighted in bold. Abbreviations used: MxL = maximum length, MxDm = maximum midshaft diameter, MnDm = minimum midshaft diameter, MnCir = minimum shaft circumference, CirHd = circumference of head, MxTDm = maximum transverse diameter of head, MxSDm = maximum sagittal diameter of head, EpBr = epicondylar breadth, TCBr = trochlea-capitulum breadth.

5.2.6. Individual asymmetry

The distribution of asymmetry at the individual level was explored for the humerus, as it was for the metacarpals and phalanges. Individual asymmetry was calculated using the method described in section 5.1.6. Figure 5.15 (below) presents the percentage of right-side dominant, left-side dominant and symmetrical humerus measurements for each individual. From Figure 5.15 it can be seen that as with the metacarpals and phalanges, there is a large degree of variation in asymmetry distribution across individuals with dominant asymmetries ranging from 50% to 100%. There is a clear trend for a right-side dominance with 48 of 55 individuals (87.3%) showing a right-side asymmetry pattern, compared to only 2 of 55 individuals (3.6%) favouring a left-side dominant asymmetry (5 of 55 individuals). Sample size is once again an issue however. With only nine variables measured it may not be possible to draw any definitive conclusions although these findings support the results of previous analyses in identifying right-side dominant asymmetry amongst the sample.

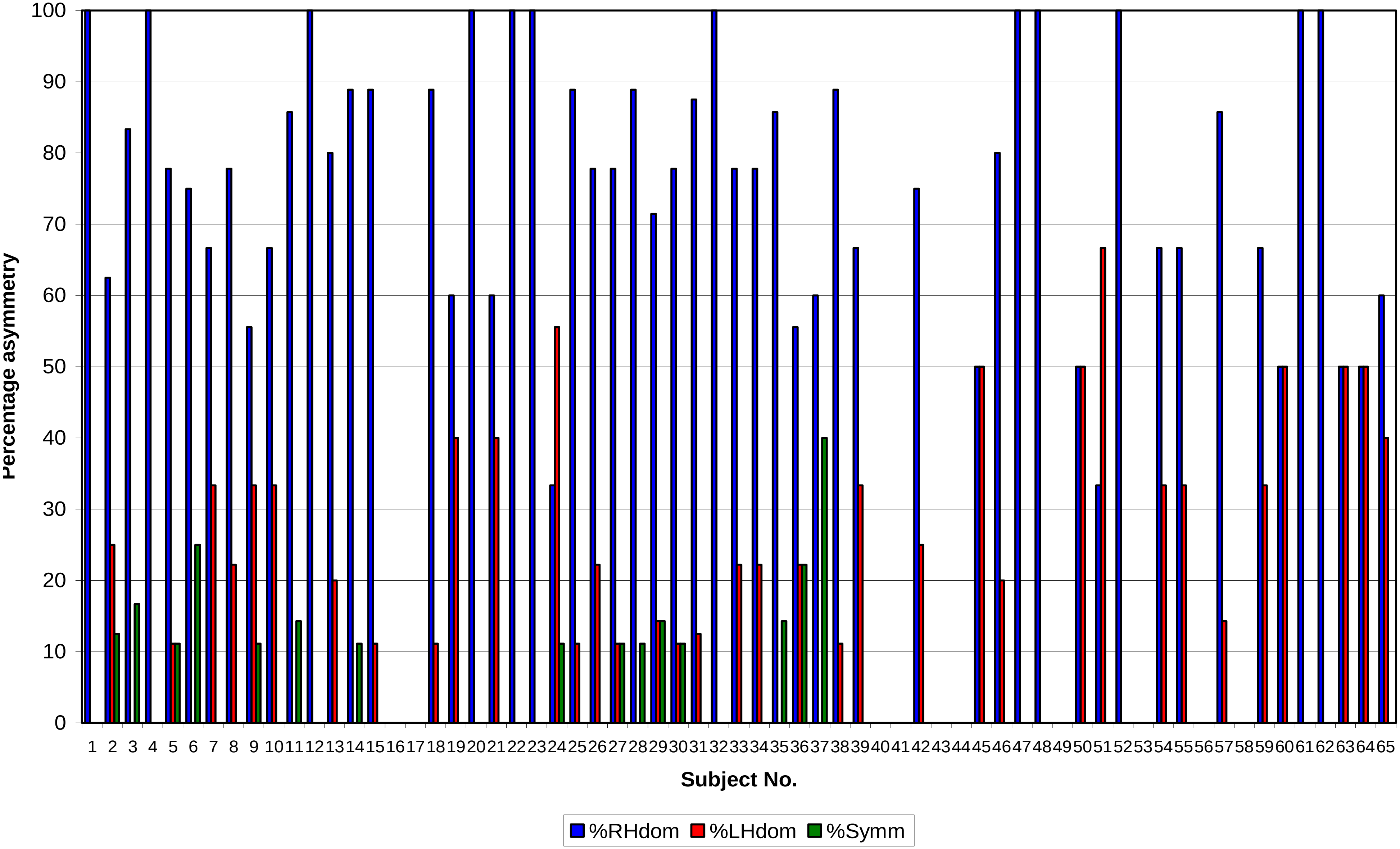


Figure 5.15. For each individual, the percentage of right-side dominant, left-side dominant and symmetric scores for all humerus measurements. Due to missing data, individual asymmetry could not be calculated for subjects 16, 17, 40, 41, 43, 44, 49, 53, 56 and 58.

5.2.7. Summary of humerus metric analysis

The analyses presented in section 5.2 show a strong right-side dominant asymmetry in the Écija humerus material which appears to be stronger than that identified in either the metacarpals or phalanges from the Écija sample. A Wilcoxon test indicated that all left and right humerus measurements are significantly different in size. An ANOVA test confirms the trends identified in the metacarpals and phalanges namely, the strong main effect of sex on all variables (with males larger than females) with very little effect of age. A significant interaction between sex and age was only found for one humerus variable. The strong sexual dimorphism identified in the ANOVA contrasts with the lack of statistically significant sexual dimorphism found in cross-sectional humeral properties (derived from external diaphyseal measurements) as assessed by Pomeroy & Zakrzewski (2009). The exact reason for these contrasting results is unclear as it is unlikely that small differences in measurement types and statistical analyses would result in such contrasting findings.

Analysis of asymmetry indicated an overall higher magnitude of right-side dominant asymmetry across the humerus variables than that found in the metacarpals and phalanges, although no specific patterns were identified in the distribution of this asymmetry. Mann-Whitney U tests for the effects of sex and age on asymmetry found very limited effects of both variables on humeral asymmetry. This mirrors the findings of Pomeroy & Zakrzewski's (2009) study of asymmetry in the Écija humeri. The reasons for the lack of sex and age effects are unclear, but the long time span of the burials represented at Écija (section 3.1.1) should be considered amongst the possible explanations. Analysis of individual asymmetry also shows a clear, albeit variable pattern of right-side dominance across individuals. However, it is worth considering that individual asymmetry scores represent asymmetry for only nine humerus measurements.

5.3. Musculoskeletal stress markers (MSM) in the hand

Development of MSM was assessed at a range of muscle insertion and origin sites on the metacarpals and phalanges for the purposes of comparison with the results of the earlier metric analysis of these bones (section 5.1). MSM development was assessed and scored following the presence/absence methodology outlined in section 3.2.2 in order to investigate whether an MSM approach can be successfully applied to the bones of the hand and in turn, the applicability of a presence/absence methodology to studies of upper limb bilateral asymmetry more generally.

The following sections will address the issue of asymmetry in MSM development between the left and right hands (and subsequently the left and right humeri). This will be done by comparing the proportions of individuals scored as 'present' for each MSM. The statistical significance of any asymmetries, plus the effects of sex and age on MSM development will also be explored. This analysis will begin with the MSM of the hands.

5.3.1. Asymmetry in hand MSM

MSM development at the insertion sites of four muscles and the origin sites of eight muscles (Table 3.4) on both the left and right hands was scored as being either ‘present’ or ‘absent’. Figure 5.16 (below) gives for the right hand (in blue) and the left hand (in red), the percentage of subjects who were scored as ‘present’ for each of the muscles. Scores of ‘absent’ or ‘not measurable’ were not included in the analysis. Data for this analysis can be found in Table C.18, Appendix C. For the purposes of analysis and reporting the four *flexor digitorum superficialis* insertions (FDS2, FDS3, FDS4 and FDS5) and the four *flexor digitorum profundus* insertions (FDP2, FDP3, FDP4 and FDP5) were each treated as one data point (referred to as FDS and FDP, respectively). During the course of data collection there were found to be no differences within the sets of flexor insertions in terms of their expression, i.e. if FDS2 was found to be present, then FDS3, 4 and 5 would also be present (and vice versa). Therefore for the purposes of brevity their data were analysed collectively.

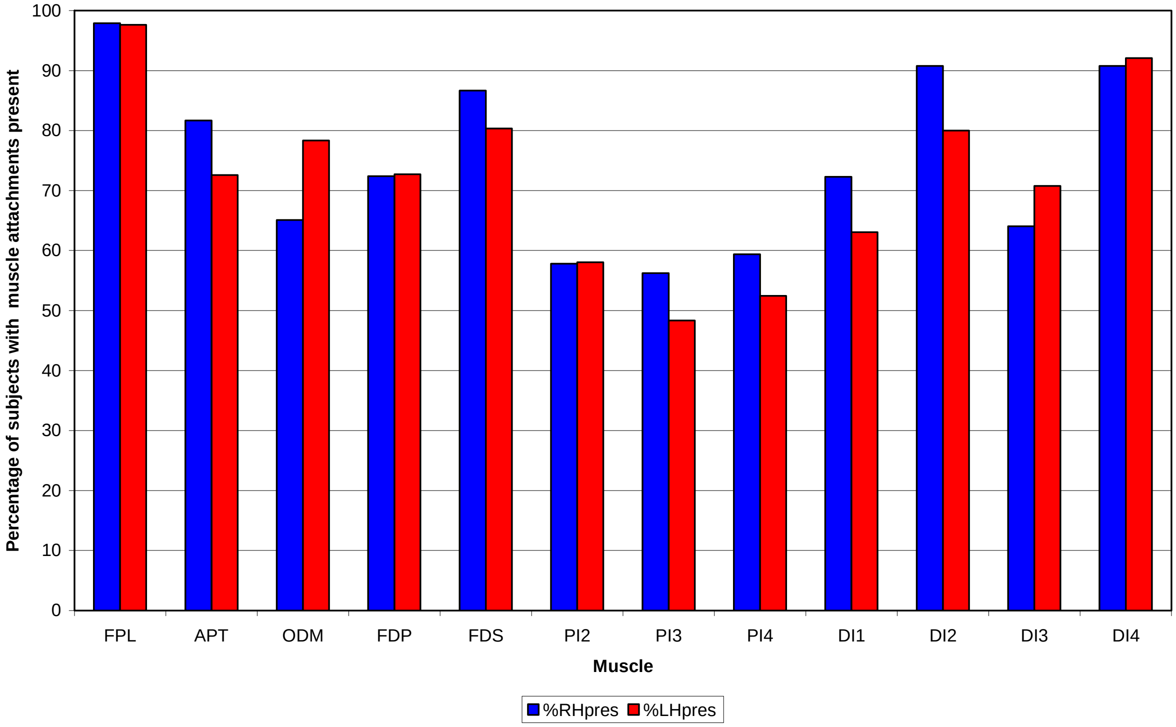


Figure 5.16. For each of the 12 hand MSM, the percentage scored as ‘present’ for the left hand (red) and the right hand (blue). Abbreviations used: FPL = flexor pollicis longus, APT = adductor pollicis (transverse head), ODM = oppenens digiti minimi, FDP = flexor digitorum profundus (2-5), FDS = flexor digitorum superficialis (2-5), PI = palmar interosseous, DI = dorsal interosseous. Further data provided in Table C.18, Appendix C.

Figure 5.16 shows that there is very little difference between the right and left paired MSM in terms of the percentage of subjects with MSM rated as ‘present’ suggesting negligible asymmetry between the sides. Of the 12 MSM scored, 7 showed a right-side dominance (i.e. they were scored as ‘present’ on the right side more frequently than on the left) and 5 showed a left-side dominance. The statistical significance of these relationships is explored in section 5.3.2. This symmetry in the MSM is in contrast to the findings of the metric analysis of the metacarpals and phalanges (section 5.1), where all measurements were clearly right-side dominant. The reasons for this trend are not clear and may reflect inconsistencies between metric and MSM approaches in their ability to identify bilateral asymmetry in the hands.

Further inspection of the data identifies a number of patterns for example, in the MSM that are right-side dominant (FPL, APT, FDS, PI3, PI4, DI1, and DI2) compared to those that are left-side dominant (ODM, FDP, PI2, DI3 and DI4). While the flexors (FPL, FDP and FDS) and the mc5-centred MSM (ODM, PI4, DI4) do not show consistent patterns of side dominance, MSM attached to the 2nd metacarpal (DI1, DI2) show a similar pattern of right-side dominance with those attached to the 3rd metacarpal (DI3, DI4) showing a similar pattern of left-side dominance. While not conclusive, this suggests a possibility of identifying links between muscle function and asymmetry. There does not seem to be any obvious differences between those MSM that represent insertion sites (FPL, FDS, FDP and ODM) and those that represent muscle origins (APT, PI2, PI3, PI4, DI1, DI2, DI3 and DI4). The muscles represented by the MSM in this study can also be considered as members of functional groups made up of prime movers and their corresponding synergists and antagonists (Table 5.13). Prime movers are muscles that initiate a movement, while synergists are muscles that contract to support a prime mover and antagonists are muscles that oppose the action of the prime mover (Moses *et al.*, 2005). Some researchers (e.g. Kennedy, 1998; Robb, 1998; Stirland, 1998) have suggested that MSM should not be studied in isolation as muscles do not operate independently of each other. Therefore, it is worthwhile considering asymmetry patterns across MSM with related functions where possible. Although only a few comparisons were possible, a simple visual comparison of the MSM scores of functionally-related MSM (identified in Table 5.13) in Figure 5.16 found no clear patterns in asymmetry between any of the prime movers and their synergists and antagonists. This suggests that for the hand MSM in this study at least, there may not be a clear link functional grouping in muscle activation and patterns of MSM asymmetry.

It is clear from Figure 5.16 that there is an observable difference between the frequencies that each MSM is rated as ‘present’ for both left and right MSM. The *palmar interossei* MSM (PI2, PI3, PI4) in particular are all rated as ‘present’ less than 60% of the time. While this may be related to the function and expression of this muscle, it may also be a result of the difficulty with which this attachment site is identified on dry bone. The FPL insertion site, by contrast, was identified as ‘present’ on approximately 98% of occasions. While this MSM is readily identifiable in skeletal material, it is also a functionally prominent muscle in the human hand (Susman, 1988; Marzke & Marzke, 2000). Further analysis is required of the remaining MSM data in this sample to further elucidate the role of functional and methodological influences on MSM expression.

Table 5.14. Functional groupings of hand muscles in current study.

Prime mover	Synergists	Antagonists
Flexor pollicis longus	Flexor pollicis brevis *Adductor pollicis*	Extensor pollicis longus Extensor pollicis brevis Abductor pollicis longus
Flexor digitorum superficialis	*Flexor digitorum profundus*	Extensor digitorum
Flexor digitorum profundus	*Flexor digitorum superficialis*	Extensor digitorum
Opponens digiti minimi	Flexor digiti minimi brevis Abductor digiti minimi	-
Adductor pollicis (transverse)	Flexor pollicis brevis *Flexor pollicis longus* Opponens pollicis	Extensor pollicis brevis Extensor pollicis longus Abductor pollicis brevis Abductor pollicis brevis
Palmar interossei	-	-
Dorsal interossei	-	-

Prime movers are those muscles included in the current study. Synergists and antagonists included in study marked in italics. Taken from Bowden & Bowden (2005).

5.3.2. Significance testing

The next stage in the analysis was to test whether any of the asymmetry (in terms of difference in left and right MSM scoring) identified in Figure 5.16 was statistically significant. As the MSM data are nominal (i.e. categorical) in nature (e.g. 'absent' = 0, 'present' = 1), a non-parametric test was necessary. Each of the subjects in the sample was scored twice, once for the left bone and once for the corresponding right bone. This produced a related-samples data set making it unsuitable for the application of a standard chi-squared (χ^2) test (which requires a between-samples data set). The McNemar test, however, is a version of the χ^2 test suitable for the analysis of paired nominal data. This technique tests the null hypothesis (H_0) that paired scores will not differ. The McNemar test will therefore only analysis data from subjects whose score changes between the two categories (left and right) (Howitt & Cramer, 1997; Kinnear & Gray, 2006). In the context of this analysis the H_0 is taken that there will be no difference between the left and right side MSM scores.

The McNemar test performed on the paired hand MSM data (see Table C.19, Appendix C) indicated that there were no statistically significant differences between the paired MSM scores. On the occasion that fewer than 25 cases showed a changed in score between left and right values, a binomial distribution is used to compute probability in the McNemar test. Due to the small sample sizes in this analysis, the binomial distribution was used for each variable. Overall, these results support the earlier observation that there is very little asymmetry in the MSM values (Fig. 5.16) and questions the usefulness of MSM development as a tool in identifying bilateral hand use.

5.3.3. Sex and hand MSM

The roles played by sex and age are of particularly interest to those analysing MSM development. Past research (Peterson, 1998; Robb, 1998; Steen & Lane, 1998; Stirland, 1998; Weiss, 2003; Eshed *et al.*, 2004; Molnar, 2006) has shown that these traits exert a strong influence on individual MSM expression and therefore the inferences that can be made regarding the distribution of asymmetry at both the individual level and the sample level. For this reason it is important to ascertain to what extent these factors can explain the patterns of asymmetry found in the Écija MSM data.

A chi-squared (χ^2) test was performed to identify any statistical association between sex and MSM score. A χ^2 test is suitable for determining association in nominal, between-subjects data (Howell, 2002; Kinnear & Gray, 2006). Left and right MSM scores were individually compared with sex so that each subject contributed to just one cell count in the χ^2 2x2 contingency table. Like the McNemar test, the χ^2 test works on the H_0 that there is no association between variables. Association is determined by comparing observed frequencies in each category with the expected frequency for each cell. Table 5.14 (below) presents the results from the χ^2 analysis. The χ^2 statistic is affected by the frequencies in each cell and can only be a measure of whether an association is present (Kinnear & Gray, 2006). Therefore, the phi value (φ) was also included for each analysis. The value for φ informs us of the strength of the χ^2 association, where 1 = perfect association and 0 = no association. In addition, where cell frequencies were small, a Fisher's Exact Test p-value was used in the place of the χ^2 p-value.

This analysis shows that the association between sex and MSM score is very weak with only left FDS, right DI1 and right DI4 showing statistically significant associations. These significant associations do not show any noticeable pattern in their distribution although it is worth noting that DI4 and ODM (approaching significance) are both located on mc5. There is no clear side preference for the significant associations. The φ values in Table 5.15 are small (the highest being 0.32 for left DI4) suggesting that, even when a significant association is present the strength of this association is weak. These results contrast with the metric analysis of the hands which found that metacarpal and phalanx size properties were clearly different between males and females although this association was not found in the analyses of asymmetry. These results raise interesting questions about the association between sex and MSM expression as they are not in keeping with existing research, which has found a strong influence of sex on MSM development (e.g. Peterson, 1998; Robb, 1998; Steen & Lane, 1998; Weiss, 2003; Eshed *et al.*, 2004; Molnar, 2006). The reasons for this discrepancy are unclear; it may reflect a lack of sexual dimorphism in MSM development in the Écija hands samples, it may also represent methodological influences such as difficulties in accurately assigning individuals to age categories or problems inherent in MSM scoring.

Table 5.15. Chi-squared (χ^2) test of association between sex and hand MSM.

MSM	Side	χ^2 value	Sig. (2-tailed)	φ value
FPL	L	1.51	p = 0.41*	0.19
	R	1.31	p = 0.44*	0.17
APT	L	0.03	p = 1.00	0.02
	R	0.57	p = 0.52	0.10
ODM	L	0.05	p = 1.00	0.03
	R	4.22	*p = 0.06*	0.26
FDP	L	0.03	p = 1.00*	0.04
	R	0.07	p = 1.00*	0.05
FDS	L	4.99	**p = 0.04***	0.30
	R	0.93	p = 0.45*	0.12
PI2	L	1.93	p = 0.20	0.18
	R	0.39	p = 0.62	0.08
PI3	L	1.13	p = 0.31	0.14
	R	2.81	p = 0.13	0.21
PI4	L	0.36	p = 0.61	0.08
	R	0.01	p = 1.00	0.01
DI1	L	4.09	*p = 0.07*	0.25
	R	4.22	**p = 0.05**	0.26
DI2	L	3.48	p = 0.12	0.23
	R	1.12	p = 0.40*	0.13
DI3	L	1.49	p = 0.28	0.15
	R	0.01	p = 1.00	0.01
DI4	L	6.37	**p = 0.02***	0.32
	R	3.68	*p = 0.09**	0.24

Significant p-values highlighted in bold and values approaching significance (between 0.055 and 0.1) highlighted in italics. Values marked with an asterisk (*) indicate where the Fisher's Exact Test p-value was used due to low cell counts (in most instances, this test provides the same results as the standard χ^2). A phi (φ) value indicates the strength of the χ^2 association. Abbreviations used: FPL = flexor pollicis longus, APT = adductor pollicis (transverse head), ODM = oppenens digiti minimi, FDP = flexor digitorum profundus (2-5), FDS = flexor digitorum superficialis (2-5), PI = palmar interosseous, DI = dorsal interosseous.

5.3.4. Age and hand MSM

With age found to have a very weak effect on the metric properties of the hand (section 5.1.2 and 5.1.5) and a limited association between sex and MSM development (section 5.3.3), it was unclear what association there would be, if any between age and MSM development. As with previous analysis in section 5.3.3, a χ^2 test was performed to measure the degree and strength of association between MSM score and age. The results from this test are presented in Table 5.16. χ^2 tests are sensitive to low cell frequencies and with only five ‘old adults’ in the sample, it was decided to exclude these individuals from the analysis.

Table 5.16. Chi-squared (χ^2) test of association between age and hand MSM.

MSM	Side	χ^2 value	Sig. (2-tailed)	φ value
FPL	L	0.67	p = 1.00*	0.13
	R	0.90	p = 1.00*	0.14
APT	L	0.02	p = 1.00	0.02
	R	1.34	p = 0.31*	0.15
ODM	L	3.44	p = 0.11	0.25
	R	4.68	**p = 0.05**	0.28
FDP	L	2.78	p = 0.16*	0.37
	R	0.07	p = 1.00*	0.05
FDS	L	2.00	p = 0.19	0.20
	R	0.14	p = 1.00*	0.05
PI2	L	0.25	p = 0.79	0.07
	R	0.05	p = 1.00	0.03
PI3	L	0.01	p = 1.00	0.01
	R	1.89	p = 0.19	0.18
PI4	L	0.001	p = 1.00	0.60
	R	0.01	p = 1.00	0.01
DI1	L	0.73	p = 0.43	0.11
	R	1.47	p = 0.26	0.16
DI2	L	0.81	p = 0.53	0.12
	R	0.19	p = 0.69*	0.06
DI3	L	1.16	p = 0.40	0.14
	R	0.06	p = 1.00	0.03
DI4	L	1.19	p = 0.38*	0.14
	R	1.05	p = 0.39*	0.13

Significant p-values highlighted in bold. Values marked with an asterisk (*) indicate where the Fisher’s Exact Test p-value was used due to low cell counts (in most instances, this test provides the same results as the standard χ^2). A phi (φ) value indicates the strength of the χ^2 association. Abbreviations used: FPL = flexor pollicis longus, APT = adductor pollicis (transverse head), ODM = oppenens digiti minimi, FDP = flexor digitorum profundus (2-5), FDS = flexor digitorum superficialis (2-5), PI = palmar interosseous, DI = dorsal interosseous.

From Table 5.16 it can be seen that the association between age and MSM development is even weaker than that found for sex (Table 5.15). Only one MSM, right ODM, shows a significant association with age ($p = 0.05$) with a φ value of 0.28 suggesting that this is a weak association. This trend for limited weak associations mirrors that found in the χ^2 test of associations with sex. It is also in keeping with the results of the earlier metric analysis (section 5.1.2 and 5.1.5) which found that age had almost no effect on metacarpal or phalanx size or asymmetry. The results are in contrast however, with the MSM literature which shows age to generally have a strong effect on MSM expression (Robb, 1998; Stirland, 1998; Weiss, 2003; Molnar, 2006). While it is possible that this trend is a particular feature of the Écija sample, it is also necessary to again consider the influence of methodological factors.

5.4. MSM in the humerus

MSM analysis in the hand (section 5.3), together with metric analysis of the hands and humeri (sections 5.1 and 5.2), support the notion of a variable expression of bilateral asymmetry across the upper limb; an asymmetry that is directly influenced by the method used to assess it. Assessment of MSM development in the humerus will help to address some of the questions posed by these earlier analyses, particularly those surrounding the trends identified in the hand MSM analysis.

5.4.1. Asymmetry in humerus MSM

Using the methods outlined in section 5.3.1, asymmetry in the Écija humerus MSM data was identified. Analyses follow the same structure as for the hand MSM (section 5.3). Figure 5.17 gives the percentage of subjects rated as ‘present’ for each of the 11 humerus MSM sites on both the left and right humerus. Data from this analysis can be found in Table C.20, Appendix C.

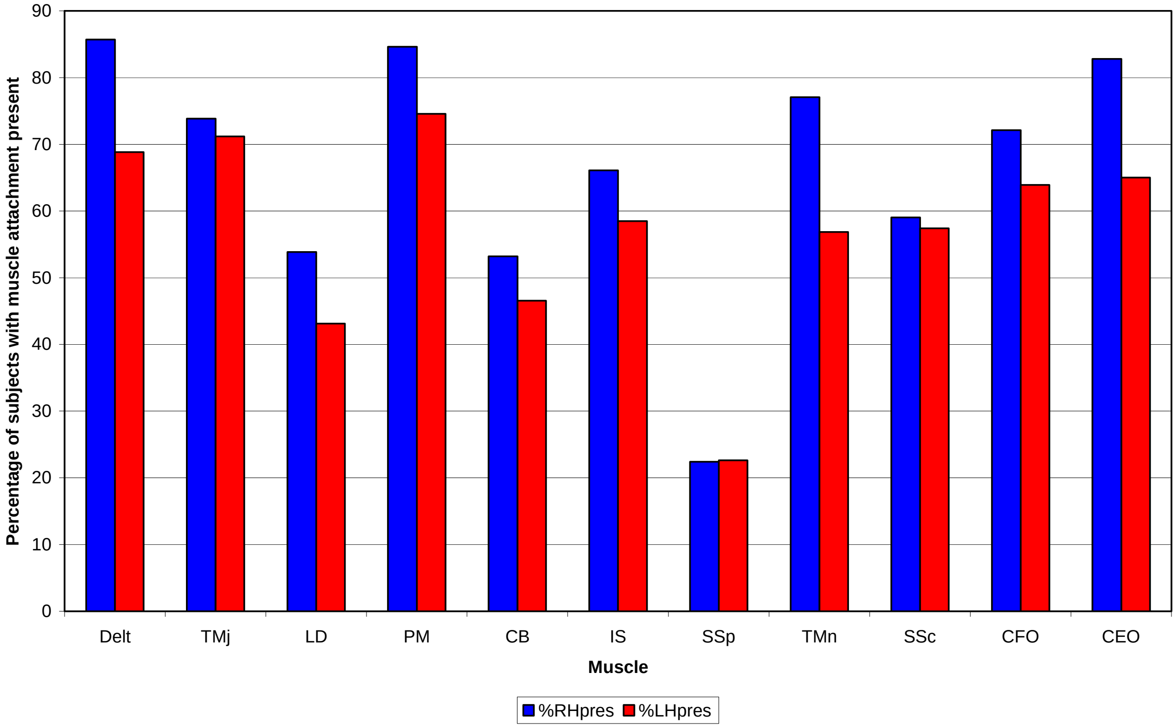


Figure 5.17. For each of the 11 humeral MSM, the percentage scored as ‘present’ muscle for the left humerus (red) and the right humerus (blue). Abbreviations used: Delt = deltoid, TMj = teres major, LD = latissimus dorsi, PM = pectoralis major, CB coracobrachialis, IS = infraspinatus, SSp = supraspinatus, TMn = teres minor, SSc = subscapularis, CFO = common flexor origin, CEO = common extensor origin. Further data available in Table C.20, Appendix C.

With the exception of *supraspinatus* (SSp) all MSM were scored as 'present' on the right humerus more frequently than the left. The magnitude of this right-side dominance is small, often less than 10% and never more than 20%. This contrasts with what was found in the metric humerus asymmetry (section 5.2.3) where the minimum right-side dominant asymmetry was never less than 30%. Although the humerus MSM in Figure 5.17 show left/right asymmetry, the degree of asymmetry in the humerus MSM is greater than that seen in the hand MSM (Fig. 5.16). This supports the trend identified in the metric asymmetry (sections 5.1.3 and 5.2.3) where the humerus was found to display greater asymmetry than that seen in either the metacarpals or phalanges. This suggests that overall, the Écija humeri are more asymmetric in their properties than either the Écija metacarpals or phalanges.

Table 5.17. Functional groupings of humeral muscles in current study.

Prime mover	**Synergists**	**Antagonists**
Deltoideus	*Supraspinatus* *Pectoralis major* (clavicular)	*Latissimus dorsi* *Pectoralis major*
Teres major	*Latissimus dorsi* *Subscapularis*	-
Latissimus dorsi	Rhomboids *Pectoralis major* *Teres major*	-
Pectoralis major	Sternal: *Latissimus dorsi* *Subscapularis* *Teres major* Clavicular: Biceps brachii *Latissimus dorsi* *Deltoid*	-
Coracobrachialis	*Pectoralis major* Biceps brachii *Deltoid*	-
Infraspinatus	*Teres minor* *Subscapularis* *Supraspinatus* *Deltoid*	-
Supraspinatus	*Deltoid*	-
Teres minor	*Infraspinatus* *Subscapularis*	-
Subscapularis	*Teres major* *Pectoralis major* *Latissimus dorsi*	-
Common flexor origin	N/A	N/A
Common extensor origin	N/A	N/A

Prime movers are those muscles included in the current study. Synergists and antagonists included in study marked in italics. Taken from Bowden & Bowden (2005).

Looking at the humerus MSM data in more detail, no clear patterns of asymmetry emerge. Muscle groups such as the *infraspinatus* (IS), *supraspinatus* and *teres minor* (TMn) of the greater tubercle (i.e. those of the ‘rotator cuff’ which stabilise and rotate the humerus) show different degrees of MSM asymmetry in terms of magnitude and direction. Muscles can also be grouped functionally in terms of prime movers and their corresponding synergists and antagonists (Table 5.16). Visually comparing the MSM of those muscles that have a functional relationship indicates that despite the inter-connectedness of many of the humeral muscles, the MSM differ greatly in terms of their magnitude. As with the comparison of hand MSM in section 5.3.1, there appears to be no strong links between these functional muscle groupings and the MSM asymmetry identified in this analysis. Such a comparison within the humerus is problematic however, particularly if the point of the analysis is to determine *variation* between the actions of the muscles due to the relationship between all the muscles under study.

Figure 5.17 shows that there are clear differences between the MSM with regards to the percentage of individuals scored as ‘present’ for each MSM. In particular the LD, *coracobrachialis* (CB) and SSp have low percentages relatively to the other MSM, with left and right SSp only scored as ‘present’ approximately 22% of the time. This may be because these muscles were not habitually stressed in this sample. However, it was noted during data collection that the LD, CB and SSp were the most difficult MSM to identify on dry bone. Therefore, it is possible that these particular results reflect this difficulty.

5.4.2 Significance testing

Compared to the MSM of the hands, greater asymmetry was found in the MSM of the humerus (Fig. 5.17). Therefore, it was possible that this asymmetry may be statistically significant. As described in section 5.3.2 a McNemar test was run to compare left and right humerus MSM data (not shown, see Table C.21, Appendix C). This test found no significant differences between any of the left and right MSM. The only MSM comparison approaching significance was for common extensor origin (CEO) ($p = 0.07$). Al-Oumaoui *et al.* (2004) also applied a presence/absence method to the study of upper limb MSM in a medieval Muslim population from Andalucía (La Torrecilla, Granada) and found that despite a trend towards right-side dominant asymmetry in the MSM studied (*pectoralis major*, *teres major* and *deltoid*), this asymmetry was not statistically significant. The lack of statistically significant asymmetry in the humerus MSM raises questions regarding the ability of MSM to accurate reflect bilateral asymmetry both in the humerus and hands. These results could represent the unsuitability of MSM for the assessment of bilateral asymmetry (compared to metric analyses). They may also reflect differences between the response of bone remodelling and MSM development to mechanical influences.

5.4.3. Sex and humerus MSM

The analysis of the association between sex and hand MSM (section 5.3.3), contrary to expectation, failed to identify many significant associations between sex and hand MSM development. A χ^2 test (as described in section 5.3.3) was performed on the humerus MSM data to assess whether this trend would also be found between sex and humerus MSM. Table 5.18 provides the results of this analysis.

Table 5.18. Chi-squared (χ^2) test of association between sex and humerus MSM.

MSM	Side	χ^2 value	Sig. (2-tailed)	φ value
Delt	L	1.36	p = 0.42*	0.17
	R	1.26	p = 0.39*	0.15
TMj	L	0.01	p = 1.00*	0.02
	R	0.07	p = 1.00	0.03
LD	L	0.09	p = 1.00	0.04
	R	0.49	p = 0.60	0.09
PM	L	2.14	p = 0.19*	0.21
	R	6.23	**p = 0.02***	0.32
CB	L	1.72	p = 0.23	0.20
	R	2.70	p = 0.12	0.22
IS	L	4.04	_p = 0.06*_	0.32
	R	4.15	_p = 0.06*_	0.30
SSp	L	0.29	p = 0.73	0.09
	R	0.003	p = 1.00	0.01
TMn	L	9.71	**p < 0.01***	0.52
	R	4.88	**p = 0.04***	0.31
SSc	L	4.27	_p = 0.06*_	0.33
	R	8.31	**p < 0.01**	0.41
CFO	L	0.50	p = 0.54	0.09
	R	2.33	p = 0.22	0.20
CEO	L	3.62	_p = 0.10_	0.27
	R	7.92	**p < 0.01***	0.37

Significant p-values highlighted in bold. P-values approaching significance (between 0.55 and 0.1) highlighted in italics. Values marked with an asterisk (*) indicate where the Fisher's Exact Test p-value was used due to low cell counts (in most instances, this test provides the same results as the standard χ^2). A phi (φ) value indicates the strength of the χ^2 association. Abbreviations used: Delt = deltoid, TMj = teres major, LD = latissimus dorsi, PM = pectoralis major, CB coracobrachialis, IS = infraspinatus, SSp = supraspinatus, TMn = teres minor, SSc = subscapularis, CFO = common flexor origin, CEO = common extensor origin.

From Table 5.18 it can be seen that the association between sex and humerus MSM is limited, as was found for the hands (Table 5.15). Significant associations with sex were found for 5/22 MSM: right PM, left and right TMn, right SSc and right CEO. This is compared to the hand where there was a significant association for only 3/24 MSM. These significant associations are distributed across the humerus (i.e. shaft and articular surfaces) suggesting that there is no specific functional pattern to the association between sex and MSM. Four out of the five significant associations are between sex and a right-side MSM. While not conclusive, it suggests that males and females may show difference in muscle expression in the, presumably dominant, right arm. The φ values for the significant are generally higher than for the corresponding analysis of the hand, but with a high value of 0.52 for left TMn, the strength of the significant associations between sex and MSM is only moderate.

In contrast to these findings, an analysis of the association between sex and humerus MSM scores for the PM, TMj and Delt in the Spanish medieval Muslim sample studied by al-Oumaoui *et al.* (2004) identified statistically significant associations between sex and MSM score for all MSM, with males being scored as 'present' more frequently than females. It is worth noting however, that al-Oumaoui *et al.* used cortical defects at the PM and TMj insertion sites as indicators of MSM 'presence' and this may explain why they were identified more frequently in males in that sample.

5.4.4. Age and humerus MSM

A χ^2 test was carried out to investigate the association between age and humerus MSM score. The results of this analysis are provided in Table 5.19 (below). As with earlier age analysis in section 5.3.4, the 'old adult' category was excluded from analysis to avoid unnecessarily low cell counts where possible.

Table 5.19 shows that there are very few significant associations between age and humerus MSM score. Only three of the MSM variables - right LD, left and right SSc – have statistically significant associations with age. The φ values for these significant associations are generally low (less than 0.50) suggesting that the strength of these associations is weak. The analysis of al-Oumaoui *et al.* (2004) also failed to identify significant differences in MSM score between age categories, although this may be related to their use of broad age categories (i.e. 'young adult' = 20 – 35 years, 'mature adult' = 36 – 50 years). The results of the current analysis are in keeping with the earlier χ^2 test for the hand MSM although proportionally, the number of significant age associations is greater for the humerus MSM. It is interesting to note that both the left and right SSc MSM in this analysis are significantly associated with age. This concurs with the results of the χ^2 test between sex and humerus MSM, which found a significant association between right SSc and sex, plus an association between left SSc and sex approaching significance ($p = 0.06$). This suggests both sexual and age-related dimorphism in the expression of the SSc muscle, which is involved in medial rotation of the humerus. Why this should be the case however, is unclear at this stage.

Table 5.19. Chi-squared (χ^2) test of association between age and humerus MSM.

MSM	Side	χ^2 value	Sig. (2-tailed)	φ value
Delt	L	2.86	p = 0.12*	0.25
	R	0.77	p = 0.64*	0.12
TMj	L	0.17	p = 0.69*	0.06
	R	0.02	p = 1.00*	0.02
LD	L	0.03	p = 1.00	0.03
	R	9.66	**p < 0.01**	0.42
PM	L	0.03	p = 1.00*	0.03
	R	3.67	*p = 0.08**	0.26
CB	L	0.87	p = 0.52	0.15
	R	1.70	p = 0.26	0.18
IS	L	3.33	p = 0.11*	0.30
	R	1.68	p = 0.40*	0.20
SSp	L	3.46	*p = 0.08**	0.31
	R	4.47	*p = 0.06**	0.32
TMn	L	2.63	p = 0.20*	0.28
	R	2.26	p = 0.28*	0.22
SSc	L	4.65	**p = 0.05***	0.35
	R	10.73	**p < 0.01***	0.48
CFO	L	0.00	p = 1.00	0.00
	R	0.25	p = 0.75*	0.07
CEO	L	1.76	p = 0.30*	0.19
	R	3.85	*p = 0.08**	0.27

Significant p-values highlighted in bold. P-values approaching significance (between 0.55 and 0.1) highlighted in italics. Values marked with an asterisk (*) indicate where the Fisher's Exact Test p-value was used due to low cell counts (in most instances, this test provides the same results as the standard χ^2). A phi (φ) value indicates the strength of the χ^2 association. Abbreviations used: Delt = deltoid, TMj = teres major, LD = latissimus dorsi, PM = pectoralis major, CB coracobrachialis, IS = infraspinatus, SSp = supraspinatus, TMn = teres minor, SSc = subscapularis, CFO = common flexor origin, CEO = common extensor origin.

5.5. Summary of MSM analysis

The analyses of both hand and humerus MSM development presented above, show that there is very little asymmetry between left and right MSM expression in either region of the upper limb. The general trend across both the hands and humerus MSM is towards right-side dominant asymmetry which is stronger in the humerus MSM compared to the hands. This mirrors the patterns of asymmetry found in the metric properties of the metacarpals, phalanges and humeri (sections 5.1 and 5.2) where the humeri were also the most strongly asymmetric elements. Despite these trends none of the MSM asymmetries identified in Figs 5.16 and 5.17 were found to be statistically significant. As discussed above, past research has found strong associations between MSM expression and both sex and age. Contrary to these findings, the current study found very limited associations between MSM score and sex and age although proportionally more significant associations were found for sex than age, and for the humerus than the hand MSM. The results of the humerus MSM analysis concur, in part, with the findings of al-Oumaoui *et al.* (2004), who were the first to apply a presence/absence methodology to MSM assessment, also on a medieval Muslim population from southern Spain. Their study failed to find significant asymmetry in a small number of humeral MSM (PM, TMj and Delt) or any associations between MSM score and age. They did however, identify significant sexual dimorphism in the humerus MSM studied, in contrast to the present study although this may be explainable by the focus of al-Oumaoui *et al.* on cortical defects as indicators of MSM 'presence'.

The results of these analyses cast some doubt on the ability of the presence/absence method and perhaps MSM analysis in general, to accurate assess the full extent of bilateral asymmetry in the upper limb. However, this does not exclude the possibility of using MSM analysis of this kind in the identification of more general patterns of muscle recruitment in the hands and humerus. Although before this can be considered, methodological issues with analysis of MSM development must be explored and resolved.

Overall, the results of the Écija metric and MSM data analysis indicate that these methods differ in the magnitude of the asymmetry that they identify. Effects of sex and age are also found to differ between the methods. These differences may result from the varying sensitivities of these methods. Alternatively, differences in the response of external bone properties and muscle attachment sites to mechanical loading may be the cause of the patterns identified above. However, both analyses tend to agree that asymmetry is reduced in the hands compared to the humeri.

Chapter 6. Greenwich Data Analysis

The site of the Greenwich Naval Hospital Cemetery, London is described in detail in section 3.1.2. Due to the unique composition of the site (Boston *et al.*, 2008), the Greenwich collection has a very specific age and sex profile, comprising almost exclusively of older male individuals. This site therefore allows for control of two key confounding variables in metric and MSM analysis: sex and age. It also provides an opportunity to study a group for whom occupation is known and thereby the range of activities engaged in by individuals can be more accurately predicted. All 31 skeletons selected for inclusion in the current study were male and classified as either 'middle adult' (approx. 30 – 45 years) or 'old adult' (approx. 45 years plus). Metric data from the Greenwich sample is dealt with in sections 6.1 and 6.2. MSM data from this sample is analysed in sections 6.3 and 6.4. Table 6.1 outlines the profile of the Greenwich sample.

Table 6.1. Age and sex profile of Greenwich sample.

	Young adult	Middle adult	Old adult	Total
Male	0	14	17	**31**
Female	0	0	0	**0**
Total	**0**	**14**	**17**	**Total sample: 31**

6.1. Metacarpal and phalanx metric analysis

Descriptive statistics for the sample, split by age, are presented in Table D.1 (Appendix D). Box-and-whisker plots were used to identify outliers within the data. If an error in data entry was identified or a possible reason for the outlying value (e.g. damage) was found then the value was excluded from further analysis. If no reason could be identified then the value was included and non-parametric tests applied where necessary. Histograms and p-p plots confirmed the general normal distribution of the data. Due to the very small amount of distal phalanx data available in this sample these measurements were excluded from all analyses. The structure of the data analysis in this section follows that of the corresponding Écija analysis in section 5.1.

6.1.1. Significance testing

Due to the presence of outliers, a non-parametric Wilcoxon test was performed to identify any significant differences between left- and right-side values for each of the metacarpal measurements. Table 6.2 provides the results of this analysis.

Table 6.2. Wilcoxon test results from the combined-age Greenwich metacarpal sample.

Measurement	Side	N	Mean	Std dev.	Sig. (2-tailed)
mc1L	L	24	43.47	2.34	*p = 0.10*
	R	25	43.82	2.55	
mc2L	L	28	65.36	3.02	p = 0.16
	R	29	65.71	2.72	
mc3L	L	27	63.65	2.72	*p = 0.06*
	R	27	63.06	2.93	
mc4L	L	23	56.12	2.42	**p = 0.04**
	R	28	56.09	2.38	
mc5L	L	21	53.25	2.22	p = 0.90
	R	24	52.49	1.86	
mc1RU	L	23	12.24	0.88	**p = 0.05**
	R	27	12.71	1.10	
mc2RU	L	30	8.49	0.65	**p < 0.01**
	R	31	8.82	0.59	
mc3RU	L	30	8.52	0.65	**p = 0.02**
	R	28	8.69	0.52	
mc4RU	L	26	6.87	0.63	**p < 0.01**
	R	30	7.34	0.60	
mc5RU	L	23	7.90	0.76	**p < 0.01**
	R	24	8.25	0.69	
mc1DP	L	23	8.99	0.95	p = 0.16
	R	28	9.16	0.94	
mc2DP	L	30	9.66	0.90	p = 0.12
	R	31	9.77	0.81	
mc3DP	L	30	9.54	0.85	**p < 0.01**
	R	29	9.81	0.72	
mc4DP	L	26	7.78	0.62	**p = 0.02**
	R	30	8.09	0.55	
mc5DP	L	25	7.11	0.76	**p = 0.01**
	R	25	7.46	0.81	
mc1PB	L	22	15.83	0.96	*p = 0.07*
	R	24	16.09	1.10	
mc2PB	L	29	17.68	0.82	p = 0.26
	R	29	17.33	1.06	
mc3PB	L	26	14.43	0.75	p = 0.57
	R	28	14.29	0.76	
mc4PB	L	21	12.71	1.03	p = 0.51
	R	29	12.94	1.07	
mc5PB	L	22	12.98	1.20	p = 0.33
	R	21	13.28	1.22	
mc1DB	L	21	15.12	0.77	**p = 0.03**
	R	23	15.44	0.75	
mc2DB	L	25	14.46	0.89	**p < 0.01**
	R	27	14.80	0.82	

Measurement	Side	N	Mean	Std dev.	Sig. (2-tailed)
mc3DB	L	25	14.13	0.94	**p = 0.02**
	R	23	14.44	0.68	
mc4DB	L	21	12.17	0.89	p = 0.22
	R	23	12.30	0.90	
mc5DB	L	22	11.89	0.78	*p = 0.10*
	R	20	12.11	1.00	

Mean and standard deviation values rounded to two decimal places. Significant p-values highlighted in bold. P-values approaching significance (between 0.055 and 0.1) highlighted in italics.List of abbreviations used: mc*L = metacarpal length, mc*RU = radio-ulnar midshaft diameter, mc*DP = dorso-palmar midshaft diameter, mc*PB = proximal breadth, mc*DB = distal breadth. Asterisk (*) denotes metacarpal number.

From Table 6.2 it can be seen that approximately half (12 of 25) the metacarpal measurements show statistically significant size differences between the left and right sides. Comparison of the mean values in Table 6.2 indicates that for 20 of 25 variables the right-side measurement is larger than that of the corresponding left-side. These results are similar to the Wilcoxon test of the Écija metacarpal data (Table 5.2) which also found the majority of right-side measurements to be significantly larger in size than those on the left-side. The occupation of the residents of the hospital is likely to have led to the reduced asymmetry found in this sample relative to the Écija sample as the daily tasks of an able seaman (section 3.1.2) are likely to have stressed both hands equally.

There appears to be no clear patterns to the asymmetries identified in Table 6.2, with significant left/right differences distributed between the variables. Only radio-ulnar diameter shows significant differences for all five metacarpals, while proximal breadth showed no significant left/right differences. None of the metacarpals had significant asymmetries across all measurements.

The Wilcoxon test was repeated for the phalanx length data to identify the presence of any significant size asymmetries. Table 6.3 (below) provides the results of this analysis and it can be seen that there are no statistically significant left/right differences for any of the phalanx length measurements suggesting a certain degree of symmetry in the size of these measurements. Comparison of the mean values found an equal distribution of side dominance with 4/9 measurements larger on the right-side, compared to 5/9 larger on the left-side. These results follow the metacarpal analysis in Table 6.2, which also showed a trend towards reduced asymmetry (relative to the Écija sample). The results in Table 6.3 are similar to those of the Écija phalanges (Table 5.3) which also identified few significant left/right size differences. Unlike the Écija sample, siding of phalanges was more secure in the Greenwich sample as hand bones were sided and bagged separately immediately after excavation. This lack of size differences suggests that rather than simply a problem with phalanx siding, the fingers do not reflect asymmetric loading in the same way as the metacarpals. From a functional perspective, the main muscle activity in the fingers is from flexors and extensors. Their tendinous attachment sites are found on the medial and lateral edges (palmar side) of the intermediate phalanges (ip2 - ip5) in the case of the *flexor digitorum superficialis* and at the distal end of the palmar surface of the distal phalanges 2 to 5 and the distal pollical phalanx for the *flexor digitorum profundus* and *flexor pollicis longus*, respectively. In this study only length measurements were taken on the phalanges, and it may be the case that these measurements do not represent the full extent of asymmetric loading in the fingers.

Table 6.3. Wilcoxon test results from the combined-age Greenwich phalanx sample.

Measurement	Side	N	Mean	Std dev.	Sig. (2-tailed)
pp1L	L	24	29.44	1.52	p = 0.31
	R	23	29.16	1.57	
pp2L	L	28	39.13	1.37	p = 0.53
	R	27	39.06	1.64	
pp3L	L	25	43.26	1.81	p = 0.59
	R	29	43.29	1.54	
pp4L	L	25	41.02	1.55	*p = 0.09*
	R	27	40.53	1.76	
pp5L	L	23	32.45	1.92	p = 0.28
	R	22	32.70	1.64	
ip2L	L	16	23.32	1.15	p = 0.48
	R	18	23.76	1.44	
ip3L	L	18	28.29	1.55	*p = 0.08*
	R	20	28.44	1.65	
ip4L	L	15	27.22	1.74	p = 0.16
	R	18	27.06	1.29	
ip5L	L	11	19.62	1.15	p = 0.38
	R	16	19.26	1.32	

Due to small sample sizes, distal phalanx data were excluded from this analysis. Mean and standard deviation values rounded to two decimal places. P-values approaching significance (between 0.055 and 0.1) highlighted in italics.List of abbreviations used: pp*L = proximal phalanx length, ip*L = intermediate phalanx length. Asterisk (*) denotes phalanx number.

6.1.2. Analysis of Variance (ANOVA)

To test the effects of age on the metric properties of the bones of the hand an Analysis of Variance (ANOVA) was performed on the Greenwich data. As there was only one variable effect to assess (and this variable only had two levels – middle adult and old adult) a one-way ANOVA was carried out. The results of this ANOVA for the Greenwich metacarpals are presented in Table 6.4 (below).

Table 6.4. One-way ANOVA for the effects of age on metacarpal metric variables.

Measurement	Side	Age	N	Mean	F	Sig. (2-tailed)
mc1L	L	mid	12	43.16	0.42	p = 0.53
		old	12	43.78		
	R	mid	11	43.05	1.84	p = 0.19
		old	14	44.42		
mc2L	L	mid	13	66.29	2.44	p = 0.13
		old	15	64.55		
	R	mid	13	65.85	0.07	p = 0.80
		old	16	65.59		
mc3L	L	mid	13	64.02	0.44	p = 0.51
		old	14	63.31		
	R	mid	12	63.90	1.86	p = 0.18
		old	15	62.38		
mc4L	L	mid	12	57.11	4.97	**p = 0.04**
		old	11	55.04		
	R	mid	13	56.29	0.17	p = 0.69
		old	15	55.92		
mc5L	L	mid	12	53.08	0.15	p = 0.71
		old	9	53.47		
	R	mid	10	53.25	3.12	*p = 0.09*
		old	14	51.95		
mc1RU	L	mid	11	12.02	1.39	p = 0.25
		old	12	12.45		
	R	mid	13	12.55	0.53	p = 0.47
		old	14	12.86		
mc2RU	L	mid	14	8.39	0.54	p = 0.47
		old	16	8.57		
	R	mid	14	8.67	1.71	p = 0.20
		old	17	8.95		
mc3RU	L	mid	14	8.42	0.55	p = 0.46
		old	16	8.60		
	R	mid	12	8.62	0.45	p = 0.51
		old	16	8.75		
mc4RU	L	mid	14	6.93	0.26	p = 0.62
		old	12	6.80		
	R	mid	14	7.31	0.06	p = 0.81
		old	16	7.36		
mc5RU	L	mid	13	7.84	0.16	p = 0.69
		old	10	7.97		
	R	mid	10	8.27	0.01	p = 0.91
		old	14	8.24		

Measurement	**Side**	**Age**	**N**	**Mean**	**F**	**Sig. (2-tailed)**
mc1DP	L	mid	11	8.75	1.45	p = 0.24
		old	12	9.22		
	R	mid	13	8.96	1.09	p = 0.31
		old	15	9.33		
mc2DP	L	mid	14	9.46	1.34	p = 0.26
		old	16	9.84		
	R	mid	14	9.71	0.12	p = 0.73
		old	17	9.82		
mc3DP	L	mid	14	9.24	3.71	*p = 0.06*
		old	16	9.81		
	R	mid	13	9.59	2.16	p = 0.15
		old	16	9.98		
mc4DP	L	mid	14	7.76	0.03	p = 0.86
		old	12	7.80		
	R	mid	14	8.04	0.28	p = 0.60
		old	16	8.14		
mc5DP	L	mid	13	7.04	0.22	p = 0.64
		old	12	7.18		
	R	mid	10	7.31	0.60	p = 0.45
		old	15	7.57		
mc1PB	L	mid	10	15.51	2.16	p = 0.16
		old	12	16.10		
	R	mid	11	15.80	1.46	p = 0.24
		old	13	16.34		
mc2PB	L	mid	14	17.71	0.04	p = 0.85
		old	15	17.65		
	R	mid	13	17.28	0.05	p = 0.82
		old	16	17.37		
mc3PB	L	mid	13	14.35	0.35	p = 0.56
		old	13	14.52		
	R	mid	13	14.20	0.32	p = 0.57
		old	15	14.37		
mc4PB	L	mid	11	12.93	1.03	p = 0.32
		old	10	12.47		
	R	mid	13	12.86	0.14	p = 0.71
		old	16	13.01		
mc5PB	L	mid	12	12.79	0.65	p = 0.43
		old	10	13.21		
	R	mid	9	13.07	0.45	p = 0.51
		old	12	13.43		

Measurement	Side	Age	N	Mean	F	Sig. (2-tailed)
mc1DB	L	mid	9	15.07	0.08	p = 0.78
		old	12	15.17		
	R	mid	11	15.45	0.00	p = 0.99
		old	12	15.44		
mc2DB	L	mid	12	14.54	0.19	p = 0.67
		old	13	14.38		
	R	mid	13	14.79	0.00	p = 0.96
		old	14	14.81		
mc3DB	L	mid	12	14.03	0.25	p = 0.62
		old	13	14.22		
	R	mid	11	14.55	0.59	p = 0.45
		old	12	14.33		
mc4DB	L	mid	12	12.37	1.37	p = 0.26
		old	9	11.91		
	R	mid	12	12.62	3.44	*p = 0.08*
		old	11	11.95		
mc5DB	L	mid	12	11.84	0.10	p = 0.75
		old	10	11.95		
	R	mid	10	12.38	1.51	p = 0.23
		old	10	11.84		

Mean values rounded to two decimal places. Significant p-values highlighted in bold. P-values approaching significance (between 0.055 and 0.1) highlighted in italics. List of abbreviations used: mc*L = metacarpal length, mc*RU = radio-ulnar midshaft diameter, mc*DP = dorso-palmar midshaft diameter, mc*PB = proximal breadth, mc*DB = distal breadth. Asterisk (*) denotes metacarpal number.

It is immediately clear from Table 6.4 that age has almost no effect on metacarpal size with only one measurement, mc4L, showing a statistically significant effect. A further three measurements (right mc5L, left mc3DP, right mc4DB) show p-values approaching significance. A comparison of the mean values for each measurement highlights a general trend for older adults to be larger than the younger adults in 33 of 50 occasions (Table D.1, Appendix D).There is no clear reason why left mc4L should show a significant age effect. Overall, these findings are to be expected, under the assumption that adult metacarpal size would not undergo an age-related change. The results of the Greenwich metacarpal ANOVA support those of the Écija metacarpal sample, where age was found to have a negligible effect on metacarpal size (Table 5.4).

Table 6.5 (below) provides the results of a one-way ANOVA performed on the effect of age on phalanx measurement.

Table 6.5. One-way ANOVA for the effects of age on phalanx metric variables.

Measurement	Side	Age	N	Mean	F	Sig. (2-tailed)
pp1L	L	mid	12	29.52	0.06	p = 0.80
		old	12	29.36		
	R	mid	11	29.00	0.21	p = 0.65
		old	12	29.31		
pp2L	L	mid	14	39.07	0.05	p = 0.82
		old	14	39.19		
	R	mid	14	39.04	0.00	p = 0.96
		old	13	39.08		
pp3L	L	mid	13	43.18	0.04	p = 0.84
		old	12	43.33		
	R	mid	14	43.24	0.03	p = 0.87
		old	15	43.34		
pp4L	L	mid	13	40.83	0.39	p = 0.54
		old	12	41.23		
	R	mid	14	40.61	0.06	p = 0.81
		old	13	40.45		
pp5L	L	mid	14	32.11	1.16	p = 0.29
		old	9	32.99		
	R	mid	13	32.61	0.10	p = 0.76
		old	9	32.83		
ip2L	L	mid	8	23.56	0.70	p = 0.42
		old	8	23.08		
	R	mid	9	23.77	0.00	p = 0.99
		old	9	23.76		
ip3L	L	mid	9	28.74	1.61	p = 0.22
		old	9	27.83		
	R	mid	10	28.18	0.46	p = 0.51
		old	10	28.69		
ip4L	L	mid	9	27.51	0.61	p = 0.45
		old	6	26.78		
	R	mid	8	27.21	0.20	p = 0.66
		old	10	26.93		
ip5L	L	mid	8	19.46	0.51	p = 0.49
		old	3	20.03		
	R	mid	7	19.30	0.01	p = 0.91
		old	9	19.22		

Mean values rounded to two decimal places. Due to small sample sizes, distal phalanx data were excluded from analysis.List of abbreviations used: pp*L = proximal phalanx length, ip*L = intermediate phalanx length. Asterisk (*) denotes phalanx number.

From the analysis in Table 6.5 it can be seen that there is no significant effect of age on phalanx length, indicating that 'middle' and 'old' adults do not differ significantly in terms of phalanx size. This is further reinforced when comparing the mean values for each measurement (Table D.1, Appendix D). These indicate that 'old' adults are larger than 'middle' adults for 10/18 measurements, with 'middle' adults larger than 'old' adults for 8/18 measurements. These results follow the findings of the ANOVA for the Écija phalanx measurements (Table 5.5), which found no effect of age on phalanx length. The results are also in keeping with the Greenwich metacarpal ANOVA (Table 6.4), which identified only one variable exhibiting a significant effect of age.

6.1.3. Asymmetry in the metacarpals and phalanges

Size-independent asymmetry was identified in the Greenwich hands using the methods described in section 5.1.3. These asymmetry equations provided measures of both directional and absolute asymmetry and this information was combined to give the metacarpal asymmetry profiles in Figures 6.1 to 6.5, below. These figures represent asymmetry in terms of the percentage of individuals displaying a right-side dominant, left-side dominant or symmetrical value for each metacarpal measurement. Each of the figures represents the asymmetry scores for one set of metacarpal measurements (e.g. mcL, mcRU, mcDP, etc.). The data from this analysis are presented in Table D.2 (Appendix D).

Figures 6.1 to 6.5 (below) indicate the presence of a clear variation in asymmetry across the Greenwich metacarpal variables. In contrast to Écija metacarpal asymmetry (Figs 5.1 to 5.5), where all measurements showed clear right-side dominance, 5 of the 25 metacarpal measurements in the Greenwich sample display left-side dominance. These left-side dominant scores were found for mc3L, mc4L, mc2PB, mc3PB and mc4PB, indicating that the concentration of left-side dominant values is in metacarpal length and proximal breadth measurements, and in metacarpals 3 and 4. The general degree of asymmetry in the Greenwich metacarpal measurements is lower than that seen in the Écija metacarpal sample, with no asymmetry values greater than 78% (and only 7/25 variables showing greater than 70% asymmetry). The presence of left-side dominant asymmetry alongside reduced right-side dominant asymmetry suggests a general trend towards reduced asymmetry in this metacarpal sample. This pattern of reduced asymmetry is in line with the results of the Wilcoxon analysis (Table 6.2), which found that only approximately half of the variables showed a statistically significant size difference between the left and right measurements.

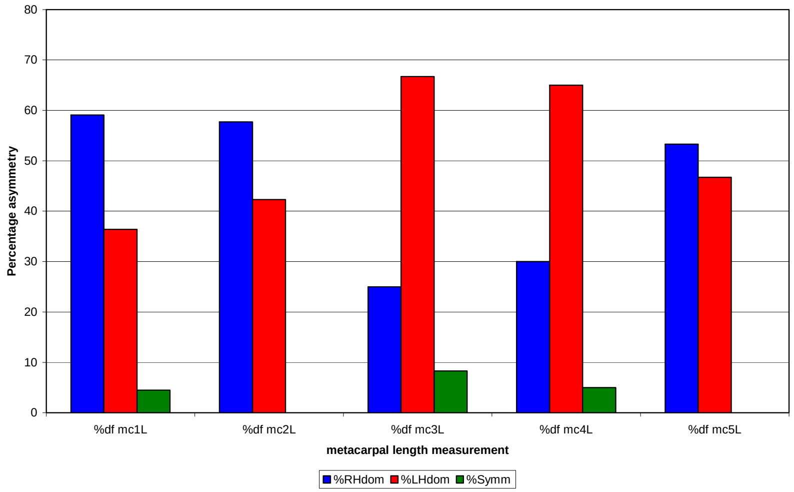


Figure 6.1.Percentage of right- and left-side dominant and symmetric individuals for metacarpal length (mc*L).

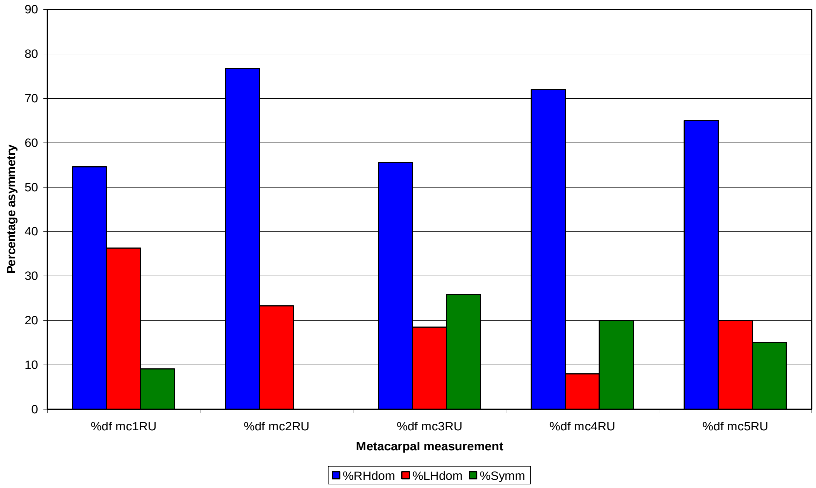


Figure 6.2.Percentage of right- and left-side dominant and symmetric individuals for metacarpal radio-ulnar diameter (mc*RU).

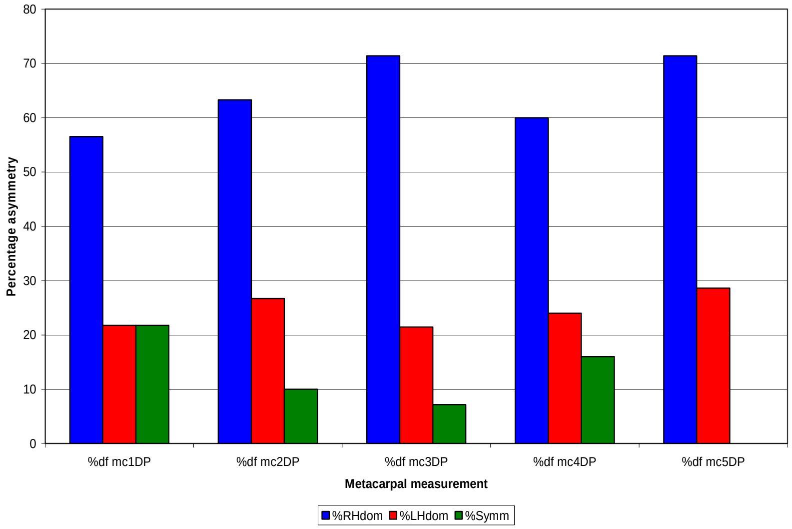


Figure 6.3. Percentage of right- and left-side dominant and symmetric individuals for metacarpal dorso-palmar diameter (mc*DP).

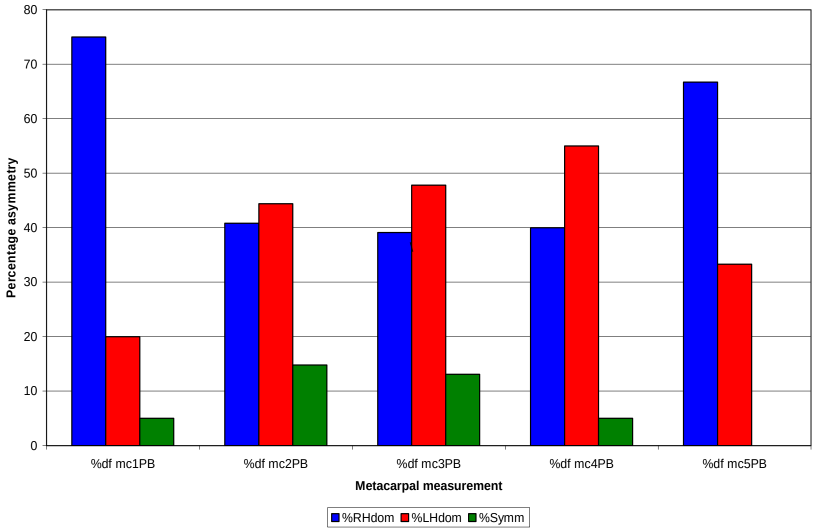


Figure 6.4. Percentage of right- and left-side dominant and symmetric individuals for metacarpal proximal breadth (mc*PB).

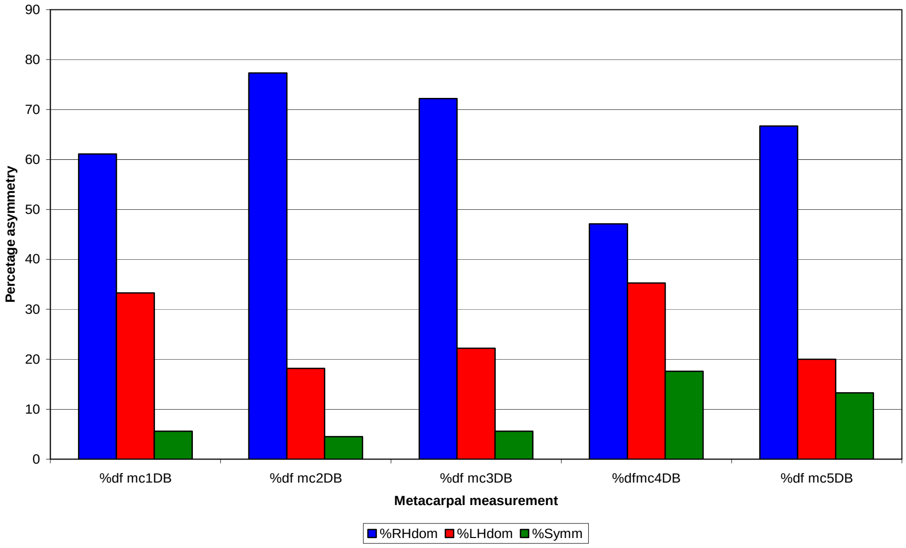


Figure 6.5. Percentage of right- and left-side dominant and symmetric individuals for metacarpal distal breadth (mc*DB). Further data for asymmetry analysis available in Table D.2, Appendix D.

Taken together, these results suggests the possibility that metacarpals 3 and 4 (and possibly metacarpal 2) were being mechanically stressed in a different manner to metacarpals 1 and 5, resulting in the differing asymmetry patterns identified above. Why metacarpal length and proximal breadth measurements should display this pattern in particular is unclear, especially as it has been suggested that the dorso-palmar plane is the primary axis of loading, in the 2nd metacarpal at least (Lazenby, 2002a). This finding is interesting when considered in the context of the specific roles of metacarpals 1 and 5 in the gripping and manipulation of objects relative to the other metacarpals (Marzke & Marzke, 2000). The reduced asymmetry seen in the Greenwich metacarpals relative to the Écija metacarpals supports the notion that stresses placed on the hands of the Greenwich seamen were more symmetrical in nature than for the Écija individuals. Evidence for the types of tasks likely to have been engaged in by the Greenwich sample appears to support this (Boston *et al.*, 2008).

The asymmetry scores presented in Figures 6.1 to 6.5 were re-plotted to reflect the overall pattern of asymmetry in each individual metacarpal. This reorganisation is presented in Figures 6.6 to 6.10 (below). These figures show that when each metacarpal is analysed separately, no obvious similarities between their asymmetry profiles emerge, as was the case for the Écija metacarpals (Figs 5.6 to 5.10). Metacarpals 3 and 4 show very ‘mixed’ asymmetry in part due to the presence of left-side dominant values. For the remaining metacarpals (1, 2 and 5) there is more similarity in the distribution of asymmetry scores, particularly for mc1 and mc5.

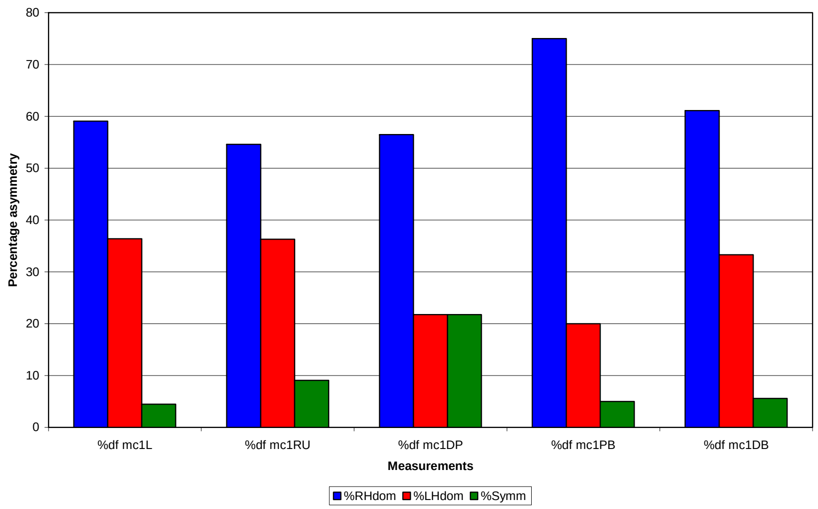


Figure 6.6. Asymmetry values for each metacarpal 1 measurement (length, radio-ulnar diameter, dorso-palmar diameter, proximal breadth and distal breadth).

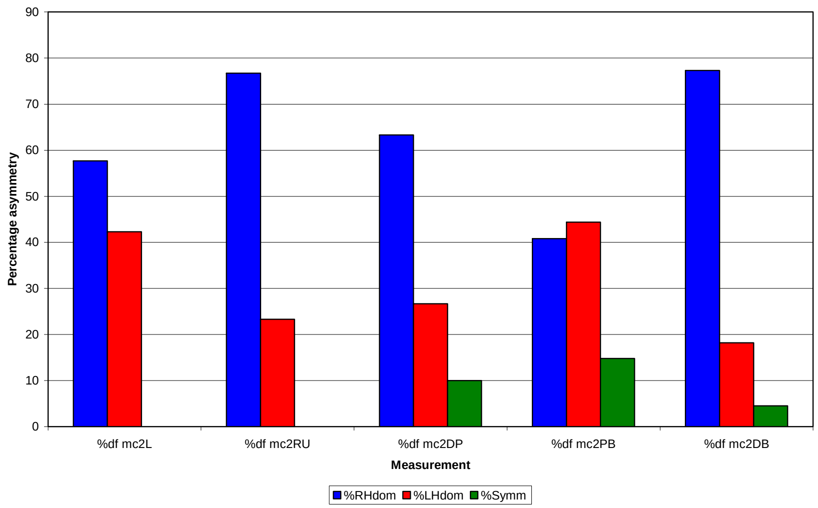


Figure 6.7. Asymmetry values for each metacarpal 2 measurement (length, radio-ulnar diameter, dorso-palmar diameter, proximal breadth and distal breadth).

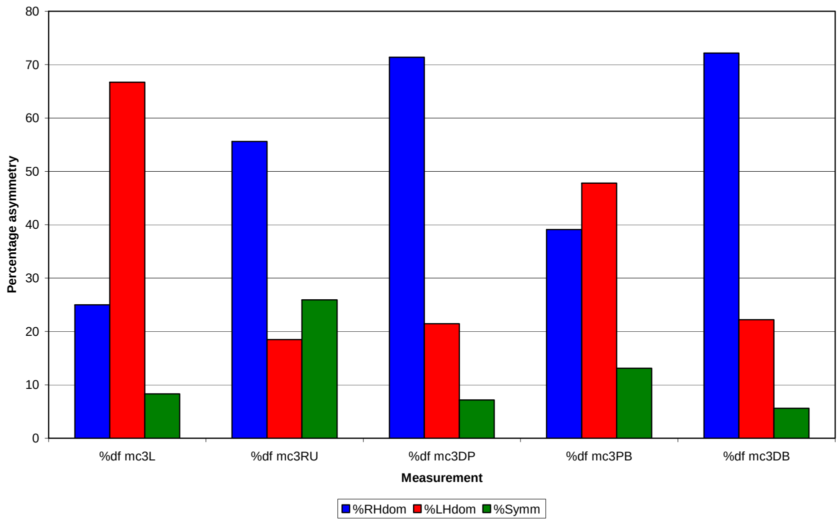


Figure 6.8. Asymmetry values for each metacarpal 3 measurement (length, radio-ulnar diameter, dorso-palmar diameter, proximal breadth and distal breadth).

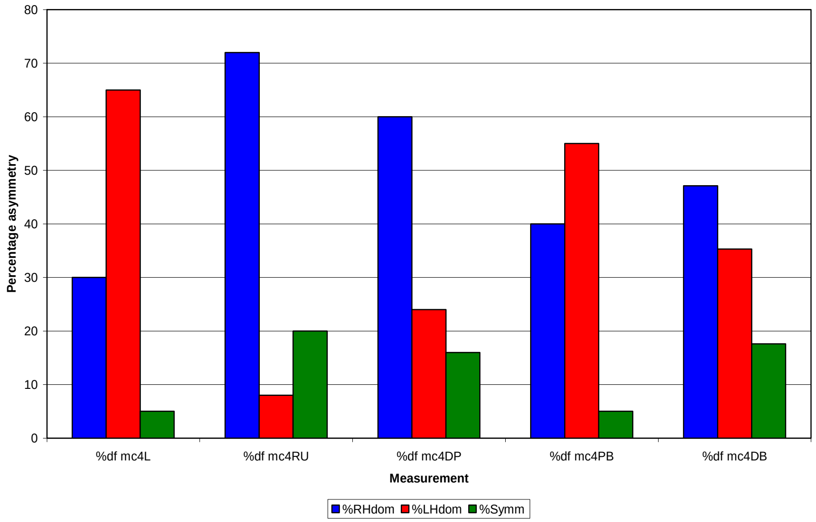


Figure 6.9. Asymmetry values for each metacarpal 4 measurement (length, radio-ulnar diameter, dorso-palmar diameter, proximal breadth and distal breadth).

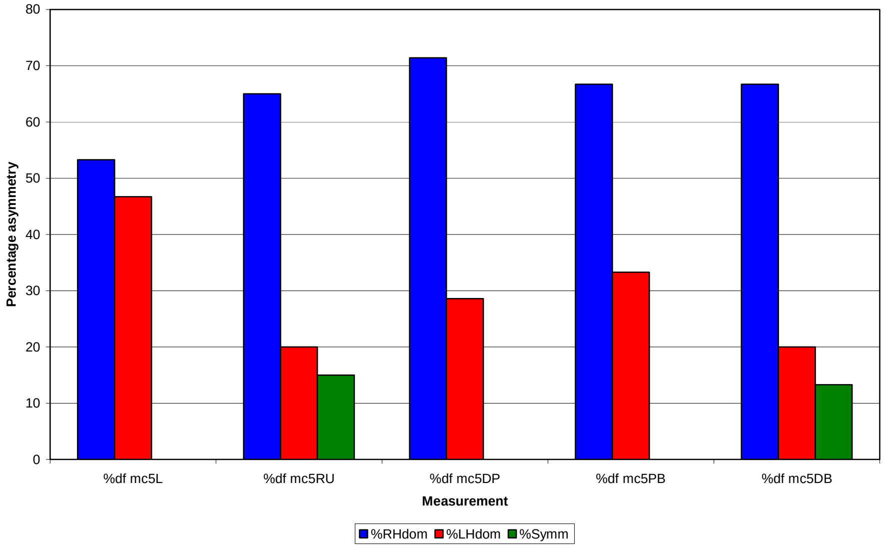


Figure 6.10. Asymmetry values for each metacarpal 5 measurement (length, radio-ulnar diameter, dorso-palmar diameter, proximal breadth and distal breadth). Further data for asymmetry analysis available in Table D.2, Appendix D.

Asymmetry scores were also calculated for each of the Greenwich phalanx length measurements using the same method as for the metacarpal sample. The results of the phalanx asymmetry analysis are presented in Figure 6.11. The data from this analysis is available in Table D.3 (Appendix D).

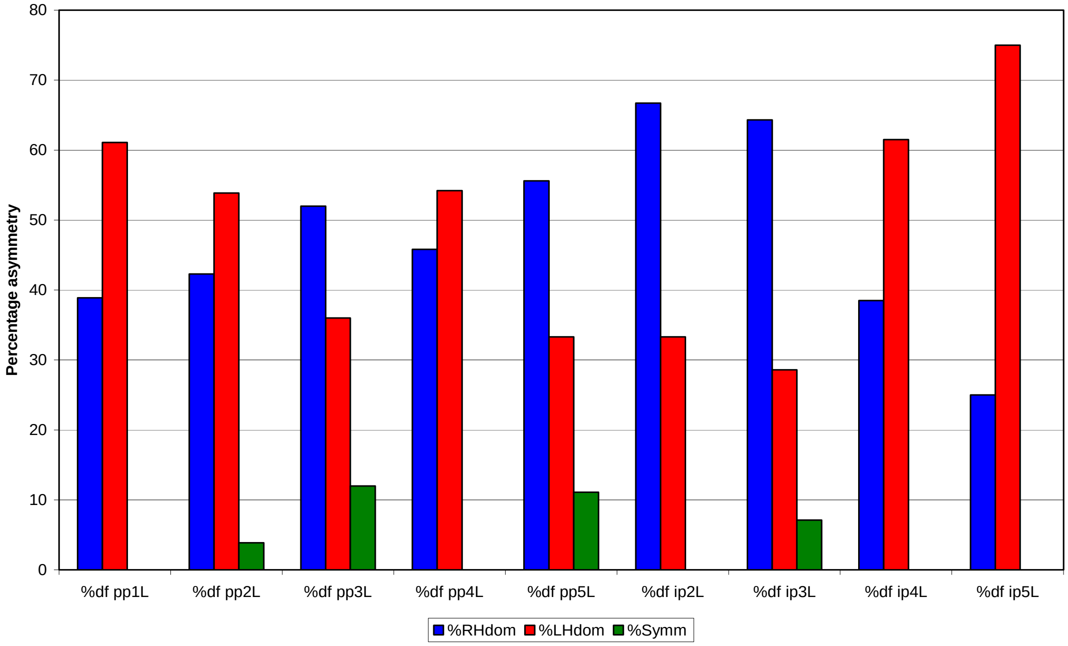


Figure 6.11. Asymmetry values for each phalanx length measurement. Due to small sample sizes, distal phalanx data were not included in this analysis. Further data for asymmetry analysis available in Table D.3, Appendix D.

It is immediately clear from Figure 6.11 that asymmetry is highly variable in the proximal and intermediate phalanges from Greenwich. There is no clear right-side dominance in this sample; in fact the overall trend is for left-side dominance (in 5/9 measurements) with only 4 measurements (pp3L, pp5L, ip2L, ip3L) showing a right-side dominance. The magnitude of the dominant asymmetry is larger in the intermediate phalanges than the proximal phalanges and the pattern of asymmetry is not always consistent within the digits. For example, pp2L is left-side dominant, but ip2L is right-side dominant; pp5L is right-side dominant, but ip5L is left-side dominant. In comparison, the Écija phalanges (Fig. 5.11) showed clear right-side dominance across all measurements.

The overall magnitude and variation in asymmetry in the Greenwich phalanges is greater than that seen in the Écija phalanges with dominant asymmetry in the Greenwich sample ranging from 52% to 75% (irrespective of variation in side dominance). As described above, siding of the Greenwich phalanges was considered to be accurate as a result of careful post-excavation curation of the bones. Therefore, the patterns identified in this analysis can be considered reflective of genuine (and not methodological) differences between the fingers. This also suggests functional differences between the Greenwich and Écija samples in the way in which each hand was used.

6.1.4. Age effects on asymmetry in the metacarpals and phalanges

The ANOVA in section 6.1.2 found virtually no effect of age on the size of metacarpal and phalanx measurements (the only exception being left mc4L, which had a p-value of 0.04). The effect of age on asymmetry as displayed in Figures 6.1 to 6.11 was assessed by conducting Mann-Whitney U tests, as described in section 5.1.4. The effect of age was assessed for both directional (i.e. left- or right-side dominance) and absolute (i.e. magnitude) asymmetry. Table 6.6 (below) provides the results of the Mann-Whitney U test performed on the Greenwich metacarpal data.

From Table 6.6 it can be seen that there is an extremely limited effect of age on both directional and absolute asymmetry in the metacarpals. There are no statistically significant effects of age on absolute asymmetry, while there is only one statistically significant effect of age on directional asymmetry, for mc4DB ($p = 0.05$). The mean rank values for the metacarpal measurements indicate that 'middle' adults are more frequently right-side dominant than 'old' adults although overall there are no obvious trends between the age categories in terms of the expression of directional or absolute asymmetry (Tables D.4 and D.5, Appendix D). Compared with the Écija metacarpals, there are fewer significant effects of age found in asymmetry in the Greenwich sample.

Table 6.6. A Mann-Whitney U test of the effects of age on directional and absolute asymmetry for each of the metacarpal measurements.

Measurement	**N**	**Directional asymmetry (cf. Steele & Mays, 1995)**				**Absolute asymmetry (cf. Trinkaus *et al.*, 1994)**			
		mean	**std dev.**	**U**	**Sig. (2-tailed)**	**mean**	**std dev.**	**U**	**Sig. (2-tailed)**
mc1L	22	0.66	2.37	55.0	p = 0.75	1.67	1.83	58.0	p = 0.89
mc2L	26	0.42	1.26	50.0	*p = 0.08*	.97	0.89	49.0	*p = 0.07*
mc3L	23	-0.61	1.49	58.0	p = 0.65	1.24	1.00	55.5	p = 0.37
mc4L	20	-0.57	1.12	38.5	p = 0.42	1.06	0.68	39.5	p = 0.47
mc5L	15	0.07	2.00	22.0	p = 0.61	1.39	1.42	16.0	p = 0.22
mc1RU	21	2.95	6.02	49.0	p = 0.71	4.52	4.70	45.5	p = 0.34
mc2RU	30	4.50	6.19	96.0	p = 0.52	6.25	4.42	100.5	p = 0.65
mc3RU	27	1.67	4.18	77.0	p = 0.54	3.15	3.38	55.5	*p = 0.09*
mc4RU	25	6.24	6.26	74.0	p = 0.89	6.67	5.79	65.0	p = 0.53
mc5RU	19	5.90	7.97	36.5	p = 0.51	6.98	6.63	36.0	p = 0.30
mc1DP	22	1.86	7.19	49.5	p = 0.49	5.51	5.43	40.0	p = 0.11
mc2DP	30	1.23	4.89	81.0	p = 0.21	3.95	3.41	111.5	p = 0.99
mc3DP	28	2.47	3.83	92.5	p = 0.83	3.79	2.57	71.5	p = 0.24
mc4DP	25	3.34	6.15	67.5	p = 0.62	5.48	4.36	58.5	p = 0.32
mc5DP	21	5.73	9.15	51.0	p = 0.81	8.95	6.04	46.5	p = 0.57
mc1PB	20	1.78	4.72	48.0	p = 0.94	4.04	3.14	40.0	p = 0.50
mc2PB	27	-1.66	5.54	87.0	p = 0.86	4.35	4.75	68.5	p = 0.28
mc3PB	23	-0.61	4.13	46.0	p = 0.24	3.30	2.82	60.0	p = 0.73
mc4PB	20	0.04	3.98	49.0	p = 1.00	3.04	2.54	42.0	p = 0.60
mc5PB	15	1.75	5.38	21.5	p = 0.48	4.44	3.46	25.5	p = 0.80
mc1DB	18	2.21	3.84	34.0	p = 0.61	3.67	2.45	36.0	p = 0.73
mc2DB	22	3.19	5.04	52.0	p = 0.63	4.66	3.76	48.0	p = 0.45
mc3DB	18	2.21	3.49	28.0	p = 0.32	3.14	2.64	26.0	p = 0.24
mc4DB	17	1.39	4.40	13.0	**p = 0.05**	3.40	3.16	26.0	p = 0.52
mc5DB	15	2.43	5.49	12.5	p = 0.14	4.77	3.78	20.5	p = 0.62

Minus values for directional asymmetry means reflects the equation used to calculate asymmetry, in which a left-side dominant individual will have a minus score. Mean and standard deviation values rounded to two decimal places. Significant p-values highlighted in bold. P-values approaching significance (between 0.055 and 0.1) highlighted in italics. List of abbreviations used: mc*L = metacarpal length, mc*RU = radio-ulnar midshaft diameter, mc*DP = dorso-palmar midshaft diameter, mc*PB = proximal breadth, mc*DB = distal breadth. Asterisk (*) denotes metacarpal number.

The effect of age on directional and absolute phalanx asymmetry was also assessed for the Greenwich phalanges using a Mann-Whitney U test. Table 6.7 (below) provides the results of this analysis and shows that there are no statistically significant effects of age on either directional or absolute asymmetry in the phalanges. Despite this, the general trend in the mean rank values (Table D.6, Appendix D) is for 'middle' adults to be more frequently right-side dominant than 'old' adults (for 6/9 variables). However, mean rank values identify no clear trends for one age category to have larger asymmetry scores than the other (Table D.7, Appendix D). Overall, age has been shown to have a negligible effect on the expression of asymmetry in the hand bones of the Greenwich sample. This could be a consequence of the difficulty in determining the difference between ‘middle’ adults and ‘old’ adults in what can be considered an ‘elderly’ population. Although it is possible that this difficulty could be compounded by the extensive pathology present in this collection, care was taken to not select individuals who exhibited pathological joint changes that altered the dimensions of metacarpal properties measured in this study.

Table 6.7. A Mann-Whitney U test of the effects of age on directional and absolute asymmetry for each of the phalanx measurements.

Measurement	N	Directional asymmetry (cf. Auerbach & Ruff, 2006)				Absolute asymmetry (cf. Trinkaus et al., 1994)			
		mean	std dev.	U	Sig. (2-tailed)	mean	std dev.	U	Sig. (2-tailed)
pp1L	18	-0.46	2.00	35.5	p = 0.71	1.70	1.15	28.5	p = 0.33
pp2L	26	-0.06	2.82	66.5	p = 0.38	1.91	2.08	58.5	p = 0.20
pp3L	25	0.13	1.99	69.0	p = 0.65	1.46	1.40	72.0	p = 0.76
pp4L	24	-0.69	1.60	43.0	p = 0.11	1.36	1.14	52.0	p = 0.27
pp5L	18	1.60	4.66	21.5	p = 0.30	2.66	4.12	27.0	p = 0.61
ip2L	9	2.20	5.90	9.0	p = 0.91	3.80	4.92	10.0	p = 1.00
ip3L	14	2.11	5.76	14.5	p = 0.24	2.47	5.60	21.5	p = 0.78
ip4L	13	-1.23	3.54	15.0	p = 0.52	2.45	3.23	13.0	p = 0.35
ip5L	8	-0.78	2.56	6.0	p = 1.00	2.20	1.44	6.0	p = 1.00

Due to small sample sizes, distal phalanx data was excluded from this analysis. Minus values for directional asymmetry means reflects the equation used to calculate asymmetry, in which a left-side dominant individual will have a minus score. Mean and standard deviation values rounded to two decimal places. List of abbreviations used: pp*L = proximal phalanx length, ip*L = intermediate phalanx length. Asterisk (*) denotes phalanx number.

6.1.5. Individual asymmetry

Asymmetry values were also calculated for each individual measured in the current study. This was done using the asymmetry equations described in section 5.1.3. These equations provided the percentage of each individual’s measurements that were right-side dominant, left-side dominant or symmetrical. Figure 6.12 (below) provides the results of this analysis for the Greenwich metacarpals. As was found for the Écija metacarpals (Fig. 5.12) there is clear variation amongst the Greenwich individuals in terms of the distribution of asymmetry and side dominance. The overall trend in this sample is for right-side dominance as seen in 18 of 30 individuals (or 60%), compared with a left-side dominance found in 10 of 30 individuals (or 33%) (2 individuals had an equal percentage of right-side dominant and left-side dominant measurements). Compared with individual asymmetry in the Écija metacarpal sample, there are many more left-side dominant individuals in the Greenwich sample. This reduction in the number of right-side dominant individuals reflects the lower levels of asymmetry identified in Figures 6.1 to 6.10. The variation in the magnitude of asymmetry is also reduced in the Greenwich individuals relative to the Écija individuals, ranging from 45% to 76% (compared with 42% to 100% in the Écija sample).

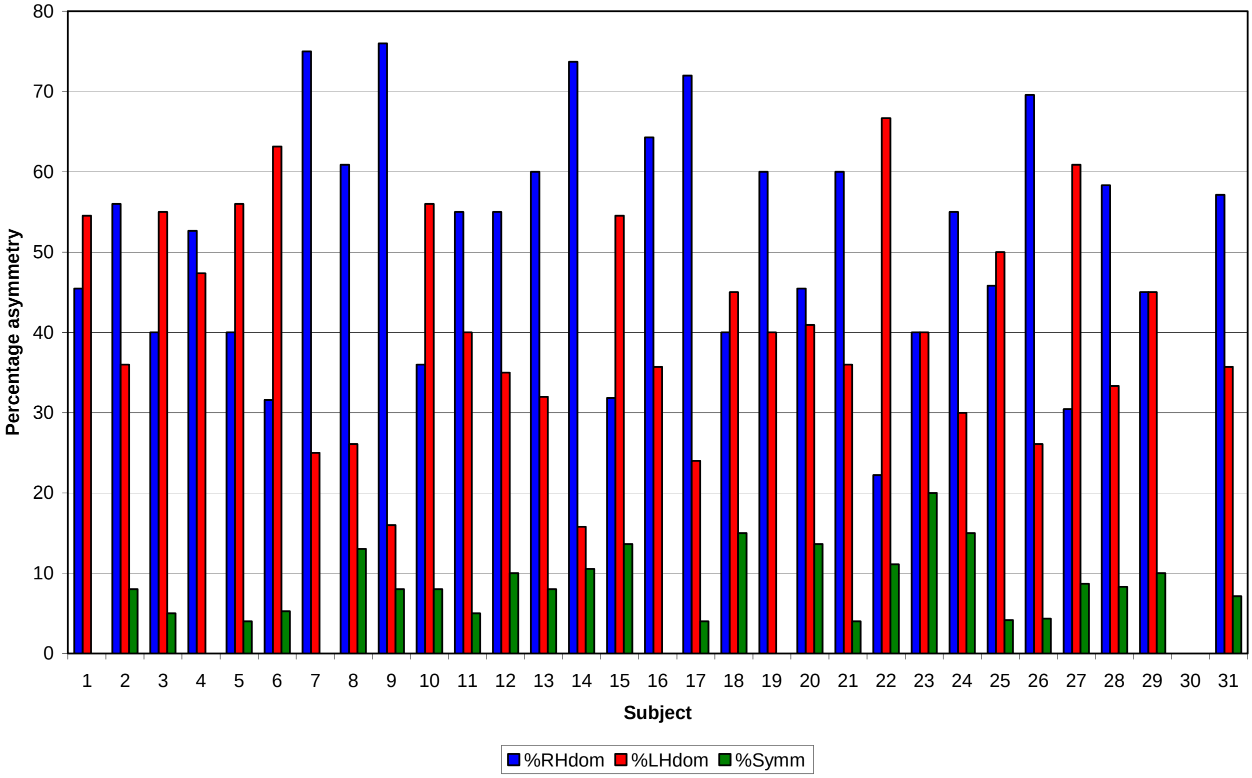


Figure 6.12. For each individual in the Greenwich sample, the percentage of right-side dominant, left-side dominant and symmetric scores for each metacarpal measurement. Due to missing data, individual asymmetry could not be calculated for subject 30.

Individual asymmetry was also calculated for phalanx length measurements in the Greenwich sample. Figure 6.13 (below) provides the results of this analysis. The majority of individuals (69% or 20/29 subjects) show a left-side dominant asymmetry for phalanx length, compared to 31% (9/29) of individuals who displayed right-side dominant asymmetry. This contrasts with individual asymmetry in the Écija phalanges (Fig. 5.13) where the majority of individuals were found to be right-side dominant. The results of the Greenwich individual asymmetry analysis support the general trend identified in Greenwich hand asymmetry for an increase in left-side dominance. These analyses imply that the hands of the Greenwich individuals were engaged in activities that have resulted in observable variation in the expression of asymmetry. It is possible that functional loading of the left hand in particular is reducing the extent of the right-side dominance in the Greenwich sample and in some cases, resulting in an increase in left-side dominant scores.

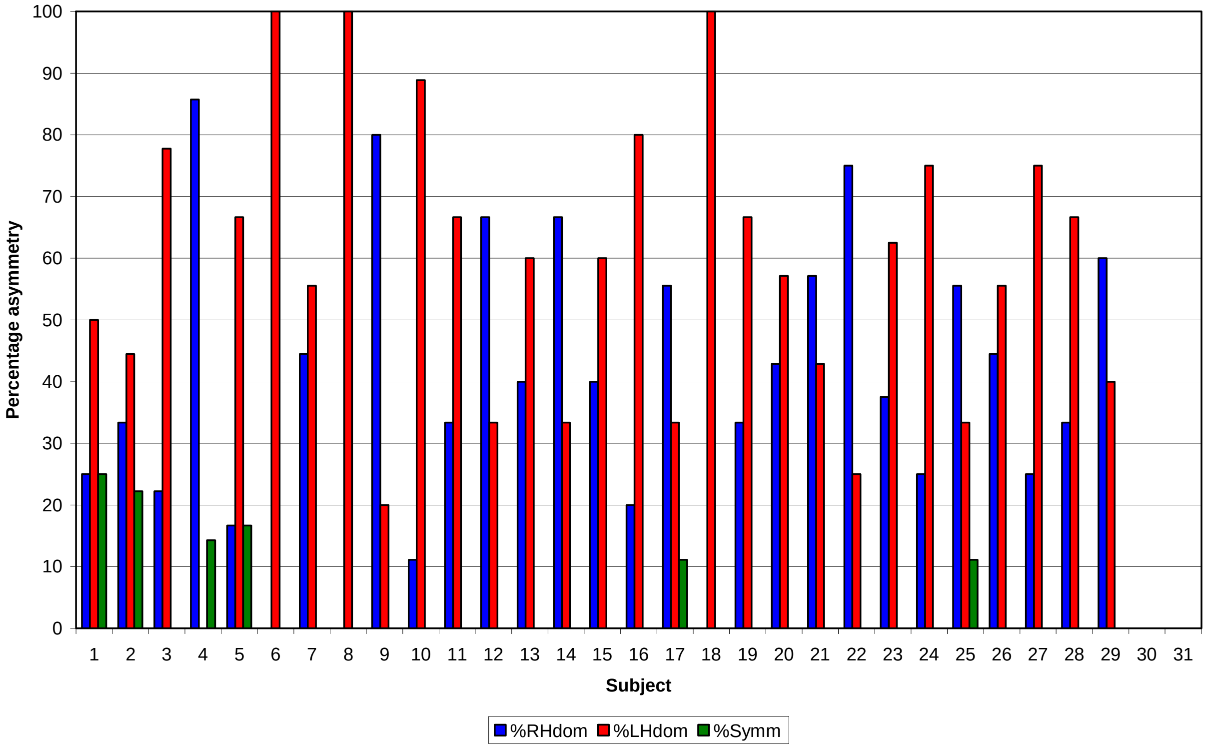


Figure 6.13. For each individual in the Greenwich sample, the percentage of right-side dominant, left-side dominant and symmetric scores for each phalanx measurement. Due to missing data, individual asymmetry could not be calculated for subjects 30 and 31.

6.1.6. Summary of metacarpal and phalanx metric analysis

The analysis of the Greenwich metacarpal and phalanx metric data indicate that there is an increased proportion of left-side dominant asymmetry present in this sample leading to an overall reduction in the level of asymmetry relative to the Écija metacarpal and phalanx sample. This trend is found in the results of the Wilcoxon tests (section 6.1.1) which identified a substantial proportion of metacarpal and phalanx measurements that showed no significant size differences between left and right measurements. In addition, ANOVA tests (section 6.1.2) found virtually no significant differences between ‘middle’-aged adults and ‘old’-aged adults in terms of measurement size. Analysis of asymmetry in the Greenwich hand bones (section 6.1.3) suggests that the intensive physical labour likely to have been engaged in by the residents of the Greenwich Naval Hospital over the course of their working lives has led to an increased proportion of left-side dominant individuals and overall left-side dominant measurements, and a reduction of the overall magnitude of right-side dominance seen in this sample relative to the Écija sample. It is possible that the trend identified by Stirland (1993) in the humeri of individuals from the *Mary Rose*, for the magnitude of observable asymmetry to decrease with age, may also contribute to the asymmetry pattern observed in the Greenwich sample. Despite this reduction in observable asymmetry in the Greenwich hands, it was noted by Boston *et al.* (2008) that there was likely to be a preponderance of right-handed individuals in the Greenwich sample, suggested by the high proportion of right-side metacarpal fractures identified. These fractures are likely to have resulted from fighting, suggesting that the right hand was often the dominant hand for punching.

Mann-Whitney U tests (section 6.1.4) have shown that there is also an extremely limited effect of age on both the direction and magnitude of asymmetry in the hands. This may reflect difficulties in making rather arbitrary age divisions in a sample comprised of older individuals. While it is possible that the level of pathology in the sample may lead to altered metacarpal dimensions, care was taken to exclude highly pathological individuals from study. Despite this, the prevalence of OA in the collection means that some degree in OA was present in the current sample.

Finally, analysis of individual asymmetry (section 6.1.5) supports the earlier observation of a reduction in the magnitude of asymmetry in the Greenwich sample and the relative increase in the proportion of left-side dominant individuals.

6.2. Humeral metric data

Metric data were also collected from the humeral material in the Greenwich collection. Descriptive statistics for this sample can be found in Table D.8 (Appendix D). Box-and-whisker plots were used to identify outliers, which were only removed from the data set if they were found to represent error in the data collection. Otherwise the data points were included in subsequent analyses and non-parametric tests applied to the data where necessary. Histograms and p-p plots confirmed the normal distribution of the data. The structure of the data analysis in this section follows that of the humeral material described in section 5.2.

6.2.1. Significance testing

A Wilcoxon test was performed on the humeral metric data to identify the presence of significant differences between the left and right measurements for each variable. Outliers were present in the data, making it unsuitable for a paired-samples t-test. Table 6.8 (below) provides the results of the Wilcoxon test performed on the combined-age sample. From Table 6.8 it can be seen that only three variables show a statistically significant difference between the left and right measurements: MxL, MxDm and TCBr, with a further two variables (MnCir and MxTDm) approaching significance. This therefore, indicates that there are few significant size differences between left and right measurements. Comparisons of mean values for each variable show that the right-side measurements are bigger than left-side measurements for all but one variable (CirHd). The presence of significant size differences between left and right MxL and MxDm suggest that the humeral diaphyses in this sample may be more influenced by bilateral asymmetry in mechanical loading than either the proximal or distal articular surfaces, as might be expected (e.g. Ruff, 2000).

Table 6.8. Wilcoxon test results for the combined-age Greenwich humerus sample.

Measurement	Side	N	Mean	Std dev.	Sig. (2-tailed)
MxL	L	29	319.38	13.38	**p = 0.05**
	R	30	321.77	12.24	
MxDm	L	31	23.27	1.65	**p < 0.01**
	R	31	23.93	1.57	
MnDm	L	31	18.86	1.60	p = 0.48
	R	31	18.94	1.31	
MnCir	L	31	65.87	4.13	*p = 0.06*
	R	31	66.35	3.57	
CirHd	L	18	145.61	6.41	p = 0.41
	R	24	144.58	6.30	
MxTDm	L	19	43.44	1.70	*p = 0.10*
	R	23	43.97	1.50	
MxSDm	L	28	47.00	2.32	p = 0.41
	R	29	47.42	1.96	
EpBr	L	25	63.46	2.95	p = 0.57
	R	24	64.11	3.26	
TCBr	L	16	47.35	2.51	**p = 0.01**
	R	25	47.96	2.07	

Mean and standard deviation values rounded to two decimal places. Significant p-values highlighted in bold. P-values approaching significance (between 0.055 and 0.1) highlighted in italics. Abbreviations used: MxL = maximum length, MxDm = maximum midshaft diameter, MnDm = minimum midshaft diameter, MnCir = minimum shaft circumference, CirHd = circumference of head, MxTDm = maximum transverse diameter of head, MxSDm = maximum sagittal diameter of head, EpBr = epicondylar breadth, TCBr = trochlea-capitulum breadth.

These results follow the pattern found in the Wilcoxon test performed on the Greenwich metacarpal and phalanx data which also identified very few significant left/right size differences. However, the results in Table 6.8 contrast with those of the corresponding Écija analysis (Table 5.10) which found that all humerus variables exhibited strong, statistically significant differences between left and right measurements. As for the Greenwich hands, it is likely that the occupations of the individuals in the sample has reduced the overall level of bilateral asymmetry in the Greenwich sample relative to that found in the Écija sample.

6.2.2. Analysis of Variance

A one-way ANOVA was performed to assess the effects of age on the metric properties of the humerus. Table 6.9 (below) provides the results of this analysis and it is apparent that, with the exception of left epicondylar breadth (EpBr), age has no statistically significant effects on humerus measurements. It is not clear why only left EpBr should show a significant effect, although it is worth noting that in the analysis of the Écija humerus material (Table X.11), age also had a significant effect on the left EpBr (and a p-value approaching significance for right EpBr).

A comparison of the mean values for EpBr (Table D.8, Appendix D) show that 'old' adults have larger values than 'middle' adults (which is also the trend for 13 of the 17 remaining variables). The medial and lateral epicondyles of the humerus are points of origin for many of the flexor and extensor muscles, respectively. It is therefore possible that increased use of these muscles over time with lead to bone remodelling on the epicondyles, which is reflected in larger metric dimensions. Section 6.4.1 will assess MSM at these sites in more detail.

Table 6.9. One-way ANOVA for the effects of age on humerus metric variables.

Measurement	Side	Age	N	Mean	F	Sig.
MxL	L	mid	13	319.15	0.01	p = 0.94
		old	16	319.56		
	R	mid	13	323.69	0.56	p = 0.46
		old	17	320.29		
MxDm	L	mid	14	22.94	1.03	p = 0.32
		old	17	23.55		
	R	mid	14	23.77	0.25	p = 0.62
		old	17	24.06		
MnDm	L	mid	14	18.59	0.75	p = 0.40
		old	17	19.09		
	R	mid	14	18.69	0.88	p = 0.36
		old	17	19.14		
MnCir	L	mid	14	65.00	1.14	p = 0.29
		old	17	66.59		
	R	mid	14	65.43	1.76	p = 0.20
		old	17	67.12		
CirHd	L	mid	9	145.11	0.10	p = 0.75
		old	9	146.11		
	R	mid	12	146.67	2.83	p = 0.11
		old	12	142.50		
MxTDm	L	mid	10	42.99	1.54	p = 0.23
		old	9	43.94		
	R	mid	12	43.93	0.01	p = 0.91
		old	11	44.01		
MxSDm	L	mid	12	46.39	1.47	p = 0.24
		old	16	47.46		
	R	mid	13	47.68	0.40	p = 0.53
		old	16	47.21		
EpBr	L	mid	12	62.25	4.41	**p = 0.05**
		old	13	64.57		
	R	mid	10	62.61	4.11	*p = 0.06*
		old	14	65.18		

Measurement	Side	Age	N	Mean	F	Sig.
TCBr	L	mid	6	47.05	0.13	p = 0.73
		old	10	47.53		
	R	mid	12	48.36	0.92	p = 0.35
		old	13	47.58		

Mean values rounded to two decimal places. Significant p-values highlighted in bold. P-values approaching significance (between 0.055 and 0.1) highlighted in italics. Abbreviations used: MxL = maximum length, MxDm = maximum midshaft diameter, MnDm = minimum midshaft diameter, MnCir = minimum shaft circumference, CirHd = circumference of head, MxTDm = maximum transverse diameter of head, MxSDm = maximum sagittal diameter of head, EpBr = epicondylar breadth, TCBr = trochlea-capitulum breadth.

6.2.3. Asymmetry in the humerus

As with the metacarpal and phalanx measurements (section 6.1.3) humeral asymmetry was assessed in the Greenwich sample in terms of the percentage of subjects displaying right-side dominant, left-side dominant or symmetrical values for each of the nine humerus measurements. This was done using the equations described in section 5.1.3. The results of this analysis are presented in Figure 6.14. Data from this analysis can be found in Table D.9 (Appendix D).

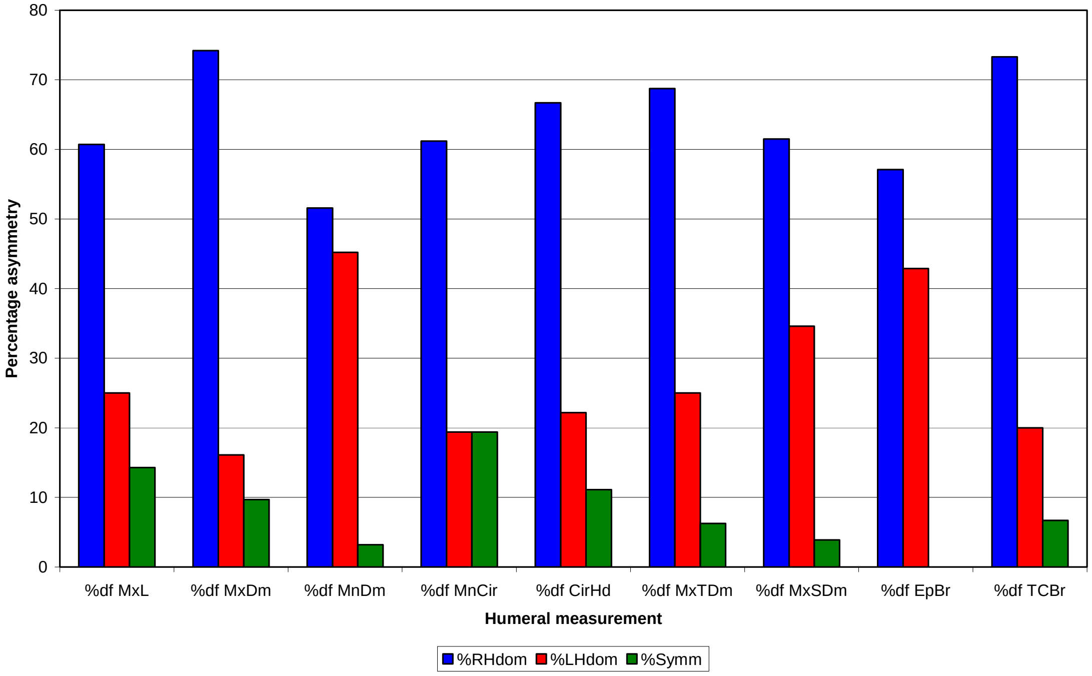


Figure 6.14. Percentage of right and left side dominant and symmetric individuals for humerus measurements. Further data available in Table D.9, Appendix D.

From Figure 6.14 it can be seen that the trend is for right-side dominant asymmetry across all the humerus measurements. However, there is clear variation in the magnitude of this right-side dominance. In the Greenwich sample only two variables exhibit right-side dominance greater than 70% (MxDm and TCBr) in contrast to the Écija humeri (Fig. 5.14) where 7 of the 9 variables show asymmetry greater than 70%. This indicates that the general magnitude of humerus asymmetry is lower in the Greenwich sample compared with that of the Écija sample. In particular, MnDm and EpBr show lower levels of right-side dominance (<60%) compared with the other measurements in the Greenwich sample. In both this analysis and that of Écija humeral asymmetry, MnDm shows the least amount of asymmetry relative to the other measurements. As long bone diaphyses are more liable to show mechanically-influenced bone remodelling than the articular surfaces (Ruff, 2000), it is possible that this trend results from the fact that MnDm is the smallest of the humerus measurements and thus has an increased potential for similar sized measurements. Despite differences in the magnitude of asymmetry the Greenwich and Écija humerus samples are similar in the pattern of asymmetry across the measurements. The noticeable exception is MxL asymmetry. In the Écija analysis MxL is highly right-side dominant (93%), but this asymmetry is much lower in the Greenwich analysis (60.7%). This suggests that while the overall pattern of asymmetry (although not the magnitude of the asymmetry) is the same between the two groups, there is a clear difference in the response of humeral length to mechanical loading. It is perhaps this measurement that gives the clearest reflection of the more symmetrical loading of the upper limb that is likely to have been common in the working live of the Greenwich seamen.

6.2.4. Age effects on asymmetry

A Mann-Whitney U test was conducted to assess the effect of age on both directional and absolute asymmetry in the Greenwich humeri. The results of this analysis are presented in Table 6.10 (below) and as was found in the analysis of age effects on hand asymmetry (section 6.1.4), age is found to have virtually no effect on asymmetry in the Greenwich humeri. There is no statistically significant differences between ‘middle’ and ‘old’ adults in the direction of their asymmetry and only one significant difference between the age categories in terms of absolute asymmetry, for MnDm ($p = 0.04$). A comparison of mean rank values from this analysis (Table D.10 and D.11, Appendix D) shows that there is a trend for ‘middle’ adults to be more frequently right-side dominant than ‘old’ adults (for 7/9 variables), but for older adults to have larger asymmetry scores than younger adults (for 7/9 variables). The negligible effect of age found in this analysis is similar to that found for the Écija humeri (section 6.2.5) as is the trend for ‘middle’ adults to be more often right-side dominant than ‘old’ adults. The samples differ however, in the trend for absolute asymmetry with the Écija humeri having larger asymmetry scores for younger adults (and vice versa for Greenwich humeri). However, as these differences are not statistically significant their meaning is difficult to interpret.

Table 6.10. Mann-Whitney U test of the effects of age on directional asymmetry and absolute asymmetry values for each of the humerus measurements.

Measurement	N	Directional asymmetry (cf. Steele & Mays, 1995)				Absolute asymmetry (cf. Trinkaus *et al*., 1994)			
		mean	std dev.	U	Sig. (2-tailed)	mean	std dev.	U	Sig. (2-tailed)
MxL	28	0.46	1.15	85.5	p = 0.64	0.93	0.82	89.5	p = 0.78
MxDm	31	2.90	3.61	82.0	p = 0.15	3.16	3.38	100.5	p = 0.47
MnDm	31	0.61	4.42	116.0	p = 0.91	3.52	2.85	67.0	**p = 0.04**
MnCir	31	0.81	2.52	116.5	p = 0.93	1.94	1.83	116.5	p = 0.93
CirHd	18	0.47	2.79	32.0	p = 0.48	2.10	1.93	29.0	p = 0.33
MxTDm	16	1.33	2.37	23.0	p = 0.41	2.21	1.54	27.0	p = 0.68
MxSDm	26	0.57	2.64	64.0	p = 0.36	2.25	1.49	76.0	p = 0.76
EpBr	21	0.32	2.62	44.5	p = 0.48	1.99	1.75	52.5	p = 0.88
TCBr	15	2.35	3.41	27.0	p = 1.00	2.97	2.85	23.0	p = 0.69

Mean and standard deviation values rounded to two decimal places. Significant p-values highlighted in bold. Abbreviations used: MxL = maximum length, MxDm = maximum midshaft diameter, MnDm = minimum midshaft diameter, MnCir = minimum shaft circumference, CirHd = circumference of head, MxTDm = maximum transverse diameter of head, MxSDm = maximum sagittal diameter of head, EpBr = epicondylar breadth, TCBr = trochlea-capitulum breadth.

6.2.5. Individual asymmetry

To examine individual asymmetry in the Greenwich humeri, the percentage of the nine humerus measurements which were right-side dominant, left-side dominant and symmetrical was calculated for each individual in the sample. The results of this analysis are presented in Figure 6.15 (below) and indicate that the general trend is for the majority of individuals (71% or 22/31 individuals) to display a right-side dominant asymmetry across humeral measurements, compared to the 22.6% (7/31) of individuals who show left-side dominant asymmetry. While this pattern is similar to that found for the Greenwich metacarpals (Fig. 6.12) it is clearly different from the Greenwich phalanges (Fig. 6.13) where individuals were predominantly left-side dominant. When compared to the Écija humeral sample however (Fig. 5.15), the magnitude of individual right-side dominance is not as large for individuals from the Greenwich sample, which supports the general observation of reduced levels of asymmetry in this sample. Finally, it is worth keeping in mind that with only nine variables contributing to individual asymmetry scores, any conclusions drawn should be treated with caution.

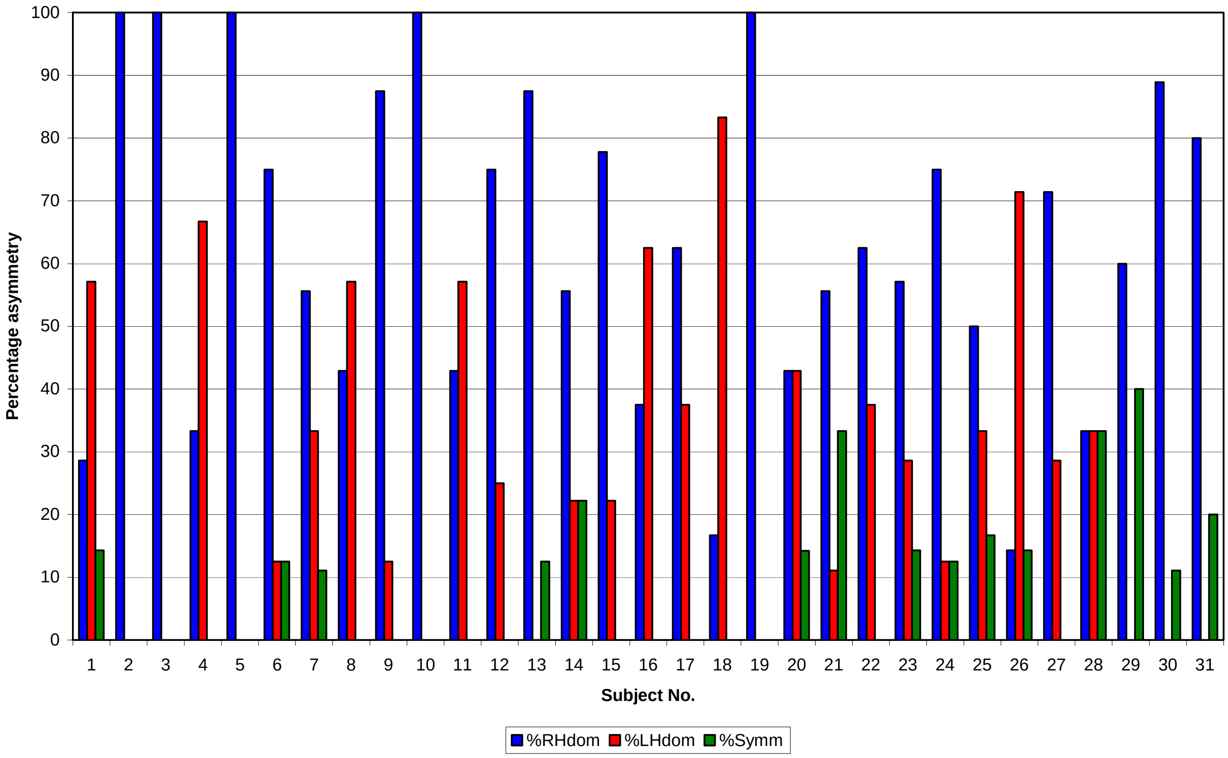


Figure 6.15. For each individual in the Greenwich sample, the percentage of right-side dominant, left-side dominant and symmetric scores for all humerus measurements.

6.2.6. Summary of humerus metric analysis

Analyses of asymmetry in the Greenwich humeri (section 6.2.3) indicate that while the overall trend in the sample is towards right-side dominant asymmetry, the scale of this asymmetry is reduced relative to that seen in the Écija humeri. This mirrors the pattern seen in the Greenwich hands, where a decrease in the strength of right-side dominance was also found (compared with the corresponding Écija sample) although the Greenwich hands also show a move towards left-side dominant asymmetry. This reduction in the magnitude of asymmetry is reflected in the findings of the Wilcoxon test (section 6.2.1) which identified significant left/right size differences for fewer than half of the humerus variables. As evidenced by the ANOVA test (section 6.2.2), age was found to have virtually no effect on the size of humerus properties. This same, limited, relationship was found for the effects of age on directional and absolute asymmetry in the humerus (section 6.2.4). Analysis of individual asymmetry (section 6.2.5) indicates that the majority of individuals show right-side dominant asymmetry across humerus measurements although once again, the magnitude of this asymmetry is reduced relative to individual asymmetry in the Écija humeri.

Overall, the results of these analyses strongly suggests that the occupation of the individuals in the Greenwich sample is likely to have reduced the degree of asymmetry observed, through more symmetrical loading of the upper limbs. As with the analysis of the Greenwich hands however, it is also possible that the increased overall age of the sample relative to the Écija humerus sample has resulted in a trend towards decreased levels of asymmetry in the Greenwich humeri (Stirland, 1993).

6.3. Musculoskeletal stress markers (MSM) in the hand

Assessment of MSM development in the Greenwich hands and humeri will provide an informative comparison with the corresponding analysis of MSM development in the Écija sample (section 5.3). The Greenwich metric analyses (sections 6.1 and 6.2) found that the level of asymmetry in these measurements was generally reduced relative to the Écija metric asymmetry (sections 5.1 and 5.2) and it is not clear at this stage whether these trends are also reflected in the Greenwich MSM data. By studying the expression of asymmetry in the Greenwich hands and humeri it will be possible to determine if such previously identified trends represent general differences between the metric and MSM methods, both in terms of their ability to identify asymmetry and the sensitivity of these bone properties to the asymmetry effects of mechanical loading. The Greenwich material poses an additional question regarding the influence of skeletal pathology on MSM development. The Greenwich collection displays a high degree of pathology (section 3.1.2) and it may be the case that this will increase the degree of MSM development identifiable in the material, as has been suggested in the case of individuals with ‘bone-forming’ diseases such as ankylosing spondylitis and DISH (diffuse idiopathic skeletal hyperostosis) (Henderson, 2008). The data analysis in this section will follow that outlined in section 5.3.

6.3.1. Asymmetry in hand MSM

Asymmetry in MSM expression in the Greenwich hands was assessed using the methods described in section 5.3.1 in order to calculate the percentage of individuals who had MSM scored as ‘present’ and ‘absent’ on both the left and right hands. To assess the degree of asymmetry in the sample the percentage of individuals scored as ‘present’ for left and right MSM was compared. As with the Écija analysis (section 5.3.1), data for the *flexor digitorum superficialis* 2-5 MSM and the *flexor digitorum profundus* 2-5 MSM were each considered as one data point. Digits 2 to 5 did not show any variation in MSM score for either muscle so data were collectively analysed. Figure 6.16 (below) presents the results of this analysis. Data from this analysis is presented in Table D.12 (Appendix D).

It can be seen from Figure 6.16 that there is variation between the MSM in terms of how often they are scored as ‘present’. However, there is also variation within the pairs of left and right MSM in how often they are identified as ‘present’. While many of the MSM exhibit the same trend found in the Écija hand MSM analysis (section 5.3.1) for very little difference between left and right MSM, a number of the Greenwich MSM show a clear left/right asymmetry (i.e. determined as a percentage difference greater than 10%). This can be seen for ODM, FDP, DI1 (right-side dominant) and PI4 (left-side dominant). Asymmetry is particularly pronounced for DI1, which shows a 34.1% difference between left and right scores. This pattern clearly contrasts that seen in the Écija hands (Fig. 5.16), where left/right differences were always below 15%. However, it is interesting to note that in the Écija sample, ODM was the MSM showing the largest left/right difference (13.2%).

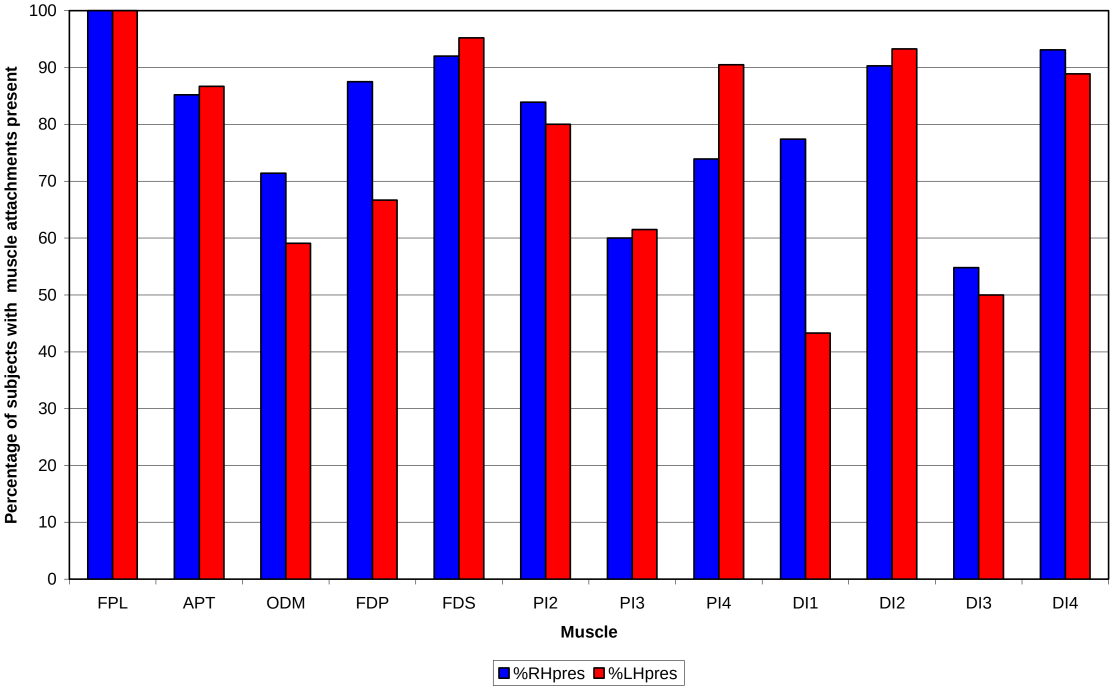


Figure 6.16. For each of the 12 MSM, the percentage scored as 'present' for the left hand (red) and the right hand (blue). Abbreviations used: FPL = flexor pollicis longus, APT = adductor pollicis (transverse head), ODM = oppenens digiti minimi, FDP = flexor digitorum profundus (2-5), FDS = flexor digitorum superficialis (2-5), PI = palmar interosseous, DI = dorsal interosseous. . Further data provided in Table D.12, Appendix D.

The numbers of right-side and left-side dominant MSM are similar to that seen in the Écija sample with 6 out of 12 MSM showing a right-side dominant asymmetry, 5 out of 12 MSM showing a left-side dominant asymmetry and 1 MSM showing symmetrical expression. This symmetrical value is for the FPL which is present in 100% of cases on both the left and right sides. The right-side dominant MSM in this sample are ODM, FDP, PI2, DI1, DI3 and DI4. With the exception of DI1, all of these MSM were found to be left-side dominant in the Écija sample. Why there should be a complete reversal in the pattern of asymmetry between the samples when the overall asymmetry direction remains the same is unclear, but suggests that there could be functional differences between the Greenwich and Écija samples in terms of muscle recruitment in the hands. However, a comparison of the asymmetry profiles of the MSM of prime movers and their synergists and antagonists, as in the previous MSM analyses (Table 5.13) finds no clear patterns linking the functionally-related MSM together. For example, FDS (prime mover) and its synergist, FDP, differ in both the degree of left/right asymmetry and the direction of their asymmetry.

As with the Écija hand sample there is variation between the MSM in terms of how often they are scored as 'present'. The FPL is distinctive, being scored as 'present' on 100% of occasions on both the left and right sides. This once more suggests that although this muscle is important for the function of the human thumb (Susman, 1988; Aiello & Dean, 1990; Marzke & Marzke, 2000), it not useful for assessments of asymmetry. At the other end of the scale, the PI3 and DI3 are scored as 'present' less frequently than the other MSM. Unlike the Écija sample (where all the PI muscles were rarely scored as 'present') this may not reflect a problem with identifying the MSM (unless it is a specific problem with identifying this particular MSM). Rather, it suggests that these muscles were recruited less often in the Greenwich sample. The functions of these muscles are flexion of the 4th digit (PI3) and abduction of the 3rd digit (DI3) (Table 3.4). It is interesting to note that in the analysis of asymmetry in the metric properties of the Greenwich metacarpals (section 6.1.3) metacarpals 3 and 4 showed an increased frequency of left-side dominant asymmetry relative to the other metacarpals. It is possible that reduced loading of the 3rd and 4th digits has led to increased left-side dominant asymmetry and reduced presence of MSM in this sample.

6.3.2. Significance testing

With a number of the hand MSM in Figure 6.16 showing clear left/right differences, a McNemar test was performed on the data to assess whether any of these differences were statistically significant. The McNemar test was the most appropriate test as the MSM data are related-samples nominal data (the χ^2 test is appropriate for between-samples data). Table 6.11 provides the results of this analysis and indicate that despite the observable asymmetry between some left and right MSM (Fig. 6.16), this difference is only statistically significant for one MSM, DI1 ($p<0.01$). Other differences are clearly non-significant. These results are in general agreement with the corresponding Écija analysis (section 5.3.2) which found no statistically significant differences between any of the left and right MSM. This suggests that asymmetry between any left and right MSM needs to be relatively large before it is identified as statistically significant. Indirectly, these findings supports the use of a nominal, presence/absence method for scoring hand MSM rather than an ordinal scaling approach such as that suggested by Hawkey & Merbs (1995), particularly when the sample size is small. An ordinal scaling approach, with its additional scoring levels, may be less sensitive to differences between left and right MSM.

Table 6.11. McNemar test of association between Greenwich left- and right-hand MSM.

MSM	N	Sig. (2-tailed)
FPL	-	-
APT	26	$p = 1.00$
ODM	16	$p = 1.00$
FDP	2	$p = 1.00$
FDS	18	$p = 1.00$
PI2	30	$p = 1.00$
PI3	25	$p = 1.00$
PI4	17	$p = 0.13$
DI1	30	**$p < 0.01$**
DI2	30	$p = 1.00$
DI3	28	$p = 1.00$
DI4	25	$p = 1.00$

N = comparisons performed. Significant p-values highlighted in bold. FPL was not included in the analysis as no individuals changed score between ‘present’ and ‘absent’ categories. Due to the low number of instances where score changed between categories, a binomial distribution was used instead of the χ^2 statistic. Abbreviations used: FPL = flexor pollicis longus, APT = adductor pollicis (transverse head), ODM = oppenens digiti minimi, FDP = flexor digitorum profundus (2-5), FDS = flexor digitorum superficialis (2-5), PI = palmar interosseous, DI = dorsal interosseous.

6.3.3. Age and hand MSM

A χ^2 test was performed to ascertain the presence of association between age and hand MSM score in the Greenwich sample. The results of this test are reported in Table D.13 (Appendix D). The χ^2 test found no statistically significant association between age and MSM score for any of the hand MSM, although right ODM was found to be approaching significance ($p = 0.06$). In the Écija analysis (section 6.3.4), right ODM was the only MSM that showed a significant association with age. Observed counts for the Greenwich ODM MSM indicate that ‘old’ adults are more likely to be scored as ‘present’ than younger adults. The implication, therefore, is that age influences the expression of the ODM muscle (on the right side at least) with its rugosity increasing with age. Why this muscle in particular should exhibit age-related change is unclear, but may be related to its involvement in the rotation of the 5th metacarpal (to bring it into opposition with the thumb) and flexion of the carpometacarpal joint (Table 3.4). The results of this analysis again contrast with the general MSM literature which has found clear age effects on MSM expression (e.g. Robb, 1998; Stirland, 1998; Wilczak, 2003; Molnar, 2006).

6.4. MSM in the humerus

Analysis of MSM asymmetry in the Greenwich hands (section 6.3) has shown that asymmetry in this sample is increased relative to that seen in the Écija hands (section 5.3), despite the general decrease in relative asymmetry found in the metric analyses (sections 6.1 and 6.2). These results suggest the possibility of a different relationship between MSM and metric asymmetry in the Greenwich sample than that seen in the Écija sample. Analysis of MSM expression in the Greenwich humeri will help to clarify the reasons for this trend, particularly the influence of age on MSM expression.

6.4.1. Asymmetry in humerus MSM

Asymmetry in the Greenwich humeral MSM was assessed using the methods outlined in section 5.4.1. Asymmetry was determined to be the percentage difference between the number of subjects with MSM scored as 'present' on the left side compared to the number scored as 'present' on the corresponding right side. Figure 6.17 presents the results of this analysis. Data from this analysis can be found in Table D.14 (Appendix D).

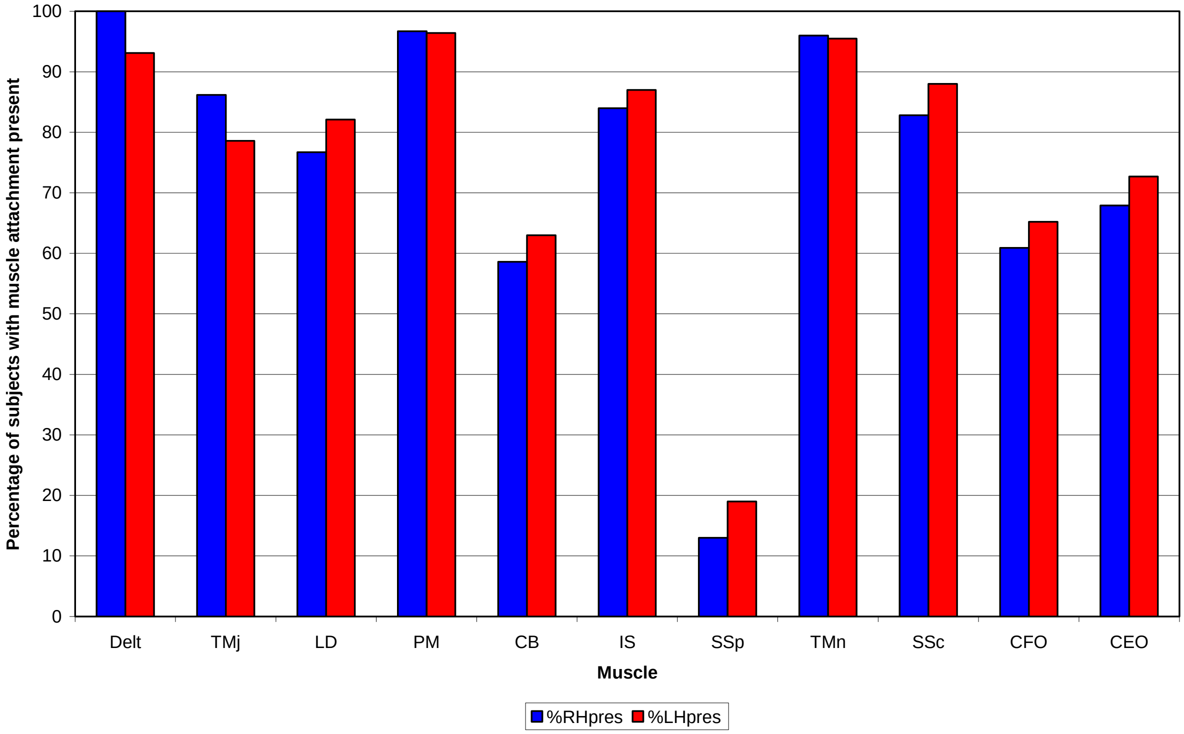


Figure 6.17. For each of the 11 humeral MSM, the percentage scored as 'present' for the left humerus (red) and the right humerus (blue). Abbreviations used: Delt = deltoid, TMj = teres major, LD = latissimus dorsi, PM = pectoralis major, CB = coracobrachialis, IS = infraspinatus, SSp = supraspinatus, TMn = teres minor, SSc = subscapularis, CFO = common flexor origin, CEO = common extensor origin. Further data available in Table D.14, Appendix D.

Looking at the results in Figure 6.17 there appears to be little difference between the left and right humeri in terms of the percentage of MSM scored as 'present'. The greatest difference is between left and right TMj (7.6%). This is clearly less than is seen in the Greenwich hand MSM (section 6.3.1), and also less than that found in the Écija humeri (section 5.4.1). This relative reduction in asymmetry in the

Greenwich humeral MSM is accompanied by a clear left-side dominance in asymmetry for 7 of 11 MSM (with 4/11 MSM showing right-side dominance). This is in contrast to the Écija humeri, where 10 of 11 MSM were right-side dominant. It does however follow the trend exhibited by the Greenwich hand MSM which were approximately evenly split between right- and left-side dominant asymmetry. In line with the metric analysis of the Greenwich humeri (section 6.2), the results in Figure 6.17 suggest that more symmetrical loading of the humeri in particular has reduced the overall level of asymmetry expressed in the humeri and increased the proportion of left-side dominant asymmetry found. It is also possible that a marked increase of left-arm loading in this sample has led to this pattern of humeral asymmetry.

Despite differences between the Greenwich and Écija samples in terms of direction and magnitude of asymmetry they display some similarities in the frequency with which certain MSM are scored as ‘present’. For example, left and right SSp are rarely scored as ‘present’ in both samples. Considering the differing age, sex and occupational profiles of the samples this suggests a degree of methodological influence on the results, with the relative ease or difficulty of identifying an MSM having a bearing on the frequency of its expression.

Finally, it is unclear how much effect individual muscle function has on MSM asymmetry. The muscles of the ‘rotator cuff’ (IS, SSp, TMm, SSc) are similar in the magnitude and direction of their asymmetry (although they clearly differ in the frequency of identification), as do the CFO and CEO of the distal humerus. However, comparison of prime movers with their synergists and antagonists (Table 5.16) does not identify clear patterns in asymmetry profiles.

6.4.2. Significance testing

A McNemar test (Table D.15, Appendix D) was performed to assess the degree of association between left and right humerus MSM scores. This test found perhaps unsurprisingly, that none of the left and right MSM pairs showed any statistically significant differences between their scores. This finding is in keeping with the results of the McNemar test on the Écija humerus MSM (section 5.4.2), which also found no statistically significant left/right MSM differences and the Greenwich hand MSM (section 6.3.2) where only one MSM variable (DI1) displayed a significant difference between left and right MSM scores.

6.4.3. Age and humerus MSM

A χ^2 test was performed to identify the presence of any associations between age and MSM development for the Greenwich humeri. This analysis (Table D.16, Appendix D) found no statistically significant association between age and MSM score for any of the humerus MSM (although right LD and right IS were approaching significance at p = 0.10). Despite the potential influence of age in increasing the frequency of identifying ‘present’ MSM this does not appear to have had an effect on the degree of asymmetry in the Greenwich sample, despite the presence of a number of significant associations between age and MSM score in the Écija humeri (section 5.4.4). It may be this difference between frequency and asymmetry in MSM that explains the discrepancy between the results of these age analyses and the findings of the wider MSM literature, which show a clear association between age and MSM development (e.g. Robb, 1998; Stirland, 1998; Wilczak, 2003; Molnar, 2006). It is also possible the general ‘elderly’ profile of the Greenwich sample, alongside high levels of skeletal pathology, has made it difficult to divide the sample into discrete age categories.

6.5. Summary of MSM analysis

The analyses of MSM asymmetry in the Greenwich hands (section 6.3) and humeri (section 6.4) show that asymmetry is more pronounced in the hands than the humeri. This is the reverse of the trend identified in the Écija MSM (sections 5.3 and 5.4) suggesting differences in the pattern of muscle recruitment in the hands and humeri in the Greenwich sample relative to the Écija sample. It is likely that the muscular strain and mechanical loading typical of the occupations of the Greenwich Naval Hospital residents have led to increased symmetry in the sample, reflected in the reduced levels of right-side dominant asymmetry in the Greenwich metric and MSM analyses (relative to Écija) and also the increased proportion of left-side dominant asymmetries in this sample. The increased asymmetry in hand MSM relative to humerus MSM in the Greenwich sample supports the notion that the humerus is more liable to be symmetrical (as a result of the recruitment of the arms in strenuous tasks) relative to the hands, which are likely to be engaged in less ‘heavy duty’ tasks which do not promote symmetry (Steele, 2000a). Despite this increased asymmetry in the hands, only one of the left/right asymmetries identified was found to be statistically significant (DI1). No significant associations were found between age and any of the MSM. While this at first seems at odds with the MSM literature, previous studies have tended to look at differences in degree of MSM expression rather than MSM asymmetry. It is possible that using a presence/absence methodology on what is a relatively small sample may not identify the full extent of age differences present. It is also possible the general ‘elderly’ status of the sample makes it difficult to identify clear age categories. Finally, the highly pathological nature of the sample may have increased the degree of MSM development identifiable across the sample, blurring the boundaries between age categories. Although individuals with debilitating upper limb pathologies were excluded from analysis, those with ‘bone-forming’ diseases (e.g. in the spine and pelvis) may remain and it has been suggested that these individuals are likely to show increased MSM development relative to ‘healthy’ individuals (Henderson, 2008).

Overall, despite the trend for reduced MSM asymmetry and metric asymmetry in the Greenwich sample relative to the Écija sample, metric asymmetry is more readily identifiable than that of MSM asymmetry in both samples. This suggests that the methods by which asymmetry is assessed are likely to influence, to a certain extent, the magnitude of the asymmetry expressed in a particular sample.

Chapter 7. Non-Human Primate Data Analysis

The analyses of modern human upper limb bilateral asymmetry in the preceding chapters highlight interesting differences in the expression of asymmetry between the hands and the humeri. They also highlight important differences between the methods by which asymmetry was assessed in these samples. Analysis of metric and MSM asymmetry in the hands and humeri of great apes will provide an opportunity to explore these trends further. It is assumed that the great ape upper limb will exhibit a lower degree of asymmetry compared with the human upper limb, as a result of the functional constraints of locomotion (leading to more symmetrical use of the upper limb in great apes) (Auerbach & Ruff, 2006; Drapeau, 2008). For this reason, the great ape samples measured in the current study serve as control groups and permit further examination of the relative influences methodology and anatomy on asymmetry profiles. The following analyses will also provide further quantification of the nature of upper limb bilateral asymmetry in great apes, a topic that to date has received relatively little attention compared to that of human groups (Sarringhaus *et al.*, 2005; Hopkins, 2008).

The great ape skeletal collections housed at the Powell-Cotton Museum in Birchington, Kent are described in more detail in section 3.1.3. From this collection, a total of 21 wild-shot adult *Pan troglodytes schweinfurthii* and 21 *Gorilla gorilla gorilla* skeletons were selected for study. Adult status was determined on the basis of complete postcranial fusion. Individuals were tentatively assigned to ‘young’, ‘middle’ and ‘old’ adult categories on the basis of information from the museum catalogue. Due to the small sample sizes and issues with the accuracy of the age category assignments, it was decided not to include age as a variable for any further analysis. The museum catalogue holds incomplete age information for individual specimens and it was not clear how well great ape age categories mapped onto to the human age categories used in the previous analyses. It was also possible that small sample sizes in each potential great ape age category would hamper statistical testing. Therefore, age was excluded as a variable to remove potential erroneous effects.

The non-human primate data was analysed separately for chimpanzees and gorillas, following the methods outlined for the Écija (Ch. 5) and Greenwich (Ch. 6) samples. The structure of the data analyses follows that of the previous human results chapters. Chimpanzee data are dealt with first: sections 7.1 (hands) and 7.2 (humeri) provide the results of the metric analyses, with sections 7.3 and 7.4 containing the results of the MSM analyses of the chimpanzee hands and humeri, respectively. The gorilla data analysis follows on from this. Results of the metric analyses are presented in sections 7.5 (hands) and 7.6 (humeri) and results from the MSM analyses can be found in sections 7.7 (hands) and 7.8 (humeri).

7.1. Chimpanzee metacarpal and phalanx metric analysis

Table 7.1 provides the age and sex profile for the chimpanzee sample. However as discussed above, age was not used as a variable in this analysis, although a tentative assignment has been made for the purposes of the table.

Table 7.1. Age and sex profile of chimpanzee sample.

	Young adult	**Middle adult**	**Old adult**	**Total**
Male	2	3	4	**9**
Female	1	6	5	**12**
Total	**3**	**9**	**9**	Total sample: **21**

Descriptive statistics for the metacarpals and phalanges, split by sex, can be found in Table E.1, Appendix E. Histograms and p-p plots confirmed the normal distribution of the data in this sample. Box-and-whisker plots identified the presence of a number of outliers. When these outliers were checked against the original data, it was confirmed that they were not a result of input error or caused by pathology or unusual morphology. Therefore none of the scores was deleted and all were included in subsequent analyses. During the conservation process, the skins were removed from the wild-shot specimens in one piece with the distal phalanges remaining inside the skin. As a result, no distal phalanges were available for study in the chimpanzee collection.

7.1.1. Significance testing

A Wilcoxon test was performed to assess whether there were any of the left and right metacarpal measurements showed significant size differences. Due to the presence of outliers in the metacarpal sample, the parametric t-test was not suitable and the non-parametric Wilcoxon test was used instead. Table 7.2 (below) presents the results of this analysis and it can be seen that there are very few statistically significant differences between the left and right metacarpal measurements in this sample. Of the 25 variables only 4 were found to show significant side differences in terms of size (mc3DP, mc4DP, mc4PB, mc3DB) indicating it is metacarpal 3 and 4 that are the most asymmetric in this sample. This may reflect the increased loads borne by the third and fourth digits during knuckle-walking (Aiello & Dean, 1990), although it is the phalanges that are directly load-bearing. Interestingly, a trend for asymmetry in metacarpal 3 and 4 measurements was also found for the Greenwich metacarpals (section 6.1.1). A comparison of the mean values in Table 7.2 shows that for the majority of variables (19/25) the right-side measurement is bigger than the left. This general lack of significant size differences contrasts with both of the modern human samples. The majority of Écija metacarpal variables (section 5.1.1) and approximately half of the Greenwich metacarpal variables showed significant left/right differences. The results reported in Table 7.2 support the assumption that the chimpanzee sample would show a lesser degree of size asymmetry compared to the modern human samples due to the locomotor constraints on great ape upper limb morphology.

Table 7.2. Wilcoxon test results for the combined-sex chimpanzee metacarpal sample.

Measurement	Side	N	Mean	Std dev.	Sig. (2-tailed)
mc1L	L	20	39.54	2.48	$p = 0.82$
	R	21	39.67	2.61	
mc2L	L	20	86.78	4.01	$p = 0.31$
	R	21	87.31	4.18	
mc3L	L	21	85.88	3.91	$p = 0.28$
	R	21	86.10	3.81	
mc4L	L	20	80.72	4.13	$p = 0.59$
	R	21	81.03	4.24	
mc5L	L	20	74.03	3.90	$p = 0.46$
	R	20	74.00	3.73	
mc1RU	L	20	8.35	1.02	$p = 0.66$
	R	21	8.35	0.86	
mc2RU	L	21	8.00	0.62	$p = 0.75$
	R	21	7.92	0.60	
mc3RU	L	21	8.47	0.64	*$p = 0.08$*
	R	21	8.59	0.53	
mc4RU	L	21	7.70	0.65	$p = 0.65$
	R	21	7.67	0.60	
mc5RU	L	20	7.24	0.74	$p = 0.48$
	R	20	7.36	0.79	
mc1DP	L	20	6.48	0.82	$p = 0.60$
	R	21	6.66	1.10	
mc2DP	L	21	8.11	0.80	$p = 0.32$
	R	21	8.25	0.83	
mc3DP	L	21	8.93	0.64	**$p = 0.02$**
	R	21	9.09	0.61	
mc4DP	L	21	7.85	0.64	**$p = 0.02$**
	R	21	8.10	0.63	
mc5DP	L	20	6.16	0.62	*$p = 0.09$*
	R	20	6.36	0.58	
mc1PB	L	20	10.71	0.95	$p = 0.92$
	R	21	10.79	0.94	
mc2PB	L	21	12.69	0.87	$p = 0.27$
	R	21	12.81	0.75	
mc3PB	L	21	13.56	0.88	$p = 0.46$
	R	21	13.50	0.81	
mc4PB	L	21	10.47	0.86	**$p < 0.01$**
	R	21	10.72	0.82	
mc5PB	L	20	9.34	1.02	$p = 0.22$
	R	20	9.56	1.11	

Measurement	Side	N	Mean	Std dev.	Sig. (2-tailed)
mc1DB	L	20	9.15	0.70	p = 0.79
	R	21	9.21	0.74	
mc2DB	L	20	12.05	0.63	p = 0.27
	R	21	12.20	0.75	
mc3DB	L	21	13.25	0.91	**p = 0.05**
	R	21	13.38	0.86	
mc4DB	L	20	11.96	0.78	p = 0.68
	R	21	12.09	0.81	
mc5DB	L	20	9.51	0.81	p = 0.39
	R	19	9.47	0.76	

Mean and standard deviation values rounded to two decimal places. Significant p-values highlighted in bold. P-values approaching significance (between 0.055 and 0.1) highlighted in italics. Abbreviations used: mc*L = metacarpal length, mc*RU = radio-ulnar midshaft diameter, mc*DP = dorso-palmar midshaft diameter, mc*PB = proximal breadth, mc*DB = distal breadth. Asterisk (*) denotes metacarpal number.

A Wilcoxon test was also performed to assess left/right side differences in chimpanzee phalanx length measurements. Table 7.3 provides the results of this analysis.

Table 7.3. Wilcoxon test results for the combined-sex chimpanzee phalanx sample.

Measurement	Side	N	Mean	Std dev.	Sig. (2-tailed)
pp1L	L	20	25.18	2.36	p = 0.17
	R	21	24.87	2.82	
pp2L	L	21	49.16	2.98	p = 0.31
	R	21	48.96	3.05	
pp3L	L	20	57.24	2.73	p = 0.84
	R	21	57.40	2.80	
pp4L	L	21	54.12	2.98	p = 0.37
	R	21	53.97	3.03	
pp5L	L	21	42.03	2.41	p = 0.81
	R	21	41.96	2.61	
ip2L	L	20	30.59	2.10	*p = 0.10*
	R	21	30.90	2.20	
ip3L	L	21	41.14	2.48	p = 0.99
	R	21	41.15	2.44	
ip4L	L	21	38.05	2.43	p = 0.27
	R	19	38.02	2.29	
ip5L	L	20	26.71	2.37	p = 0.62
	R	21	26.99	2.34	

Mean and standard deviation values rounded to two decimal places. P-values approaching significance (between 0.055 and 0.1) highlighted in italics. As a result of the conservation process, no distal phalanges were available for study. Abbreviations used: pp*L = proximal phalanx length, ip*L = intermediate phalanx length. Asterisk (*) denotes phalanx number.

The results of the Wilcoxon test in Table 7.3 show no statistically significant size differences between left and right phalanx length measurements. A comparison of mean values indicates that 5 of the 9 phalanx measurements are larger on the left side suggesting a degree of symmetry in size between the phalanges. These findings follow the trend identified in the Greenwich and Écija phalanges. Due to the careful preservation and curation of the Powell-Cotton skeletal collections the siding of the phalanges in this sample can be considered secure. Therefore, the reduced size asymmetry seen in the phalanges relative in the metacarpals in both the chimpanzee and human samples suggests a genuine difference in the degree of asymmetry in these bones. However, as discussed previously (section 6.1.1), it is possible that the phalanx length measurement may not reflect the full extent of asymmetry in this bone.

7.1.2. Analysis of Variance (ANOVA)

A one-way ANOVA was performed to assess the effects of sex on hand bone measurements in the chimpanzee sample. This ANOVA was suitable for the purposes of the analysis due to the exclusion of age as a variable. Table 7.4 presents the results of this analysis for the metacarpals.

Table 7.4. One-way ANOVA for the effect of sex on chimpanzee metacarpal variables.

Measurement	Side	Sex	N	Mean	F	Sig. (2-tailed)
mc1L	L	male	8	39.68	0.04	p = 0.85
		female	12	39.45		
	R	male	9	40.01	0.27	p = 0.61
		female	12	39.41		
mc2L	L	male	8	87.63	0.58	p = 0.46
		female	12	86.22		
	R	male	9	88.87	2.33	p = 0.14
		female	12	86.14		
mc3L	L	male	9	87.40	2.58	p = 0.13
		female	12	84.73		
	R	male	9	87.70	3.09	*p = 0.10*
		female	12	84.89		
mc4L	L	male	8	82.23	1.86	p = 0.19
		female	12	79.71		
	R	male	9	82.87	3.27	*p = 0.09*
		female	12	79.66		
mc5L	L	male	8	75.56	2.19	p = 0.16
		female	12	72.74		
	R	male	8	75.89	3.95	*p = 0.06*
		female	12	73.01		

Measurement	Side	Sex	N	Mean	F	Sig. (2-tailed)
mc1RU	L	male	8	8.78	2.58	$p = 0.13$
		female	12	8.06		
	R	male	9	8.61	1.51	$p = 0.23$
		female	12	8.15		
mc2RU	L	male	9	8.33	5.59	**$p = 0.03$**
		female	12	7.75		
	R	male	9	8.30	8.67	**$p < 0.01$**
		female	12	7.63		
mc3RU	L	male	9	8.87	8.45	**$p < 0.01$**
		female	12	8.17		
	R	male	9	8.93	9.54	**$p < 0.01$**
		female	12	8.33		
mc4RU	L	male	9	8.16	12.26	**$p < 0.01$**
		female	12	7.35		
	R	male	9	8.11	14.16	**$p < 0.01$**
		female	12	7.33		
mc5RU	L	male	8	7.83	14.65	**$p < 0.01$**
		female	12	6.84		
	R	male	8	7.94	10.91	**$p < 0.01$**
		female	12	6.97		
mc1DP	L	male	8	7.11	13.01	**$p < 0.01$**
		female	12	6.05		
	R	male	9	7.22	4.99	**$p = 0.04$**
		female	12	6.23		
mc2DP	L	male	9	8.61	8.34	**$p < 0.01$**
		female	12	7.74		
	R	male	9	8.61	3.31	*$p = 0.09$*
		female	12	7.98		
mc3DP	L	male	9	9.21	3.35	*$p = 0.08$*
		female	12	8.73		
	R	male	9	9.29	1.82	$p = 0.19$
		female	12	8.93		
mc4DP	L	male	9	8.00	0.82	$p = 0.38$
		female	12	7.74		
	R	male	9	8.11	0.00	$p = 0.95$
		female	12	8.09		
mc5DP	L	male	8	6.35	1.29	$p = 0.27$
		female	12	6.03		
	R	male	8	6.51	0.97	$p = 0.34$
		female	12	6.25		
mc1PB	L	male	8	10.80	0.11	$p = 0.74$
		female	12	10.65		

	Side	Sex	N	Mean	F	Sig. (2-tailed)
	R	male	9	10.92	0.30	p = 0.59
		female	12	10.69		
mc2PB	L	male	9	13.33	14.66	**p < 0.01**
		female	12	12.20		
	R	male	9	13.26	7.18	**p = 0.02**
		female	12	12.48		
mc3PB	L	male	9	13.76	0.79	p = 0.38
		female	12	13.41		
	R	male	9	13.82	2.59	p = 0.12
		female	12	13.27		
mc4PB	L	male	9	10.78	2.10	p = 0.16
		female	12	10.24		
	R	male	9	10.91	0.81	p = 0.38
		female	12	10.58		
mc5PB	L	male	8	9.68	1.51	p = 0.24
		female	12	9.11		
	R	male	8	9.94	1.64	p = 0.22
		female	12	9.30		
mc1DB	L	male	8	9.30	0.59	p = 0.45
		female	12	9.05		
	R	male	9	9.57	4.16	*p = 0.06*
		female	12	8.95		
mc2DB	L	male	8	12.23	1.08	p = 0.31
		female	12	11.93		
	R	male	9	12.56	3.97	*p = 0.06*
		female	12	11.94		
mc3DB	L	male	9	13.67	3.83	*p = 0.07*
		female	12	12.93		
	R	male	9	13.81	4.73	**p = 0.04**
		female	12	13.05		
mc4DB	L	male	8	12.26	2.13	p = 0.16
		female	12	11.76		
	R	male	9	12.43	3.11	*p = 0.09*
		female	12	11.83		
mc5DB	L	male	8	9.86	2.84	p = 0.11
		female	12	9.27		
	R	male	7	9.74	1.50	p = 0.24
		female	12	9.31		

Mean and standard deviation values rounded to two decimal places. Significant p-values highlighted in bold. P-values approaching significance (between 0.055 and 0.1) highlighted in italics. Abbreviations used: mc*L = metacarpal length, mc*RU = radio-ulnar midshaft diameter, mc*DP = dorso-palmar midshaft diameter, mc*PB = proximal breadth, mc*DB = distal breadth. Asterisk (*) denotes metacarpal number.

It can be seen from Table 7.4 that there is a limited effect of sex on metacarpal measurement size with only 14 of the 25 variables showing a statistically significant effect. An additional 9 variables were found to be approaching significance. The effect of sex is most prominent for radio-ulnar diameter measurements. It is possible that the significant sex differences found for radio-ulnar diameter reflect increased development of the *dorsal interossei* muscles located in this region and which can influence the dimensions of this measurement. Section 7.3 will explore the expression of MSM in the chimpanzee hands in more detail. Metacarpal length and distal breadth measurements are those variables most often approaching statistical significance in this sample.

A comparison of mean values in Table 7.4 indicates that males are larger than females across all measurements. It can be seen that the effect of sex on the chimpanzee metacarpal size is reduced compared with the Écija metacarpal sample (section 5.1.2). This finding is likely explained by the observation that the level of sexual dimorphism is not high in *Pan troglodytes* (relative to the other great apes *Pongo* and *Gorilla*) but similar to that that seen in *H. sapiens* (Fleagle, 1999).

A further one-way ANOVA test was performed to assess the effect of sex on chimpanzee phalanx length (see Table E.2, Appendix E). This analysis found no significant effects of sex for any of the phalanx length measurements. As with the metacarpals in Table 7.4 this pattern contrasts with the findings of the Écija phalanx ANOVA (Table 5.5) which found a significant sex effect for the majority of phalanx variables. This again seems to reflect the absence of strong sexual dimorphism in chimpanzees. In contrast to the chimpanzee metacarpal ANOVA, a comparison of the mean values in Table E.2 shows that females have larger phalanx length measurements than males for 13 of the 18 phalanx variables. Why this trend exists is unclear but may be a consequence of the low levels of sexual dimorphism in this species. However, the small sample sizes in the analysis must be borne in mind when drawing conclusions based on these results.

7.1.3. Asymmetry in the metacarpals and phalanges

The Wilcoxon tests in section 7.1.1 indentified few significant size differences between the left and right metacarpals and phalanges. This suggests a generally low level of asymmetry in this sample. To understand this trend in the chimpanzee hands in more detail, the difference between each left and right measurement was calculated as a percentage asymmetry using the equations described in section 5.1.3. The results of directional and absolute asymmetry equations were combined to provide an asymmetry profile for each of the metacarpal measurements and presented in Figures 7.1 to 7.5 (below). The data from this analysis can be found in Table E.3 (Appendix E).

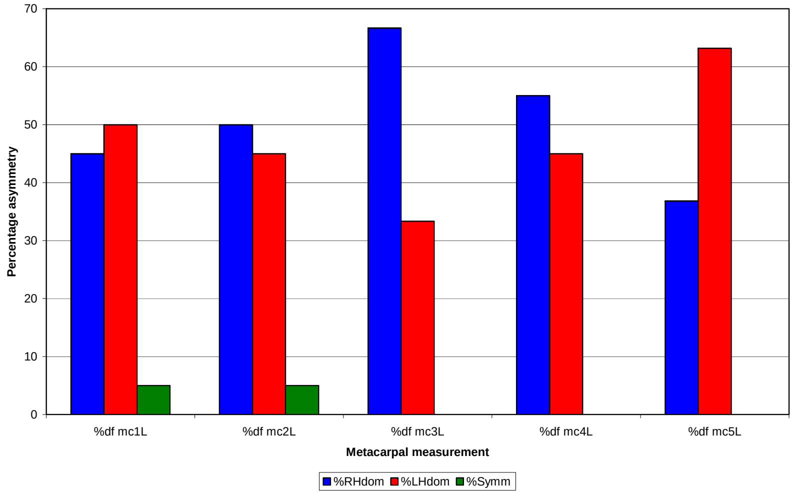


Figure 7.1.Percentage of right- and left-side dominant and symmetric individuals for chimpanzee metacarpal length (mc*L).

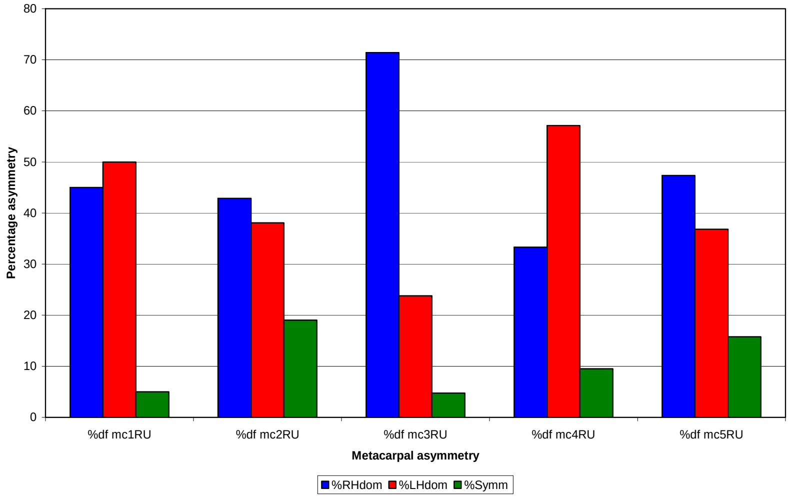


Figure 7.2.Percentage of right- and left-side dominant and symmetric individuals for chimpanzee metacarpal radio-ulnar diameter (mc*RU).

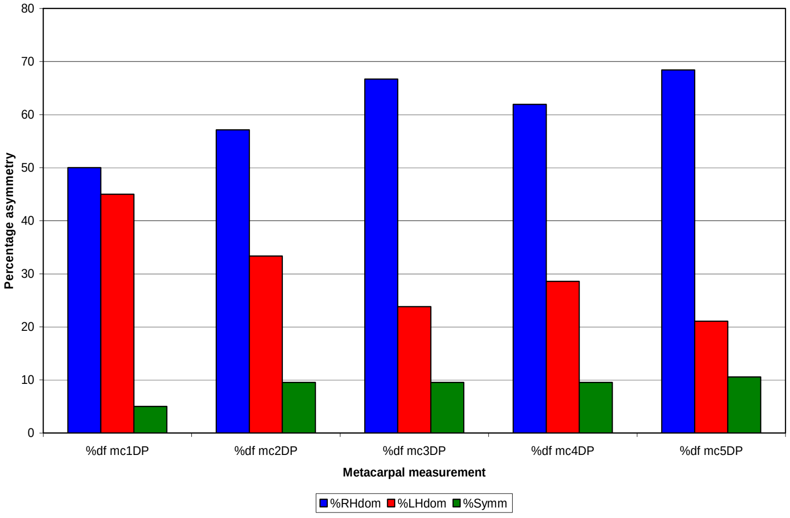


Figure 7.3. Percentage of right- and left-side dominant and symmetric individuals for chimpanzee metacarpal dorso-palmar diameter (mc*DP).

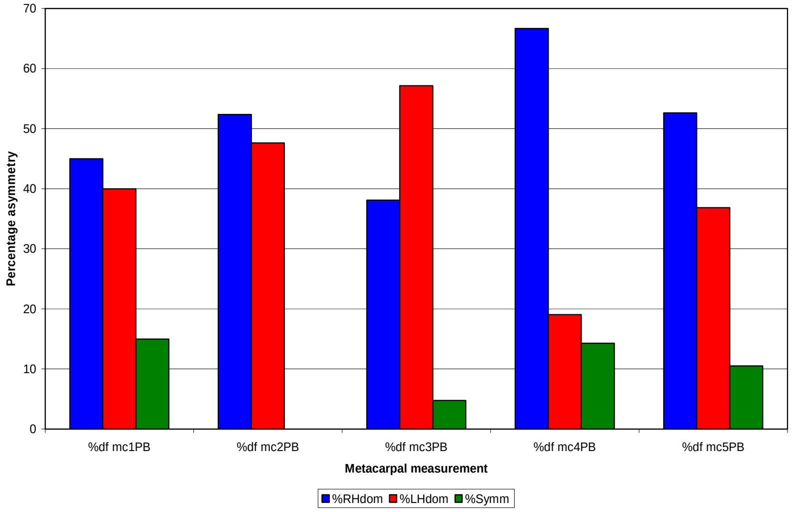


Figure 7.4. Percentage of right- and left-side dominant and symmetric individuals for chimpanzee metacarpal proximal breadth (mc*PB).

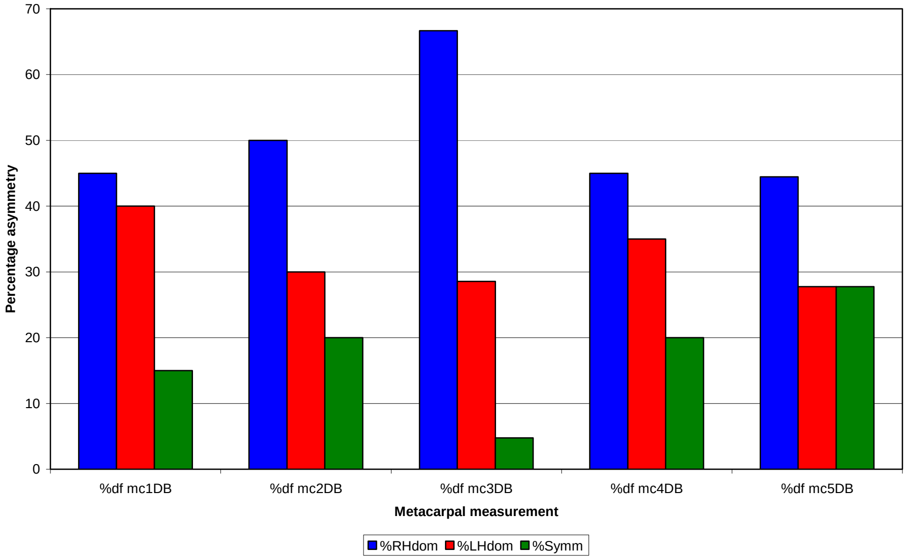


Figure 7.5. Percentage of right- and left-side dominant and symmetric individuals for chimpanzee metacarpal distal breadth (mc*DB). Further data available in Table E.3, Appendix E.

In Figures 7.1 to 7.5 it appears that while there is variation between the metacarpal variables in terms of their asymmetry, the magnitude of this asymmetry is generally low when compared to the Écija metacarpals (section 5.1.3) but similar to that seen in the Greenwich metacarpals (section 6.1.3).The magnitude of chimpanzee metacarpal asymmetry ranges from 42.9% to 71.4% with only one variable (mc3RU) displaying asymmetry scores greater than 70%. This is fewer than for the Greenwich metacarpals where 7 variables were identified as having greater than 70% asymmetry scores. Although the general trend in the chimpanzee sample is towards right-side dominant asymmetry, 5 of the 20 variables exhibit a left-side dominant asymmetry (mc1L, mc5L, mc1RU, mc4RU, mc3PB). This is the same proportion as identified in the Greenwich sample. The chimpanzee left-side dominant values do not appear to favour a particular metacarpal, but are focused on the metacarpal length and radio-ulnar diameter measurements. Metacarpal length also displayed left-side dominant asymmetry in the Greenwich metacarpals.

Examining the pattern of asymmetry distribution across the metacarpal measurements, asymmetry appears to be at its lowest for metacarpal 1 measurements with subsequent peaks at the metacarpal 3 measurements. To examine this trend more closely the data used to construct Figures 7.1 to 7.5 were re-plotted to produce graphs combining the various measurements for each individual metacarpal. The results of this analysis are presented in Figures 7.6 to 7.10 (below).

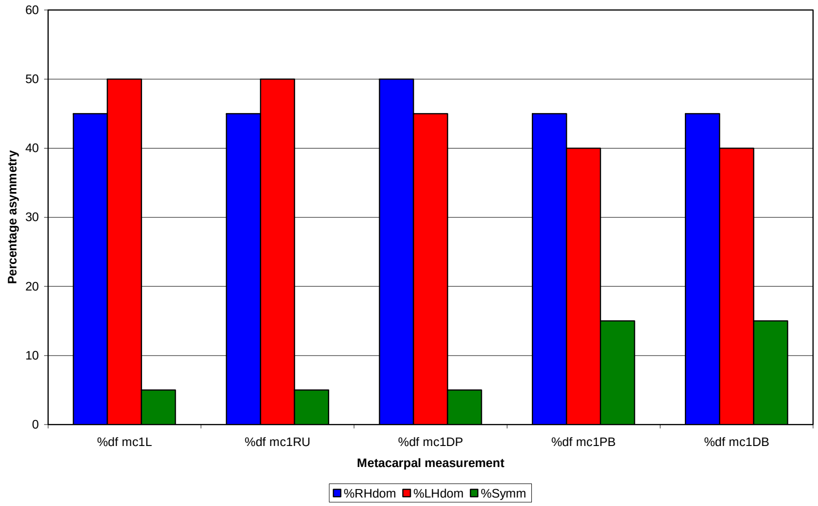


Figure 7.6. Asymmetry values for each chimpanzee metacarpal 1 measurement (length, radio-ulnar diameter, dorso-palmar diameter, proximal breadth and distal breadth).

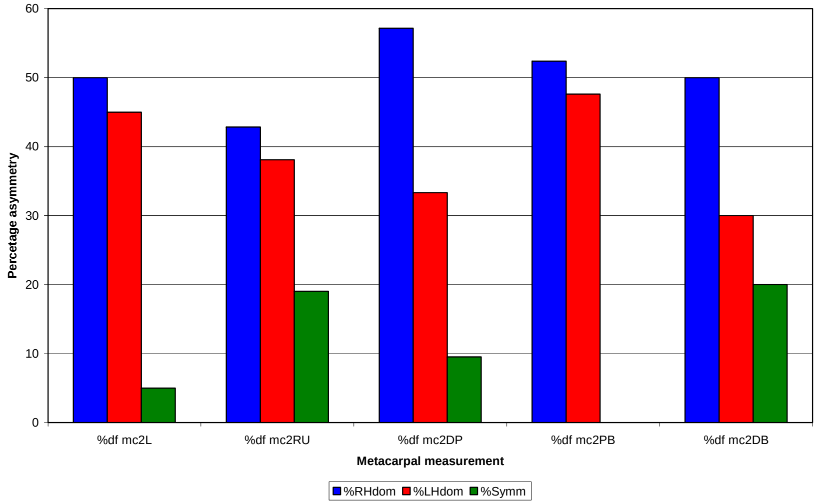


Figure 7.7. Asymmetry values for each chimpanzee metacarpal 2 measurement (length, radio-ulnar diameter, dorso-palmar diameter, proximal breadth and distal breadth).

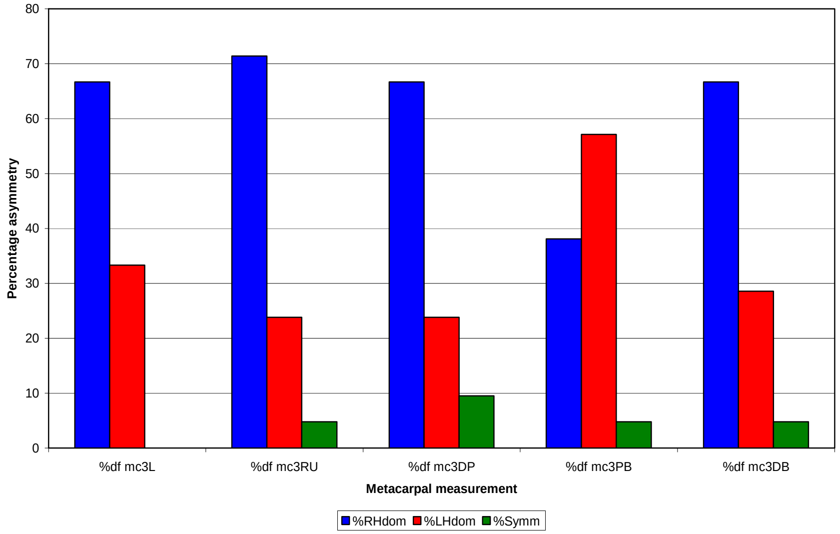


Figure 7.8. Asymmetry values for each chimpanzee metacarpal 3 measurement (length, radio-ulnar diameter, dorso-palmar diameter, proximal breadth and distal breadth).

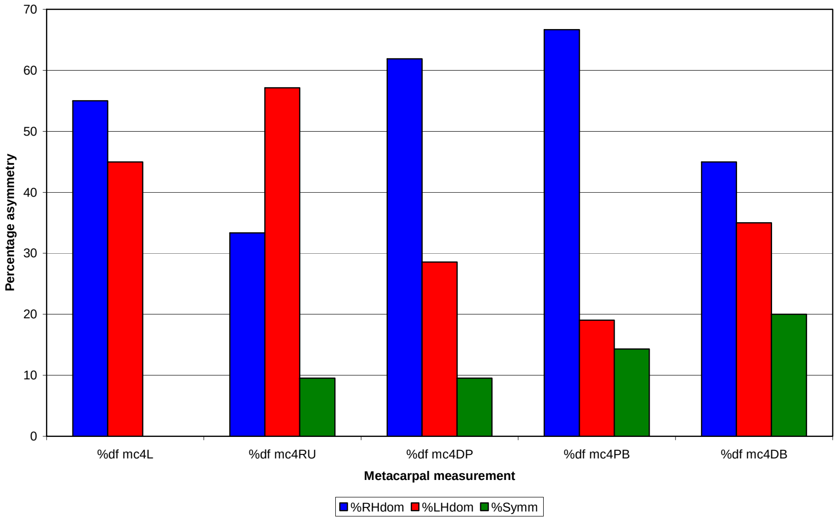


Figure 7.9. Asymmetry values for each chimpanzee metacarpal 4 measurement (length, radio-ulnar diameter, dorso-palmar diameter, proximal breadth and distal breadth).

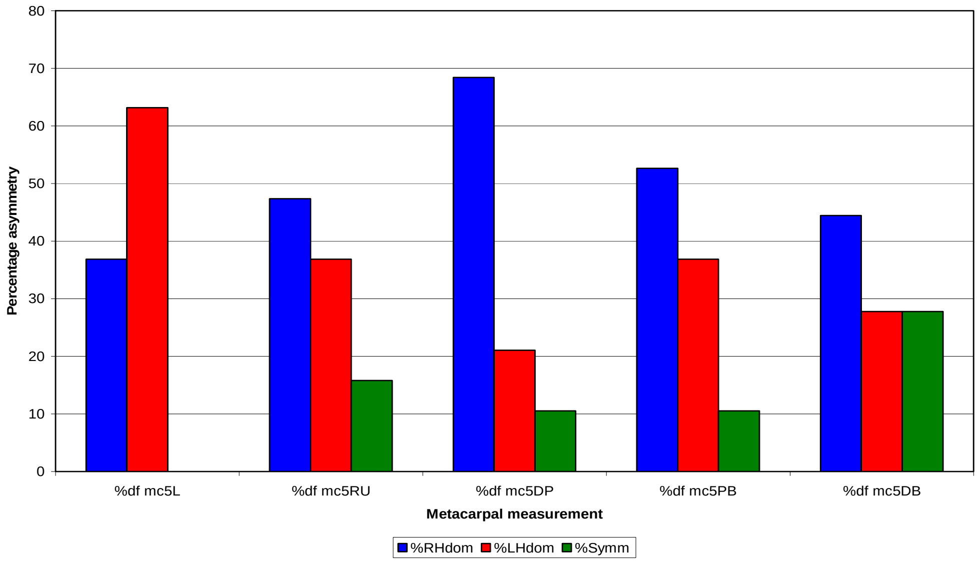


Figure 7.10. Asymmetry values for each chimpanzee metacarpal 5 measurement (length, radio-ulnar diameter, dorso-palmar diameter, proximal breadth and distal breadth). Further data available in Table E.3, Appendix E.

Figures 7.6 to 7.10 suggest that, on the whole, there is little within-metacarpal variation in asymmetry. Differences between the metacarpals are more readily identifiable. As indicated in Figures 7.1 to 7.5 metacarpal 1 has a low level of asymmetry (less than 50% in all cases). This was also the case for Écija metacarpal 1 asymmetry (Fig. 5.6). The move towards symmetry in the chimpanzee metacarpal 1 is reflected in the fact that two of the measurements (mc1L and mc1RU) display a slight left-side dominance. That the chimpanzee thumb should show much less bilateral asymmetry compared to the human samples is to be expected, given the unique role of the human thumb in manipulatory activities (Aiello, 1994; Susman, 1994; Marzke, 1997). It can be seen from Figure 7.8 that metacarpal 3 has the highest overall levels of asymmetry. This suggests this bone is subject to particularly asymmetric loading relative to the other metacarpals, although the reasons why this should be the cases in this sample are unclear. It is interesting to note that metacarpal 2 is the only metacarpal for which each variable is right-side dominant. Strong right-side asymmetry for second metacarpal subperiosteal area was identified by Sarringhaus *et al.* (2005). This suggests that there is perhaps some directional asymmetry acting on this bone, promoting a shift to the right side.

An asymmetry profile was created for the chimpanzee proximal and intermediate phalanx length measurements. The results are presented in Figure 7.11 (below). Data from this analysis can be found in Table E.4 (Appendix E). Similar to what was found in Figures 7.1 to 7.10, Figure 7.11 indicates that there is a low degree of asymmetry in chimpanzee phalanx length, with no variable displaying an asymmetry score greater than 60%. This mirrors the trend identified in the Écija phalanges (Fig. 5.11), although the magnitude of asymmetry in the chimpanzee phalanges is slightly reduced relative to that seen in the Greenwich phalanges (Fig. 6.11). It is clear from Figure 7.11 that there is a left-side dominant asymmetry in phalanx length with only three variables (pp5L, ip2L, ip4L) showing right-side dominant asymmetry. The Greenwich phalanges were found to show a slight predominance of left-side dominant asymmetry (for 5 of the 9 variables). In contrast, the Écija phalanges were all right-side dominant in their asymmetry.

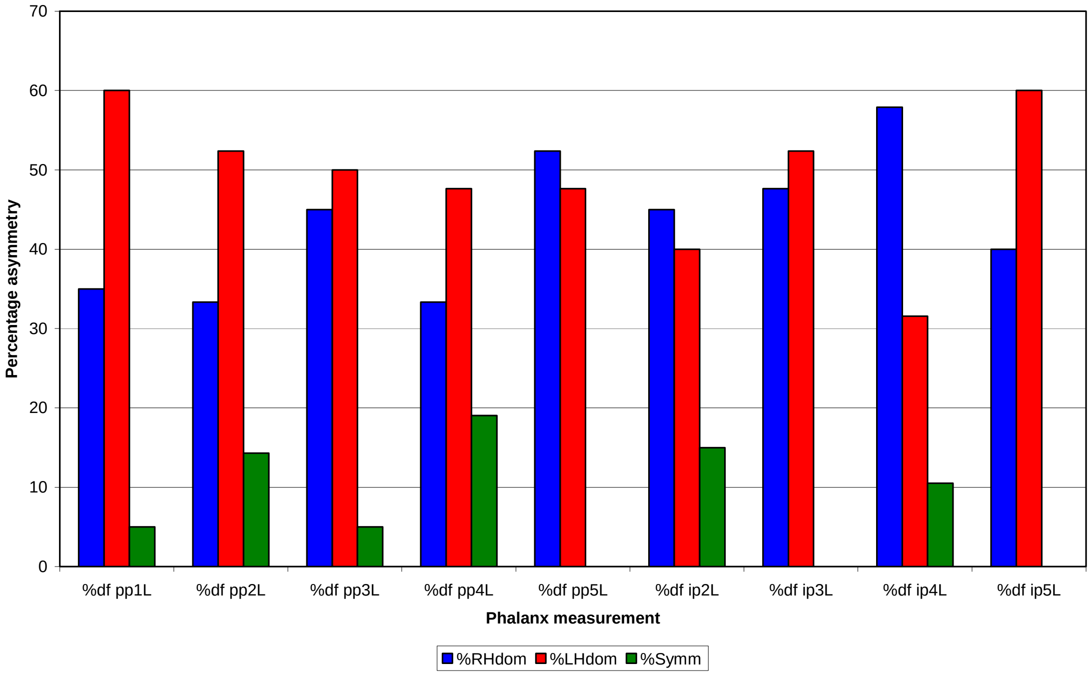


Figure 7.11. Asymmetry values for each chimpanzee phalanx length measurement. Due to the nature of the conservation process in this sample, no distal phalanges were available for study. Further data available in Table E.4, Appendix E.

Comparing the asymmetry seen in Figure 7.11 with that of the chimpanzee metacarpals shows a disparity between metacarpal and phalanx asymmetry. For example, pp1L has a higher degree of asymmetry (60%) than seen in any of the metacarpal 1 measurements (largest asymmetry = 50%). The strong mc3 asymmetry (Fig. 7.8) is not reflected in either pp3L or ip3L. Additionally, it can be seen that there is contrasting asymmetry between the proximal and intermediate phalanges, i.e. pp2L is left-side dominant while ip2L is right-side dominant, pp5L is right-side dominant but ip5L is left-side dominant. The analysis of chimpanzee phalanx asymmetry supports the presence of clear differences in the expression of asymmetry between the metacarpals and phalanges which is observable even when the overall levels of asymmetry are low.

7.1.4. Sex effects on asymmetry in the metacarpals and phalanges

The ANOVAs in section 7.1.2 indicate that there is little sexual dimorphism in the chimpanzee sample in terms of metacarpal and phalanx size. To assess the degree to which males and females differed in the direction and size of asymmetry, a Mann-Whitney U test was performed on the data. Table 7.5 (below) presents the results of this analysis for the chimpanzee metacarpals.

Table 7.5. A Mann-Whitney U test of the effects of sex on directional and absolute asymmetry for each of the chimpanzee metacarpal measurements.

Measurement	N	Directional asymmetry (cf. Steele & Mays, 1995)				Absolute asymmetry (cf. Trinkaus *et al.*, 1994)			
		mean	std dev.	U	Sig. (2-tailed)	mean	std dev.	U	Sig. (2-tailed)
mc1L	20	-0.14	1.48	47.0	p = 0.95	1.26	0.77	36.0	p = 0.37
mc2L	20	0.18	1.10	36.5	p = 0.39	1.26	0.77	42.0	p = 0.67
mc3L	21	0.27	1.28	40.0	p = 0.35	0.84	0.73	7.0	**p < 0.01**
mc4L	20	0.10	0.81	32.0	p = 0.23	0.99	0.84	45.5	p = 0.87
mc5L	19	-0.37	1.74	42.0	p = 1.00	0.64	0.49	26.0	p = 0.20
mc1RU	20	-0.27	4.40	25.0	*p = 0.08*	1.47	1.02	32.5	p = 0.25
mc2RU	21	-0.86	5.16	45.0	p = 0.54	3.81	2.35	51.0	p = 0.85
mc3RU	21	1.62	3.74	42.0	p = 0.42	3.87	4.16	50.0	p = 0.81
mc4RU	21	-0.25	3.77	53.5	p = 0.99	3.30	2.38	43.0	p = 0.45
mc5RU	19	1.56	7.51	39.5	p = 0.85	3.10	2.23	24.5	p = 0.15
mc1DP	20	1.62	8.67	41.0	p = 0.62	4.91	6.00	27.5	p = 0.12
mc2DP	21	1.86	6.37	44.0	p = 0.50	6.24	6.33	53.0	p = 0.96
mc3DP	21	1.78	3.08	36.0	p = 0.21	4.71	4.69	25.5	**p = 0.04**
mc4DP	21	3.36	6.06	29.5	*p = 0.09*	2.83	2.11	47.5	p = 0.67
mc5DP	19	3.09	6.11	39.0	p = 0.82	4.66	5.09	36.0	p = 0.64
mc1PB	20	0.05	3.26	40.0	p = 0.57	5.62	3.96	31.0	p = 0.21
mc2PB	21	1.15	3.94	32.0	p = 0.13	2.60	2.04	32.5	p = 0.13
mc3PB	21	-0.30	3.36	34.0	p = 0.17	3.22	2.52	43.0	p = 0.46
mc4PB	21	2.51	3.60	36.0	p = 0.22	2.72	2.00	47.0	p = 0.64
mc5PB	19	2.34	6.61	41.5	p = 0.98	3.15	3.04	36.5	p = 0.67
mc1DB	20	0.38	4.20	24.0	*p = 0.07*	5.47	4.41	34.0	p = 0.30
mc2DB	20	0.61	2.28	41.5	p = 0.64	3.08	2.94	31.0	p = 0.20
mc3DB	21	1.01	2.15	51.0	p = 0.86	1.69	1.63	36.0	p = 0.22
mc4DB	20	0.37	2.84	43.0	p = 0.72	1.98	1.28	25.0	*p = 0.08*
mc5DB	18	0.42	1.93	35.0	p = 0.96	2.03	2.03	17.0	*p = 0.08*

Minus values for directional asymmetry means reflects the equation used to calculate asymmetry, in which a left-side dominant individual will have a minus score. Mean and standard deviation values rounded to two decimal places. Significant p-values highlighted in bold. P-values approaching significance (between 0.055 and 0.1) highlighted in italics. Abbreviations used: mc*L = metacarpal length, mc*RU = radio-ulnar midshaft diameter, mc*DP = dorso-palmar midshaft diameter, mc*PB = proximal breadth, mc*DB = distal breadth. Asterisk (*) denotes metacarpal number.

Table 7.5 indicates that males and females, on the whole, do not differ substantially in the direction or size of their metacarpal asymmetry. For directional asymmetry, no statistically significant sex effects were found, although three variables (mc1RU, mc4DP, mc1DB) were approaching significance. For absolute asymmetry, two variables, mc3L and mc3DP, showed statistically significant sex effects. When the mean rank values for the Mann-Whitney U test were compared (see Table E.5 and E.6, Appendix E), no clear trends were identified. For directional asymmetry, mean rank values are larger for females than males for 14 of 25 variables. For absolute asymmetry, females had larger mean rank values than males for 14 of 25 variables, although for mc3L (which showed a significant sex effect), males had larger asymmetry values than females. This general trend for females to be more frequently right-side dominant and to have larger asymmetry values than males was also found in the Écija metacarpal sample (section 5.1.4).

A Mann-Whitney U test was performed to assess the effects of sex on asymmetry in chimpanzee phalanx length. The results of this analysis are presented in Table 7.6.

Table 7.6. A Mann-Whitney U test of the effects of sex on directional and absolute asymmetry for each of the chimpanzee phalanx measurements.

Measurement	**N**	**Directional asymmetry (cf. Steele & Mays, 1995)**				**Absolute asymmetry (cf. Trinkaus *et al.*, 1994)**			
		mean	**std dev.**	**U**	**Sig. (2-tailed)**	**mean**	**std dev.**	**U**	**Sig. (2-tailed)**
pp1L	20	-1.56	4.69	42.0	p = 0.68	3.60	3.97	36.0	p = 0.38
pp2L	21	-0.41	1.58	38.0	p = 0.28	1.09	1.26	52.0	p = 0.90
pp3L	20	-0.14	1.25	28.0	p = 0.13	0.90	0.88	41.0	p = 0.61
pp4L	21	-0.28	1.06	45.5	p = 0.57	0.80	0.76	35.0	p = 0.19
pp5L	21	-0.17	2.03	51.0	p = 0.85	1.57	1.31	52.0	p = 0.90
ip2L	20	0.66	1.42	43.0	p = 0.73	1.11	1.09	45.5	p = 0.87
ip3L	21	0.04	1.17	51.5	p = 0.87	1.01	0.57	25.0	**p = 0.04**
ip4L	19	0.27	1.03	28.5	p = 0.21	0.77	0.73	41.0	p = 0.83
ip5L	20	0.68	5.93	38.0	p = 0.47	3.48	4.88	38.0	p = 0.47

No distal phalanx data was available for this analysis. Minus values for directional asymmetry means reflects the equation used to calculate asymmetry, in which a left-side dominant individual will have a minus score. Mean and standard deviation values rounded to two decimal places. Significant p-values highlighted in bold. Abbreviations used: pp*L = proximal phalanx length, ip*L = intermediate phalanx length Asterisk (*) denotes phalanx number.

As can be seen from Table 7.6, sex has a negligible effect on asymmetry in the chimpanzee phalanx sample with no effect found on directional asymmetry and only one variable, ip3L, showing a significant sex effect on absolute asymmetry. This trend was also found for the chimpanzee metacarpals (Table 7.5). A more substantial sex effect was found for the Écija phalanges (Table 5.7), which was more pronounced for directional asymmetry than absolute asymmetry. Comparing the mean rank values for the chimpanzee phalanges (Table E.7 and E.8, Appendix E) shows that for directional asymmetry there is no general trend for males or females to be more right-side dominant, with males having larger mean rank values for 4 of the 9 phalanx length measurements and females for 5 of 9 measurements. For absolute asymmetry, the trend is for males to have larger asymmetry scores than females (in 7 of the 9 phalanx variables), although the mean rank value is larger for males for ip3L (the only variable to show significant sex effect). These results indicate that in addition to low sexual dimorphism in chimpanzee metacarpal and phalanx size, there is also very little sexual dimorphism in asymmetry for these bones.

7.1.5. Individual asymmetry

The relationship between group-level and individual-level asymmetry in non-human primates is of particular interest for those interested in the development of hand preference in modern humans. Research into chimpanzee hand use suggests that individuals are clearly behaviourally lateralised, preferring the use of one hand across tasks (e.g. McGrew & Marchant, 1997). However, research attempting to identify this trend at the population-level has yet to prove conclusive (e.g. McGrew & Marchant, 1997; Hopkins & Cantalupo, 2005). Analysis of individual asymmetry in the hand bones of this chimpanzee sample therefore provides an opportunity to assess differences in the distribution of asymmetry at the individual-level compared to the sample-level. To assess individual asymmetry the data from section 7.1.3 was used to calculate the percentage of variables that show right-side dominant, left-side dominant and symmetrical scores for each individual. Figure 7.12 presents the results of this analysis for the metacarpals.

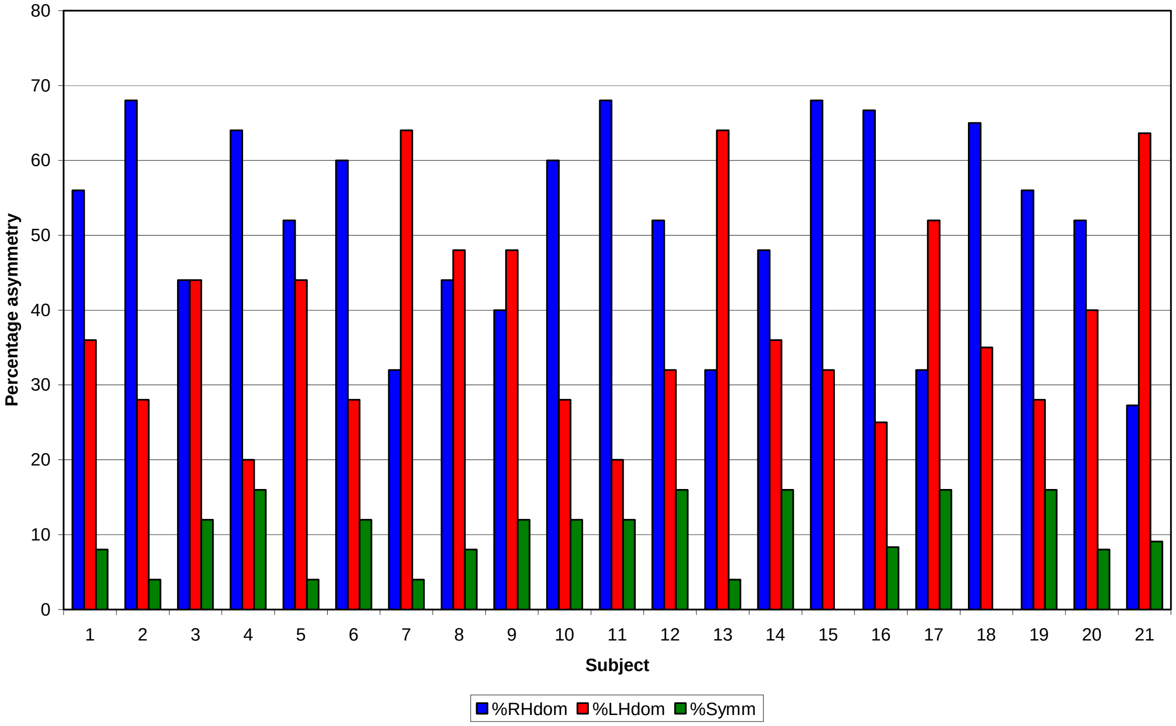


Figure 7.12. For each individual in the chimpanzee sample, the percentage of right-side dominant, left-side dominant and symmetric scores for all 25 metacarpal measurements. Each number along the x axis represents an individual's asymmetry profile.

Figure 7.12 shows that there is a general right-side dominance in chimpanzee individual asymmetry with 14 of 21 individuals (66.7%) showing an overall right-side dominant asymmetry for their metacarpal measurements. This trend is similar to that seen for Greenwich individual metacarpal asymmetry (section 6.1.5) where 60% of individuals showed right-side dominance. The chimpanzee sample contrasts with the Écija individual metacarpal asymmetry (section 5.1.5) where 92.3% of individuals were right-side dominant. The magnitude of individual asymmetry for chimpanzees is generally low with no individual exhibiting side dominance greater than 68%. These findings lend support to the observation (e.g. McGrew & Marchant, 1997) that chimpanzees preferentially use one hand for tasks, but that this individual laterality does not necessarily extend to identification of clear group- or population-level hand preference. These findings also once again highlight the symmetrical nature of the chimpanzee sample.

Individual asymmetry was also calculated for the chimpanzee phalanx length measurements. Figure 7.13 provides the results of this analysis and shows that the general trend in individual chimpanzee phalanx asymmetry is towards left-side dominance, with 11 of 21 (52.4%) individuals showing overall left-side dominant asymmetry (compared with 7 right-side dominant individuals and 3 symmetrical individuals). Given the clear left-side dominant asymmetry evident in Figure 7.11, this trend is to be expected. Although this pattern of individual phalanx asymmetry contrasts with the right-side dominance seen in the Écija phalanges (Fig. 5.13), it is in keeping with the left-side dominant trend identified in the Greenwich phalanges (Fig. 6.13). With the exception of individual 4 and individual 12, the magnitude of the individual asymmetry in the phalanges is lower than that seen in the human samples, but in line with that found in the chimpanzee metacarpals (Fig. 7.12).

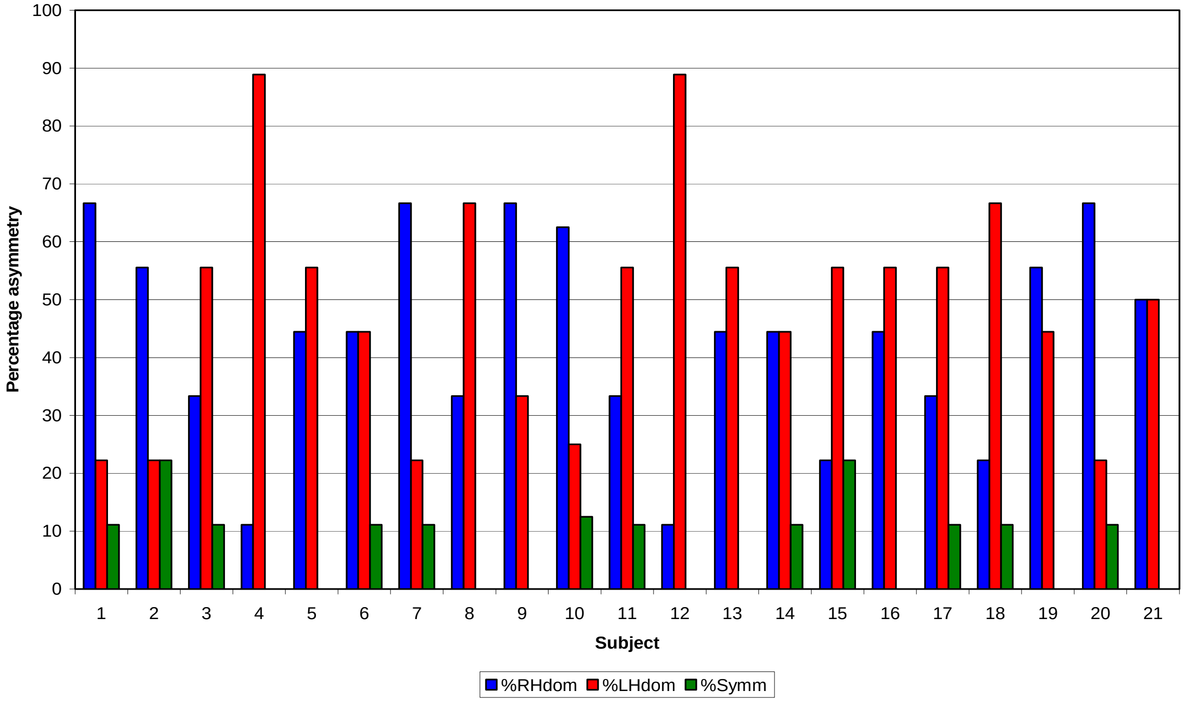


Figure 7.13. For each individual in the chimpanzee sample, the percentage of right-side dominant, left-side dominant and symmetric scores for all 9 phalanx length measurements. Each number along the x axis represents an individual's asymmetry profile.

7.1.6. Summary of chimpanzee metacarpal and phalanx metric analysis

Analysis of the chimpanzee metacarpals and phalanges has found that asymmetry between the left and right sides is generally low (sections 7.1.1 and 7.1.3) relative to the Écija human sample. The asymmetry present in the chimpanzee hands bones appears more comparable to that seen in the Greenwich sample, although the overall magnitude of asymmetry is still slightly less for the chimpanzees. Despite this, the trend remains towards right-side dominant asymmetry in the metacarpals, but left-side dominant asymmetry in the phalanges. The reduced asymmetry in the chimpanzee hand supports the hypothesis that the great ape samples will exhibit less upper limb asymmetry than the human samples due to the functional constraints of locomotion placed on the arm and hand bones. The ANOVA tests in section 7.1.2 and the Mann-Whitney U tests in section 7.1.4 confirm that there are very few differences between male and female chimpanzees in terms of size and asymmetry. Analysis of individual asymmetry in the chimpanzee metacarpals and phalanges showed that approximately 67% of individuals were right-side dominant for metacarpal measurements and approximately 52% of individuals were left-side dominant for phalanx measurements. This finding supports the notion that while individual hand preference is observed in chimpanzees the presence of population-level hand preference has not been firmly supported by the available evidence.

Despite the reduced levels of asymmetry in this chimpanzee sample relative to the Écija and Greenwich human samples the general pattern and direction of this asymmetry appears to be consistent, for the most part, across the species. This may be suggestive of general similarities in the way in which asymmetries are expressed in the upper limb with between-sample differences being reflected in the magnitude of the asymmetry. This trend may also represent methodological biases which influence the expression of asymmetry. Study of asymmetry in the chimpanzee humerus in the following section will be able to confirm whether this trend holds across both components of the chimpanzee upper limb.

7.2. Chimpanzee humerus metric analysis

In order to facilitate comparisons of upper limb asymmetry within and between species, data were collected from the humeral material corresponding to the hand bone material analysed in section 7.1. Descriptive statistics for the chimpanzee humerus sample can be found in Table E.9 (Appendix E). Box-and-whisker plots identified a small number of outliers present in the data. As with previous analyses, these outliers were not removed unless they were a result of error in the data collection process. Therefore, non-parametric tests were applied to the data where necessary. Histograms and p-p plots confirmed the normal distribution of the sample. The structure of the data analysis in this section follows that of the humeral material in the previous sections.

7.2.1. Significance testing

Due to the presence of outliers in the sample a non-parametric Wilcoxon test was performed to identify any statistically significant size differences between the left and right humerus measurements. As with the analysis of the hand bones in section 7.1 the test was performed on the combined-sex sample. Age was not used as a variable in the chimpanzee humerus analyses. Table 7.7 provides the results of this Wilcoxon test.

Table 7.7. Wilcoxon test results for the combined-sex chimpanzee humerus sample.

Measurement	Side	N	Mean	Std dev.	Sig. (2-tailed)
MxL	L	21	300.71	11.38	p = 0.69
	R	21	301.05	11.60	
MxDm	L	21	24.20	1.91	p = 0.67
	R	21	24.24	2.00	
MnDm	L	21	21.04	1.83	p = 0.34
	R	21	20.95	1.81	
MnCir	L	21	70.48	5.31	p = 0.62
	R	21	70.33	5.18	
CirHd	L	21	123.71	6.78	*p = 0.09*
	R	21	123.19	6.62	
MxTDm	L	21	40.19	2.52	p = 0.23
	R	21	40.47	2.50	
MxSDm	L	21	39.84	2.20	**p = 0.04**
	R	21	39.48	2.21	
EpBr	L	21	62.96	3.77	*p = 0.10*
	R	21	62.67	3.77	
TCBr	L	21	45.92	2.13	**p < 0.01**
	R	21	46.42	2.26	

Mean and standard deviation values rounded to two decimal places. Significant p values highlighted in bold. P values approaching significance (between 0.055 and 0.1) highlighted in italics. Abbreviations used: MxL = maximum length, MxDm = maximum midshaft diameter, MnDm = minimum midshaft diameter, MnCir = minimum shaft circumference, CirHd = circumference of head, MxTDm = maximum transverse diameter of head, MxSDm = maximum sagittal diameter of head, EpBr = epicondylar breadth, TCBr = trochlea-capitulum breadth.

Table 7.7 shows that there is little difference between the left and right humerus measurements in terms of size. Only MxSDm and TCBr show statistically significant differences between the left and right side. This clearly contrasts with the pattern seen for the Écija humeri (section 5.2.1) where all the measurements showed significant side differences, but similar to the Greenwich humeri (section 6.2.1), where few statistically significant differences were identified. The lack of significant size differences between the chimpanzee humeri mirrors the trend seen in the chimpanzee metacarpals and phalanges (section 7.1.1). A comparison of mean values indicates that there is no clear pattern in side dominance with 5 of the 9 measurements being larger on the left side and 4 of 9 measurements larger on the right side. For the two variables that displayed statistically significant side differences, MxSDm was larger on the left side, and TCBr was larger on the right side. Both MxSDm and TCBr are articular surface measurements (of the proximal and distal humerus, respectively) and finding significant size asymmetry in these variables is in contrast to the observation that diaphyseal properties display more asymmetry than articular surface dimensions (Ruff, 2000). However, Plochocki *et al.* (2006) suggests that joint morphology can be affected by mechanical loading and Rafferty & Ruff (1994) observe that articular surface size reflects joint mobility in primates, suggesting that the asymmetry seen in the articular measurements in this chimpanzee sample may in fact represent differential recruitment of the arms for these individuals.

7.2.2. Analysis of Variance (ANOVA)

A one-way ANOVA was performed to assess the effect of sex on chimpanzee humerus metric properties. Table 7.8 (below) presents the results of this analysis and it can be seen that a number of variables show significant differences between males and females (left and right CirHd, left and right MxSDm, right EpBr, right TCBr). Interestingly, these variables are all measures of articular surface dimensions. Unlike the Écija humerus sample (section 5.2.2), chimpanzee diaphyseal properties were not significantly affected by sex. The effect of sex was found to be weaker in the chimpanzee humerus than for the Écija sample, but stronger than for the Greenwich humeri (section 6.2.2). A comparison of mean values from the ANOVA shows that males have larger humerus measurements than females for 16 of 18 measurements. The pattern found for the chimpanzee humeri is comparable in strength and direction to that of the chimpanzee metacarpals, but differs from the phalanges (section 7.1.2) where no significant sex effect were found although the trend was for females to have larger mean values than males.

Table 7.8. One-way ANOVA for the effect of sex on chimpanzee humerus variables.

Measurement	Side	Sex	N	Mean	F	Sig. (2-tailed)
MxL	L	male	9	300.78	0.00	p = 0.98
		female	12	300.67		
	R	male	9	300.33	0.06	p = 0.81
		female	12	301.58		
MxDm	L	male	9	24.37	0.12	p = 0.74
		female	12	24.08		
	R	male	9	24.20	0.01	p = 0.94
		female	12	24.27		
MnDm	L	male	9	21.76	2.57	p = 0.13
		female	12	20.51		
	R	male	9	21.54	1.79	p = 0.20
		female	12	20.50		

Measurement	Side	Sex	N	Mean	F	Sig. (2-tailed)
MnCir	L	male	9	72.00	1.32	p = 0.26
		female	12	69.33		
	R	male	9	72.11	1.94	p = 0.18
		female	12	69.00		
CirHd	L	male	9	127.33	5.49	**p = 0.03**
		female	12	121.00		
	R	male	9	126.44	4.46	**p = 0.05**
		female	12	120.75		
MxTDm	L	male	9	41.19	2.70	p = 0.12
		female	12	39.43		
	R	male	9	41.51	3.00	*p = 0.10*
		female	12	39.69		
MxSDm	L	male	9	41.14	7.24	**p = 0.01**
		female	12	38.87		
	R	male	9	40.58	4.64	**p = 0.04**
		female	12	38.65		
EpBr	L	male	9	64.69	3.75	*p = 0.07*
		female	12	61.67		
	R	male	9	64.54	4.59	**p = 0.05**
		female	12	61.27		
TCBr	L	male	9	46.71	2.29	p = 0.15
		female	12	45.33		
	R	male	9	47.66	5.84	**p = 0.03**
		female	12	45.49		

Mean values rounded to two decimal places. Significant p values highlighted in bold. P values approaching significance (between 0.055 and 0.1) highlighted in italics. Abbreviations used: MxL = maximum length, MxDm = maximum midshaft diameter, MnDm = minimum midshaft diameter, MnCir = minimum shaft circumference, CirHd = circumference of head, MxTDm = maximum transverse diameter of head, MxSDm = maximum sagittal diameter of head, EpBr = epicondylar breadth, TCBr = trochlea-capitulum breadth.

7.2.3. Asymmetry in the humerus

The percentage of individuals that were right-side dominant, left-side dominant or symmetrical for each of the humerus variables was calculated using the equations described in 5.1.3. The results of this analysis are presented in Figure 7.14 (below). Data from this analysis can be found in Table E.10 (Appendix E).

It is immediately evident from Figure 7.14 that asymmetry is highly variable in these chimpanzee humeri. The magnitude of dominant asymmetry ranges from 38.1% (for MxL) up to 81% (for TCBr). This variation in asymmetry is greater than that seen in either of the modern human humeral samples (sections 5.2.3 and 6.2.3). The variation is also greater than that seen in the chimpanzee metacarpals and phalanges (section 7.1.3). In this humeral sample MxL shows the lowest magnitude of asymmetry of any of the measurements, although it is MxL that shows some of the highest levels of asymmetry in both the Écija and Greenwich humerus samples. As might be expected, given the results in sections 7.2.1 and 7.2.2, the articular dimensions MxSDm, EpBr and TCBr show the highest degree of asymmetry across the chimpanzee humerus variables. With the exception of TCBr the humeral variables in this analysis do not exhibit dominant asymmetry values greater than 67%. Therefore, the magnitude of asymmetry in the chimpanzee humeri is more variable, but generally lower than that seen in the Écija and Greenwich humeri, as well as the chimpanzee metacarpals and phalanges.

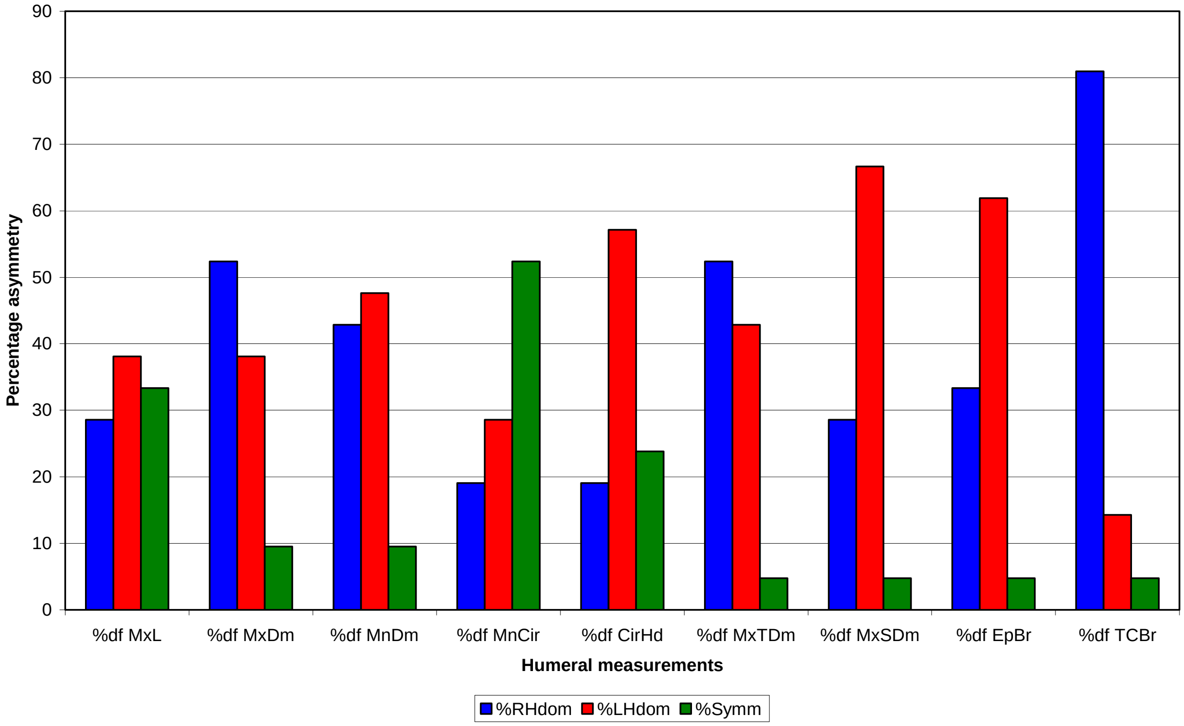


Figure 7.14. Percentage of right- and left-side dominant, plus symmetric individuals for each chimpanzee humerus measurement. Further data available in Table E.10, Appendix E.

Unlike the Écija and Greenwich humerus samples (which were both right-side dominant for all measurements) 5 of the 9 humerus measurements in Figure 7.14 are left-side dominant, with 3 variables exhibiting right-side dominant asymmetry and one variable (MnCir) showing predominantly symmetrical individuals. A pattern of left-side dominant variables was identified for the chimpanzee phalanges (Fig. 7.11) although the overall trend for the chimpanzee metacarpals is towards right-side dominance (Figs 7.1 to 7.5). This shift towards left-side dominant asymmetry in chimpanzee metric humeral dimensions mirrors the trend identified in Sarringhaus *et al.* (2005) for left-side dominant asymmetry in diaphyseal subperiosteal area in their chimpanzee sample. They also noted the comparison with second metacarpal asymmetry which showed a clear right-side dominant asymmetry. This same pattern can also be seen in the second metacarpal in the current chimpanzee sample (Figure 7.7).

The results displayed in Figure 7.14 show that asymmetry in the chimpanzee humeri is highly variable in terms of magnitude, with a general trend towards left-side dominance. The clearer right-side dominant asymmetry seen in the chimpanzee metacarpals (but not the phalanges) may represent the presence of more asymmetric loading in this region. The presence of stronger asymmetry in the articular surfaces of the humerus compared to the diaphysis runs contrary to the notion of reduced articular surface plasticity indicated by Ruff (2000) but supports the observation of mechanical loading influences on articular surface morphology proposed by Plochocki *et al.* (2006). This may in part reflect aspects of joint mobility in primates (Rafferty & Ruff, 1994).

7.2.4. Sex effects on asymmetry in the humerus

A Mann-Whitney U test was performed to assess the effects of sex on directional and absolute asymmetry in the chimpanzee humeri. Table 7.9 provides the results of this analysis.

Table 7.9. Mann-Whitney U test of the effects of sex on directional asymmetry and absolute asymmetry values for each of the chimpanzee humerus measurements.

Measurement	N	Directional asymmetry (cf. Steele & Mays, 1995)				Absolute asymmetry (cf. Trinkaus *et al.*, 1994)			
		mean	std dev.	U	Sig. (2-tailed)	mean	std dev.	U	Sig. (2-tailed)
MxL	21	0.11	0.79	44.5	p = 0.51	0.52	0.59	42.5	p = 0.42
MxDm	21	0.14	1.56	22.5	**p = 0.02**	1.26	0.92	53.0	p = 0.96
MnDm	21	-0.43	1.95	42.0	p = 0.41	1.59	1.24	52.5	p = 0.93
MnCir	21	-0.18	1.34	41.5	p = 0.35	0.88	1.04	46.5	p = 0.59
CirHd	21	-0.40	1.65	49.0	p = 0.74	1.21	1.18	39.0	p = 0.30
MxTDm	21	0.73	2.05	38.5	p = 0.29	1.32	1.72	48.5	p = 0.72
MxSDm	21	-0.90	2.18	44.5	p = 0.52	1.87	1.48	49.5	p = 0.77
EpBr	21	-0.46	1.18	43.0	p = 0.45	0.98	0.81	43.0	p = 0.45
TCBr	21	1.08	1.53	18.0	**p < 0.01**	1.52	1.07	31.0	p = 0.11

Minus values for directional asymmetry means reflects the equation used to calculate asymmetry, in which a left-side dominant individual will have a minus score. Mean and standard deviation values rounded to two decimal places. Significant p-values highlighted in bold. Abbreviations used: MxL = maximum length, MxDm = maximum midshaft diameter, MnDm = minimum midshaft diameter, MnCir = minimum shaft circumference, CirHd = circumference of head, MxTDm = maximum transverse diameter of head, MxSDm = maximum sagittal diameter of head, EpBr = epicondylar breadth, TCBr = trochlea-capitulum breadth.

Table 7.9 shows that there is a limited effect of sex on asymmetry in the chimpanzee humeri with only MxDm and TCBr showing a significant sex effect for directional asymmetry. There are no significant sex effects on absolute asymmetry for any of the humerus variables. This is the reverse of the trend seen in the chimpanzee metacarpals and phalanges (where there were more significant sex effects for absolute asymmetry than directional asymmetry) (section 7.1.4) but similar to that seen for the Écija humeri (section 5.2.4). When mean rank values are compared (Tables E.11 and E.12, Appendix E), a trend is identified for females have larger mean rank values than males for directional asymmetry in 5 of 9 humerus variables and for absolute asymmetry in 6 of 9 variables. However, for TCBr, males are right-side dominant more frequently than females. Overall, these results indicate that there is an underlying trend, albeit a statistically insignificant one, for female chimpanzees to be right-side dominant more frequently than males, and to exhibit a larger degree of asymmetry. It is possible that with larger sample sizes, these trends would be found to be statistically significant. However, these trends for humeral asymmetry are in line with those found for the chimpanzee metacarpals although they differ somewhat from the chimpanzee phalanges and the Écija humeri.

7.2.5. Individual asymmetry

For each individual in the chimpanzee sample asymmetry for each humerus measurement was combined to find the percentage of these measurements that were right-side dominant, left-side dominant and symmetrical. The results of this analysis are presented in Figure 7.15.

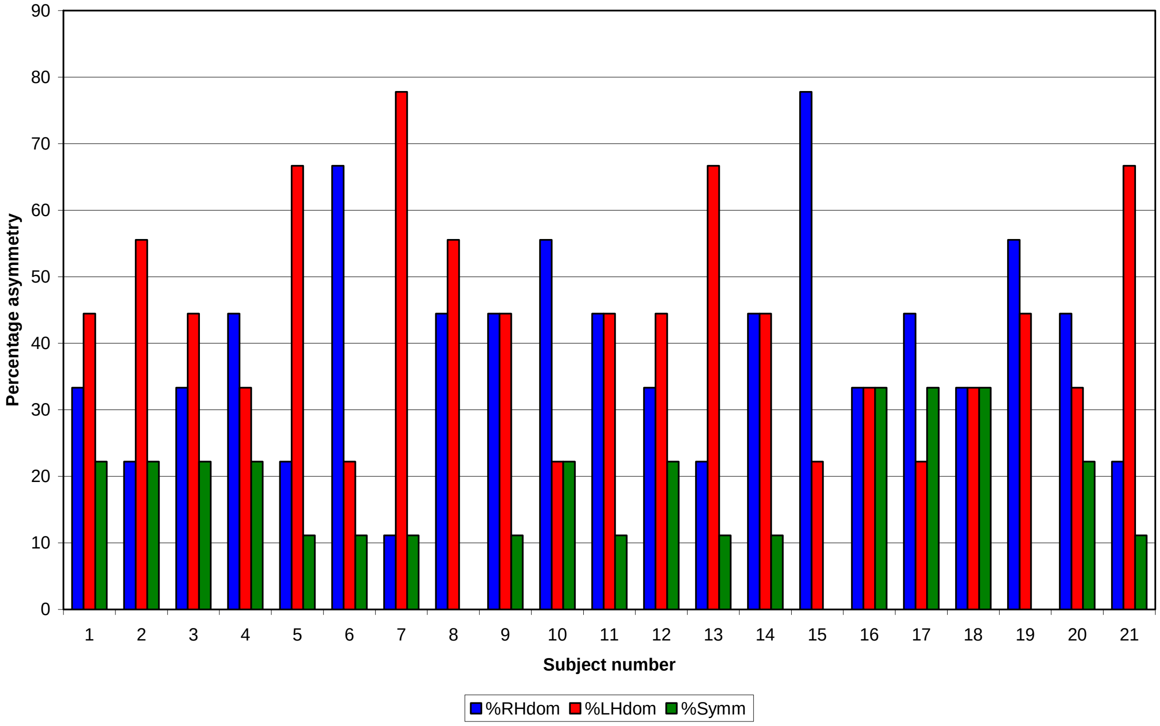


Figure 7.15. For each individual in the chimpanzee sample, the percentage of right-side dominant, left-side dominant and symmetric scores for all humerus measurements.

Figure 7.15 shows that there is a weak trend across the chimpanzee sample for individuals to exhibit predominantly left-side dominant asymmetry with 9 of 21 individuals exhibiting this pattern. However, 7 of the 21 individuals show right-side dominance and 5 individuals show an equal number of left- and right-side dominant measurements. There is variation in asymmetry between individuals, ranging from equality between the number of left- and right-side dominant measurements and symmetrical measurements up to 78% dominant asymmetry. The magnitude of this variation is reduced however, compared to that seen in the Écija and Greenwich individuals. The move towards individual left-side dominance for the chimpanzee humerus also contrasts with the general pattern in these samples. This reduction in the magnitude of individual humeral asymmetry and less variation between individuals might be expected in the chimpanzee sample given the distribution of behavioural lateralisation seen in live chimpanzees which is divided proportionally between the left and right sides (McGrew & Marchant, 1997).

7.2.6. Summary of chimpanzee humerus metric analysis

The pattern of asymmetry identified in the chimpanzee humeri highlights interesting differences between this non-human primate sample and the modern human samples from Écija and Greenwich. The left and right chimpanzee humeri differ little in terms of size (section 7.2.1) and do not show much sexual dimorphism (section 7.2.2). In terms of bilateral asymmetry the humeri show a trend towards left-side dominant asymmetry (Fig. 7.14) similar to that seen in the chimpanzee phalanges (Fig. 7.11) but the opposite to that of the chimpanzee metacarpals (Figs 7.1 to 7.5). This reversal of asymmetry between the humerus and the metacarpals is in keeping with the pattern of bilateral asymmetry found by Sarringhaus *et al.* (2005) in their study of chimpanzee upper limb cross-sectional properties. Males and females in the current analysis were found to show very few statistically significant differences in either directional or absolute asymmetry (section 7.2.4). Calculation of individual asymmetry (Fig. 7.15) supports the observation of low levels of asymmetry in the humerus measurements and the trend for left-side dominance.

The analyses in section 7.2 indicate that humeral asymmetry is reduced compared to that of the Écija and Greenwich humeral material, and also show a move towards left-side dominant asymmetry. This is contrary to the pattern of right-side dominance seen in the modern human humeri. This pattern is likely to reflect the lack of directional mechanical loading placed on the chimpanzee upper limb resulting in a more fluctuating asymmetry profile in this sample. However, differences in the direction of asymmetry between the humerus and the hands may in fact reflect behavioural influences in the use of the upper limb in chimpanzees with the left arm providing postural support and the right hand engaging in manipulative activities (Sarringhaus *et al.*, 2005). Contrary to the observations of Ruff (2000), articular surface dimensions in the chimpanzee humerus appear to be more asymmetric than the corresponding diaphyseal properties. Plochocki *et al.* (2006) indicate that articular surface properties may in fact be influenced by mechanical loading to a greater extent than previously expected. This finding may also be to differences in joint mobility in this group (Rafferty & Ruff, 1994).

Together, the results of the analyses in sections 7.1 and 7.2 paint a complex picture regarding the nature of asymmetry expression in the chimpanzee upper limb which requires further examination. Sections 7.3 and 7.4 will now address the nature of musculoskeletal stress marker development in the chimpanzee hand and arm.

7.3. Musculoskeletal stress markers (MSM) in the chimpanzee hand

The analyses of MSM expression in both the Écija and Greenwich samples (sections 5.3 and 6.3, respectively) have highlighted the difference between metric and muscle marker methods in terms of their ability to identify asymmetry. These analyses have identified relatively little asymmetry between left and right MSM expression in comparison to the clear asymmetry found in the corresponding metric analyses. To investigate the ability of the MSM method to identify differences between samples for which differences in asymmetry profile are already established, this approach was applied to MSM expression in the chimpanzee hand and humeri samples. Assumptions held about the more symmetrical nature of the chimpanzee upper limb were borne out with observation of reduced levels of asymmetry identified in the metric analysis (sections 7.1 and 7.2). It now remains to be tested whether this translates into reduced MSM asymmetry, particularly given the relative increase in chimpanzee forelimb muscle strength compared to humans but the relative reduction in strength of chimpanzee hand muscles compared to humans (Marzke *et al.*, 1999; Ogihara *et al.*, 2005). The structure of the data analysis in this section will follow that of the MSM analyses in the previous chapters.

7.3.1. Asymmetry in chimpanzee hand MSM

In order to ascertain asymmetry, the percentage of individuals who scored as ‘present’ for each MSM was compared between the right and left hands. The results of this comparison are presented in Figure 7.16 (below). Due to the lack of distal phalanges in this sample, the *flexor digitorum profundus* MSM could not be scored. The *flexor pollicis longus* muscle is not present in non-human primates (Aiello & Dean, 1990; Hamrick e*t al.*, 1998) and therefore its MSM did not form part of the analysis. As with the analyses of the human MSM data the *flexor digitorum superficialis* 2, 3, 4 and 5 MSM showed no inter-digit variation in ‘present’ or ‘absent’ scores and were therefore analysed as one data point. Data from this analysis can be found in Table E.13 (Appendix E).

From Figure 7.16 it can be seen that there are a number of MSM that display substantial (i.e. greater than 10%) difference between left and right ‘present’ scores, namely ODM, DI1 and DI3. ODM and DI1 were also found to exhibit greater than 10% asymmetry in both the Écija and Greenwich samples (Figs 5.16 and 6.16, respectively) highlighting a commonality between these MSM in their asymmetry across the samples. The reasons for such a pattern are unclear at present. ODM shows a right-side asymmetry in the chimpanzee and Greenwich samples but left-side dominant asymmetry in the Écija sample. Conversely, DI1 displays left-side dominant asymmetry in the chimpanzee sample but right-side dominant asymmetry in both the human samples. The ODM muscle is involved in bringing the 5th metacarpal into opposition with the thumb, as well as flexing the carpometacarpal joint at the fifth digit (Table 3.4). The DI1 muscle is involved in the abduction of the 2nd digit from the midline of the hand (Table 3.4) suggesting asymmetry in pinch grip-like actions between the hands in all the samples studied. Due to the availability of certain MSM for study, it was not possible to compare the MSM of prime movers included in this study with their corresponding synergists and antagonists.

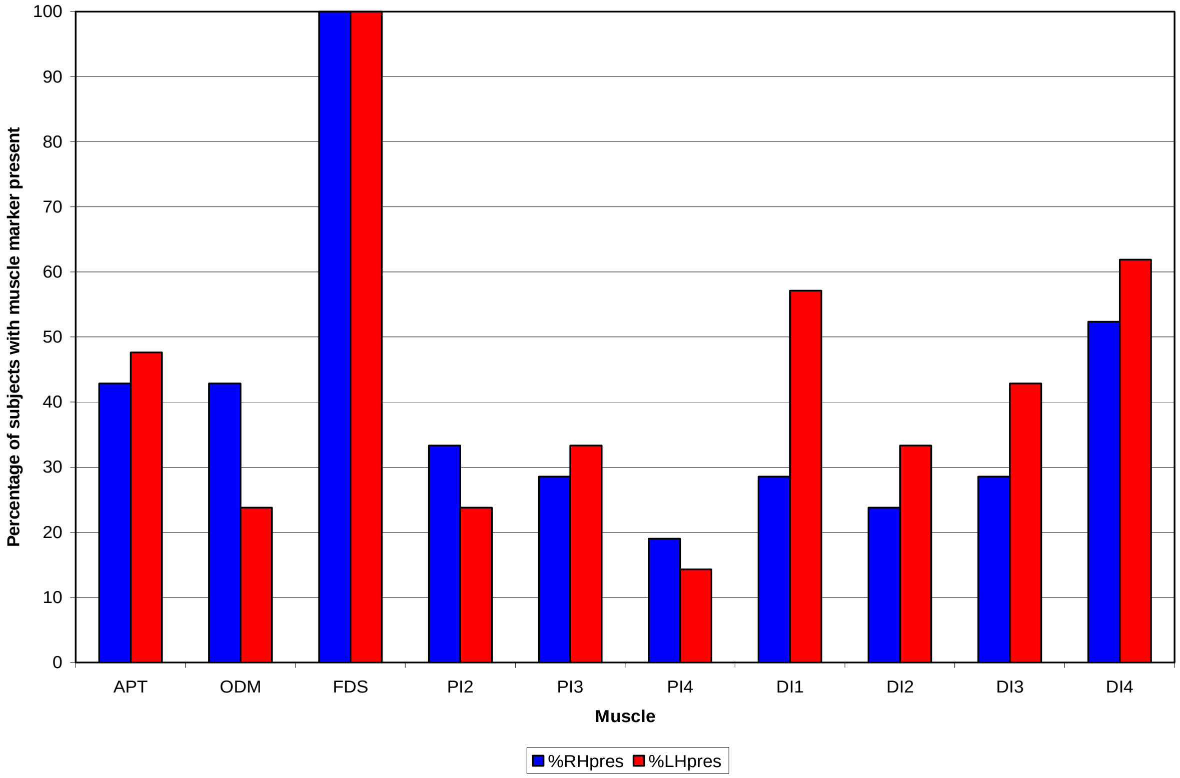


Figure 7.16. For each of the 10 chimpanzee MSM, the percentage scored as 'present' for the left hand (red) and the right hand (blue). Abbreviations used: APT = adductor pollicis (transverse head), ODM = oppenens digiti minimi, FDS = flexor digitorum superficialis (2-5), PI = palmar interosseous, DI = dorsal interosseous. Due to the absence of distal phalanges in the chimpanzee sample, it was not possible to score the flexor digitorum profundus MSM. Further data provided in Table E.13, Appendix E.

In terms of the direction of asymmetry 6 of the 10 MSM (APT, PI3, DI1, DI2, DI3, DI4) show left-side dominant asymmetry with only 3 MSM (ODM, PI2, PI4) showing right-side dominance. One MSM, FDS, shows no difference between the frequency of left and right 'present' scores. This contrasts with both the Écija and Greenwich samples where the overall trend was towards right-side dominance (although it is worth noting that this is only a slight difference in the numbers of right- and left-side dominant asymmetries in both samples). With the exception of FDS, all the MSM in Figure 7.16 are located on the metacarpals. Therefore this trend towards left-side dominant asymmetry contrasts with the chimpanzee metric analyses which identified a right-side asymmetry in the metacarpals (although the chimpanzee phalanges were found to display predominantly left-side dominant asymmetry). This trend may be a reflection of the presence of a more fluctuating asymmetry between the left and right hands, resulting from reduced directional loading on these extremities.

It is clear from Figure 7.16 is that there is marked variation in the frequency with which MSM were rated as 'present' with the FDS in particular scored as 'present' on 100% of occasions. Even with this

MSM excluded from analysis, a 42.9 point difference remains between the lowest 'dominant' asymmetry value (for PI4) and the highest (for DI4). This pattern suggests that the flexor muscles are particularly functionally stressed in the chimpanzee sample which may reflect the role of the phalanges in knuckle-walking in this species (Tuttle, 1967; Richmond *et al.*, 2001). Unfortunately the distal phalanges were not available in this sample to allow comparison of the FDP MSM. Similar to the Greenwich and Écija samples, the *dorsal interossei* appear to be scored as 'present' more frequently than the *palmar interossei*. It is likely that this trend reflects the difficulty in identifying the MSM of the generally gracile *palmar interossei*, which are often located in close proximity to the more readily observable *dorsal interossei* (Fig. 3.4 and 3.5).

7.3.2. Significance testing

To identify whether any of the left/right MSM differences seen in Figure 7.16 reflected statistically significant differences in MSM expression, a McNemar test was performed on the data. The McNemar test is a related-samples test for nominal data derived from the chi-squared test. Table 7.10 presents the results of this test on the chimpanzee hand MSM data.

Table 7.10. McNemar test of association between chimpanzee left- and right-hand MSM.

MSM	N	Sig. (2-tailed)
APT	21	p = 1.00
ODM	19	p = 0.45
FDS	-	-
PI2	21	p = 0.63
PI3	21	p = 1.00
PI4	19	p = 1.00
DI1	21	*p = 0.07*
DI2	21	p = 0.63
DI3	21	p = 0.45
DI4	21	p = 0.69

N = comparisons performed. P-values approaching significance (between 0.055 and 0.1) highlighted in italics. FDS not included in analysis as no individuals changed score between 'present' and 'absent' categories. Due to the low number of cases where score changed between categories, a binomial distribution was in place of the χ^2 statistic. Abbreviations used: APT = adductor pollicis (transverse head), ODM = oppenens digiti minimi, FDS = flexor digitorum superficialis (2-5), PI = palmar interosseous, DI = dorsal interosseous.

Table 7.11 clearly shows that there are no statistically significant differences between any of the paired left and right MSM in terms of their 'present' and 'absent' scoring. This indicates that any asymmetry identified in Figure 7.16 is not statistically significant. However, for DI1, which showed the largest asymmetry between left and right 'present' scores, this asymmetry is approaching significance (p = 0.07). In the Greenwich sample (section 6.3.2) DI1 was the only MSM that displayed a statistically significant difference between left and right scores.

7.3.3. Sex and hand MSM

A χ^2 test was performed to ascertain whether any association was present between sex and hand MSM score for the chimpanzee sample. The results of this analysis are presented in Table 7.11.

Table 7.11. Chi-squared (χ^2) test of association between sex and chimpanzee hand MSM.

MSM	Side	χ^2 value	Sig. (2-tailed)	φ value
APT	L	4.07	*p = 0.08**	0.44
	R	2.74	p = 0.18*	0.36
ODM	L	4.44	*p = 0.06**	0.47
	R	0.30	p = 0.67*	0.12
FDS	L	-	-	-
	R	-	-	-
PI2	L	0.02	p = 1.00*	0.03
	R	0.00	p = 1.00*	0.00
PI3	L	0.00	p = 1.00*	0.00
	R	0.18	p = 1.00*	0.09
PI4	L	0.07	p = 1.00*	0.06
	R	0.21	p = 1.00*	0.10
DI1	L	0.58	p = 0.66*	0.17
	R	0.31	p = 0.66*	0.12
DI2	L	0.00	p = 1.00*	0.00
	R	0.79	p = 0.61*	0.19
DI3	L	0.02	p = 1.00*	0.03
	R	0.31	p = 0.66*	0.12
DI4	L	5.45	**p = 0.03***	0.51
	R	2.29	p = 0.20*	0.33

Significant p-values in bold. P-values approaching significance (between 0.055 and 0.1) highlighted in italics. FDS was not included in the analysis as no individuals changed score between ‘present’ and ‘absent’ categories. Values marked with an asterisk (*) indicate where the Fisher’s Exact Test p-value was used due to low cell counts (in most instances, this test provides the same results as the standard χ^2). A phi (φ) value indicates the strength of the χ^2 association. Abbreviations used: APT = adductor pollicis (transverse head), ODM = oppenens digiti minimi, FDS = flexor digitorum superficialis (2-5), PI = palmar interosseous, DI = dorsal interosseous.

It can be seen from Table 7.11 that only left DI4 shows a statistically significant association with sex with left APT and left ODM approaching significance (p = 0.08 and p = 0.06, respectively). This indicates that there is little difference between males and females in terms of their MSM development suggesting minimum dimorphism in muscle recruitment. The phi (φ) value for the significant association between sex and left DI4 is 0.51 indicating only a moderate association between the variables (where 0 = no association and 1 = perfect association). The association between sex and left DI4 arises from females being scored as ‘present’ more often than males. In the Écija sample left DI4 was also found to have a significant association with sex. The DI4 is involved in abduction of the 4th digit from the midline of the hand (Table 3.4) and it is unclear why males and females would differ in the use of this muscle in particular. The overall weak association between sex and MSM score in the chimpanzee hand sample is similar to the trend identified in the corresponding Écija analysis. It remains unclear as to why sex should not be found to have a significant influence on MSM expression, as has been identified in other analyses (e.g. Robb, 1998; Stirland, 1998; Wilczak, 2003; Molnar, 2006). Small samples sizes in the chimpanzee analysis may be an influence but further clarification is required.

7.4. MSM in the chimpanzee humerus

The metric analysis of the chimpanzee upper limb (sections 7.1 and 7.2) found that the hands and the humeri differ predominantly in the direction of their asymmetry. The preceding analysis of chimpanzee hand MSM (section 7.3) found that similar to the Écija and Greenwich hand samples, there was little significant asymmetry between left and right MSM. The samples differed however, in the direction of asymmetry with a move towards left-side dominant asymmetry in the chimpanzee hands. Interestingly, this contrasted with the right-side dominant asymmetry identified in the chimpanzee metacarpals. Therefore, with varying relationships between and within hand and humerus asymmetry in all the samples studied, it is necessary to now examine the nature of MSM asymmetry in the chimpanzee humerus in order to ascertain how this asymmetry fits in with the patterns of asymmetry previously identified. The structure of the data analysis in this section will follow that of the preceding MSM analyses.

7.4.1. Asymmetry in humerus MSM

Asymmetry in humeral MSM was assessed by calculating the percentage of individuals for which MSM were scored as ‘present’ or ‘absent’, for each MSM. Asymmetry was determined through comparison of the left and right percentages of ‘present’ scores for each MSM. The results of this analysis are presented in Figure 7.17 (below). Data from this analysis can be found in Table E.14 (Appendix E).

Figure 7.17 confirms that there is minimal asymmetry between left and right humerus MSM in terms of how often they are scored as ‘present’. Only SSp exhibits a substantial left/right asymmetry (i.e. greater than 10%). This is an interesting finding when one considers that this MSM shows very little asymmetry in either the Écija or Greenwich samples. The function of the SSp is to abduct the arm and to stabilise the humeral head in the glenoid cavity (Table 3.5). Therefore it is possible that this asymmetry in this MSM may reflect preferential use of the left arm in postural support while the right hand engages in manipulative actions, as proposed by Sarringhaus *et al.* (2005).

This low degree of asymmetry present in chimpanzee humerus MSM is low relative to that seen in the modern human sample (Figs 5.17 and 6.17) and also that of the chimpanzee hands (Fig. 7.16). This trend in humerus MSM asymmetry supports the findings of Drapeau (2008) who also identified relatively lower levels of asymmetry in her chimpanzee humerus MSM sample compared to her human sample. There is no clear trend in Figure 7.17 the direction of asymmetry. Right-side dominance was identified in 4 of the 11 MSM with 3 MSM displaying left-side dominance and 4 MSM showing equal percentages of left and right ‘present’ scores. This contrasts with both the Écija humeral MSM which were predominantly right-side dominant, and the Greenwich humeral MSM which were predominantly left-side dominant. It also contrasts with the chimpanzee hand MSM which favoured left-side dominance. These findings are in keeping with the metric analysis of the chimpanzee humerus (section 7.2) which identified reduced metric asymmetry but with a general trend towards left-side dominant asymmetry. Taken together, these results suggests that the mechanical constraints of locomotion on the chimpanzee arm has indeed led to reduced asymmetry in musculature and bone robusticity, as might be expected. It is interesting to note that the hands appear to remain more asymmetric than the humeri in both metric and MSM properties.

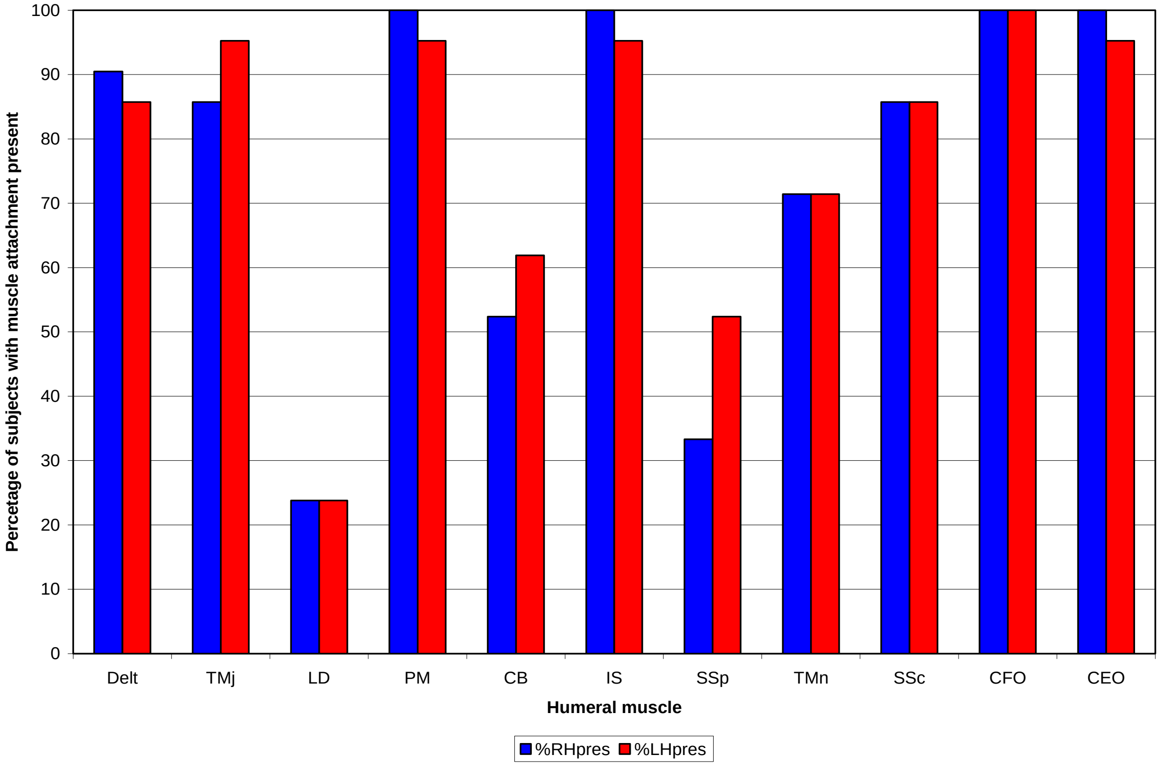


Figure 7.17. For each of the 11 MSM, the percentage scored as ‘present’ for the left humerus (red) and the right humerus (blue). Abbreviations used: Delt = deltoid, TMj = teres major, LD = latissimus dorsi, PM = pectoralis major, CB coracobrachialis, IS = infraspinatus, SSp = supraspinatus, TMn = teres minor, SSc = subscapularis, CFO = common flexor origin, CEO = common extensor origin. Further data available in Table E.4, Appendix 4.

Compared to the other humerus MSM analyses, many of the MSM in Fig. 7.17 are notable for the frequency with which they were scored as ‘present’, with the majority (7 out of 11) observable in more than 85% of individuals. For right PM, right IS, left and right CFO and right CEO in particular, MSM were rated as ‘present’ for all individuals. However, the LD, CB and SSp were scored as ‘present’ much less frequently than other MSM and the LD in particular was identified very infrequently compared to both the human samples. In comparison, the SSp, CFO and CEO were rated as ‘present’ for many more individuals in the chimpanzee sample relative to the Écija and Greenwich samples. The difficulties or relative ease of identifying certain MSM in the larger (relative to modern humans) chimpanzee humerus may in part account for the asymmetry profile displayed in Figure 7.17. It is also likely that the particular nature of chimpanzee upper limb function contributes to this asymmetry profile. The increased ‘presence’ of the IS and SSp in the chimpanzee sample may be related to the role of these muscles in the stabilisation of the humeral head in the glenoid cavity. The increased ‘presence’ of the CFO and CEO could be linked to the role of the finger flexors and extensors in knuckle-walking and brachiation in chimpanzees (Richmond *et al.*, 2001). Finally, no clear patterns of asymmetry could be identified between the MSM of prime movers and their corresponding synergists and antagonists (Table 5.16).

7.4.2. Significance testing

Despite a low degree of chimpanzee humeral asymmetry identified in section 7.4.1, a McNemar test was performed to test whether any of the asymmetries were statistically significant (see Table E.15, Appendix E). This test found no statistically significant differences between any of the left/right MSM pairs. This finding was not surprising when it is considered that none of the asymmetries were as large as those identified in the chimpanzee hand MSM analysis (section 7.3.2), which found only one value approaching statistical significance. This result is consistent with McNemar tests performed on the Écija and Greenwich humeri MSM (sections 5.4.2 and 6.4.2, respectively).

7.4.3. Sex and humerus MSM

To test the association between sex and MSM expression in the chimpanzee humerus, a chi-squared test was performed (see Table E.16, Appendix E). The results of this analysis show that there are no statistically significant associations between sex and any of the MSM, although a number of analyses were not possible due to the fact that some MSM scores did not vary between the left and right side. Only one variable, left CB, was found to be approaching significance ($p = 0.07$). In comparison, a number of significant associations were found between sex and Écija humerus MSM (section 5.4.3), suggesting some degree of dimorphism in muscle recruitment in that sample.

7.4.4. Summary of chimpanzee MSM analysis

What emerges from the analyses of MSM expression across the chimpanzee upper limb is the complex nature of the asymmetry in this region. Both the hand and humerus MSM analyses highlight the same generally low levels of asymmetry relative to both the chimpanzee metric asymmetry and the Écija and Greenwich MSM analyses. The low levels of MSM asymmetry relative to the human samples supports similar findings described by Drapeau (2008). The pattern of hand MSM asymmetry (Fig. 7.16) indicates that chimpanzees show particular asymmetry in MSM likely to be related to pinch-gripping, as has also been found in the modern human samples. The trend towards left-side dominant asymmetry in the hand MSM contrasts with the right-side dominant asymmetry seen in the metric properties of the chimpanzee metacarpals (but is similar to that found in the chimpanzee phalanx metric analysis). Additionally, the left-side dominant asymmetry evident in the chimpanzee humerus metric analysis is not present in the humerus MSM which shows almost equivalent numbers of right-side dominant, left-side dominant and symmetrical MSM. With relatively strong symmetrical forces placed on the hands and arms in terms of their engagement in locomotion, identifiable asymmetry in the data may be a result of fluctuating asymmetry influences.

Analyses found that none of the asymmetries observed in the hands and humerus MSM was statistically significant. In addition, a very weak association was found between sex and MSM in both the hands and the humerus. While this trend is consistent with the findings of the modern human MSM analysis, sexual dimorphism in MSM development would not be expected in the chimpanzee upper limb due to the role of this limb in locomotor activities in both sexes. The relatively low level of sexual dimorphism in size in this species is also reflected in this result.

Taking the data available from the preceding analyses of MSM expression, a few questions begin to emerge regarding the most appropriate application of MSM techniques. It would seem that MSM can inform us regarding the direction of asymmetry (i.e. whether a sample is left- or right-side dominant), but is perhaps of less practical use for identifying asymmetries within single MSM. Differences between the samples suggest that MSM techniques may be best applied to more global questions of between-group differences in larger samples, rather than more subtle, smaller scale analyses.

The second half of this chapter will now focus on the results of the gorilla data analyses, beginning with the metric analysis of the gorilla metacarpals and phalanges.

7.5. Gorilla metacarpal and phalanx metric analysis

There is currently little work addressing gorilla skeletal upper limb bilateral asymmetry (Drapeau, 2008 being one of the few examples). It is therefore unclear how asymmetry will be expressed in the gorilla data collected for the current study. This analysis provides an opportunity to address this paucity of research and compare asymmetry in the gorilla hand and arm with that seen in both chimpanzees and modern humans.

The age and sex profile of the gorilla sample is presented in Table 7.12 (below). As with the chimpanzee analysis, age was excluded as a variable from analysis (although a tentative assignment has been made in the table below). This was due to the incompleteness of age data available in the museum catalogue for the individuals included in the current study, difficulties in accurately assigning each skeleton to the correct age category and issues surrounding small sample sizes in each age category.

Table 7.12. Age and sex profile of the gorilla sample.

	Young adult	**Middle adult**	**Old adult**	**Total**
Male	0	2	8	**10**
Female	1	6	4	**11**
Total	**1**	**8**	**12**	Total sample: **21**

Descriptive statistics for the gorilla metacarpal and phalanx sample can be found in Table E.17, Appendix E. Box-and-whisker plots (plotted for males and females separately) identified the presence of a number of outliers in the sample. As with previous analyses, each outlier was checked for the presence of measurement or recording error. Where this was the case, the value was excluded from analysis. If no error was identified then the outlier was included in the data set. Due to the large degree of sexual dimorphism observed in gorilla groups (Fleagle, 1998), histograms and p-p plots were performed on male and female data separately. These plots confirmed the overall normal distribution of the sample. As with the chimpanzee sample, due to the nature of curation of the primate collection at the Powell-Cotton Museum, no distal phalanges were available to study in this gorilla sample.

7.5.1. Significance testing

Due to the presence of outliers in the gorilla sample it was necessary to perform a non-parametric Wilcoxon test to identify the presence of significant size differences between left and right metacarpal measurements. Table 7.13 provides the results of this analysis.

Table 7.13. Wilcoxon test results for the combined-sex gorilla metacarpal sample.

Measurement	**Side**	**N**	**Mean**	**Std dev.**	**Sig. (2-tailed)**
mc1L	L	21	46.17	6.00	**$p < 0.01$**
	R	21	46.05	6.19	
mc2L	L	21	89.27	9.69	$p = 0.85$
	R	21	89.37	9.96	
mc3L	L	21	87.97	9.69	$p = 0.91$
	R	20	88.80	9.26	
mc4L	L	21	85.67	9.49	$p = 0.92$
	R	20	86.44	9.27	
mc5L	L	21	82.23	9.98	*$p = 0.09$*
	R	21	81.65	9.79	
mc1RU	L	21	11.22	2.20	$p = 0.43$
	R	21	11.02	1.86	
mc2RU	L	21	11.30	1.49	$p = 0.22$
	R	21	11.20	1.62	

Measurement	Side	N	Mean	Std dev.	Sig. (2-tailed)
mc3RU	L	21	10.70	1.18	p = 0.35
	R	20	10.87	1.35	
mc4RU	L	21	9.86	1.45	p = 0.26
	R	20	10.08	1.29	
mc5RU	L	21	10.21	1.82	p = 0.48
	R	21	10.39	2.25	
mc1DP	L	21	8.30	1.34	p = 0.11
	R	21	8.57	1.41	
mc2DP	L	21	10.58	1.77	p = 0.33
	R	21	10.68	1.82	
mc3DP	L	21	12.80	2.06	p = 0.15
	R	20	12.71	1.95	
mc4DP	L	21	10.79	1.41	p = 0.26
	R	20	10.70	1.57	
mc5DP	L	21	9.10	1.19	p = 0.18
	R	19	8.75	1.08	
mc1PB	L	21	15.76	2.40	p = 0.50
	R	21	15.63	2.32	
mc2PB	L	21	17.72	2.76	**p< 0.01**
	R	21	18.28	2.59	
mc3PB	L	21	16.60	2.28	p = 0.78
	R	20	16.72	2.29	
mc4PB	L	21	14.70	1.91	p = 0.16
	R	20	15.01	2.03	
mc5PB	L	21	14.03	2.12	p = 0.19
	R	21	13.90	2.44	
mc1DB	L	21	13.50	2.37	p = 0.84
	R	21	13.46	2.20	
mc2DB	L	21	16.55	2.10	**p< 0.01**
	R	21	16.75	2.16	
mc3DB	L	21	17.62	2.34	p = 0.77
	R	20	17.72	2.40	
mc4DB	L	21	16.19	2.29	p = 0.15
	R	20	16.11	2.08	
mc5DB	L	21	14.12	2.17	p = 0.23
	R	21	14.24	2.24	

Mean and standard deviation values rounded to two decimal places. Significant p- values highlighted in bold. P-values approaching significance (between 0.055 and 0.1) highlighted in italics. Abbreviations used: mc*L = metacarpal length, mc*RU = radio-ulnar midshaft diameter, mc*DP = dorso-palmar midshaft diameter, mc*PB = proximal breadth, mc*DB = distal breadth. Asterisk (*) denotes metacarpal number.

From Table 7.13 it can be seen that only three metacarpal variables show a statistically significant difference between the left and right measurements: mc1L, mc2PB and mc2DB. When the mean values for each metacarpal variable are compared it can be seen that 14 of the 25 measurements are bigger on the right-side than the left, with 11 measurements bigger on the left-side. For the three statistical significant differences mc1L is bigger on the left than right, with both mc2PB and mc2DB bigger on the right than left. It is unclear why the 2nd metacarpal proximal and distal bases should be larger on the right-side, but it may reflect increased weight-bearing in this digit. The overall trend for the right-side metacarpal measurements to be larger than the left follows the trends identified in both the human and the chimpanzee samples. However, the general lack of significant size differences in the gorilla metacarpals contrasts with the large number of significant differences found for the Écija and Greenwich metacarpals (section 5.1.1 and 6.1.1, respectively). The chimpanzee metacarpal Wilcoxon test (section 7.1.1) also found few significant left/right differences (although these were identified for metacarpals 3 and 4).

Table 7.14 provides the results of the Wilcoxon test for the gorilla phalanx data.

Table 7.14. Wilcoxon test results for the combined-sex gorilla phalanx sample.

Measurement	Side	N	Mean	Std dev.	Sig. (2-tailed)
pp1L	L	21	25.90	3.34	*p = 0.06*
	R	20	25.74	3.21	
pp2L	L	21	49.80	5.03	p = 0.96
	R	21	49.72	5.04	
pp3L	L	21	56.54	5.71	p = 0.29
	R	21	56.25	5.83	
pp4L	L	21	53.68	5.59	p = 0.73
	R	20	54.12	5.46	
pp5L	L	21	44.66	4.93	p = 0.47
	R	21	44.63	5.00	
ip2L	L	20	32.19	3.71	p = 0.47
	R	19	32.01	3.13	
ip3L	L	20	39.49	3.94	p = 0.67
	R	19	39.86	3.79	
ip4L	L	20	37.90	4.14	p = 0.31
	R	19	37.86	4.36	
ip5L	L	20	28.82	4.37	p = 0.22
	R	20	28.90	4.20	
Mean and standard deviation values rounded to two decimal places. P-values approaching significance (between 0.055 and 0.1) highlighted in italics. No distal phalanges were available for study. Abbreviations used: pp*L = proximal phalanx length, ip*L = intermediate phalanx length. Asterisk (*) denotes phalanx number.					

Table 7.14 clearly shows that there are no statistically significant size differences between any of the left and right phalanx measurements. Only pp1L is approaching significance (p = 0.06). When the mean values for each measurement are compared it can be seen that 6 of the 9 phalanx length measurements are bigger on the left side than the right. This trend follows that found in the chimpanzee and (section 7.1.1) Greenwich phalanges (section 6.1.1) (the Écija phalanges show an equal division between left-side and right-side dominance). This trend contrasts with that of the gorilla metacarpals

which were generally larger on the right-side. As highlighted in the corresponding analysis of the chimpanzee hand there appears to be a discrepancy between the metacarpals and phalanges, both in terms of the degree of size differences they exhibit between left and right, plus the direction of this difference.

7.5.2. Analysis of Variance (ANOVA)

With the large degree of sexual dimorphism exhibited by gorilla species (Fleagle, 1998), it is expected that the gorilla metacarpals and phalanges will show observable sexual dimorphism in size dimensions. To test whether this is indeed the case a one-way ANOVA was performed on the data. Table 7.15 presents the results of this analysis for the gorilla metacarpals.

Table 7.15. One-way ANOVA for the effect of sex on gorilla metacarpal variables.

Measurement	Side	Sex	N	Mean	F	Sig. (2-tailed)
mc1L	L	male	10	51.29	43.28	**p < 0.01**
		female	11	41.51		
	R	male	10	51.59	61.81	**p < 0.01**
		female	11	41.01		
mc2L	L	male	10	97.85	56.71	**p < 0.01**
		female	11	81.46		
	R	male	10	98.32	63.69	**p < 0.01**
		female	11	81.24		
mc3L	L	male	10	96.33	46.92	**p < 0.01**
		female	11	80.36		
	R	male	10	96.44	45.37	**p < 0.01**
		female	10	81.16		
mc4L	L	male	10	94.00	53.04	**p < 0.01**
		female	11	78.09		
	R	male	10	94.32	57.32	**p < 0.01**
		female	10	78.56		
mc5L	L	male	10	91.08	57.15	**p < 0.01**
		female	11	74.18		
	R	male	10	90.43	62.46	**p < 0.01**
		female	11	73.67		
mc1RU	L	male	10	13.09	42.54	**p < 0.01**
		female	11	9.52		
	R	male	10	12.62	45.13	**p < 0.01**
		female	11	9.56		
mc2RU	L	male	10	12.39	19.68	**p < 0.01**
		female	11	10.32		
	R	male	10	12.53	34.71	**p < 0.01**
		female	11	9.98		

Measurement	**Side**	**Sex**	**N**	**Mean**	**F**	**Sig. (2-tailed)**
mc3RU	L	male	10	11.66	31.98	**$p < 0.01$**
		female	11	9.84		
	R	male	10	11.81	19.43	**$p < 0.01$**
		female	10	9.92		
mc4RU	L	male	10	10.88	17.14	**$p < 0.01$**
		female	11	8.93		
	R	male	10	11.02	22.43	**$p < 0.01$**
		female	10	9.14		
mc5RU	L	male	10	11.66	28.95	**$p < 0.01$**
		female	11	8.90		
	R	male	10	12.27	38.28	**$p < 0.01$**
		female	11	8.68		
mc1DP	L	male	10	9.38	30.90	**$p < 0.01$**
		female	11	7.32		
	R	male	10	9.68	28.24	**$p < 0.01$**
		female	11	7.55		
mc2DP	L	male	10	12.08	41.06	**$p < 0.01$**
		female	11	9.22		
	R	male	10	12.26	48.86	**$p < 0.01$**
		female	11	9.25		
mc3DP	L	male	10	14.61	53.77	**$p < 0.01$**
		female	11	11.15		
	R	male	10	14.36	55.93	**$p < 0.01$**
		female	10	11.05		
mc4DP	L	male	10	11.90	28.47	**$p < 0.01$**
		female	11	9.77		
	R	male	10	11.84	22.53	**$p < 0.01$**
		female	10	9.56		
mc5DP	L	male	10	9.99	22.23	**$p < 0.01$**
		female	11	8.28		
	R	male	8	9.70	25.60	**$p < 0.01$**
		female	11	8.05		
mc1PB	L	male	10	18.03	112.95	**$p < 0.01$**
		female	11	13.69		
	R	male	10	17.75	74.84	**$p < 0.01$**
		female	11	13.71		
mc2PB	L	male	10	20.35	121.61	**$p < 0.01$**
		female	11	15.33		
	R	male	10	20.71	99.40	**$p < 0.01$**
		female	11	16.07		

Measurement	Side	Sex	N	Mean	F	Sig. (2-tailed)
mc3PB	L	male	10	18.65	63.75	**p < 0.01**
		female	11	14.74		
	R	male	10	18.70	67.77	**p < 0.01**
		female	10	14.74		
mc4PB	L	male	10	16.49	98.73	**p < 0.01**
		female	11	13.06		
	R	male	10	16.80	81.98	**p < 0.01**
		female	10	13.21		
mc5PB	L	male	10	15.85	45.71	**p < 0.01**
		female	11	12.37		
	R	male	10	15.91	34.72	**p < 0.01**
		female	11	12.07		
mc1DB	L	male	10	15.38	28.55	**p < 0.01**
		female	11	11.79		
	R	male	10	15.17	26.17	**p < 0.01**
		female	11	11.90		
mc2DB	L	male	10	18.46	72.36	**p < 0.01**
		female	11	14.81		
	R	male	10	18.74	79.03	**p < 0.01**
		female	11	14.95		
mc3DB	L	male	10	19.86	133.15	**p < 0.01**
		female	11	15.58		
	R	male	10	19.82	77.12	**p < 0.01**
		female	10	15.61		
mc4DB	L	male	10	18.27	72.99	**p < 0.01**
		female	11	14.29		
	R	male	10	17.89	61.76	**p < 0.01**
		female	10	14.33		
mc5DB	L	male	10	15.94	38.94	**p < 0.01**
		female	11	12.46		
	R	male	10	16.21	52.89	**p < 0.01**
		female	11	12.45		

Mean values rounded to two decimal places. Significant p values highlighted in bold.Abbreviations used: mc*L = metacarpal length, mc*RU = radio-ulnar midshaft diameter, mc*DP = dorso-palmar midshaft diameter, mc*PB = proximal breadth, mc*DB = distal breadth. Asterisk (*) denotes metacarpal number.

It is evident from Table 7.15 that males and females show statistically significant size differences for all metacarpal variables, as might be expected considering the sexual size dimorphism observed in live gorilla groups. When the mean values in Table 7.15 are compared males are found to have larger metacarpal properties than females for all variables. These results clearly contrast with the relatively small numbers of significant size differences found between chimpanzee metacarpal measurements (section 7.1.2), most likely as a result of the moderate sexual dimorphism exhibited in this genus

(Fleagle, 1998). The Écija metacarpal sample also displayed strong sexual dimorphism (section 5.1.2), which may reflect both biological variation and occupational divisions between males and females in that population.

Table 7.16 (below) provides the results of the one-way ANOVA performed to assess the effects of sex on phalanx length in the gorilla sample. As found for the gorilla metacarpals (Table 7.15), there is a strong effect of sex on gorilla phalanx length with males and females showing statistically significant size differences for all variables. A comparison of mean values indicates that males have larger phalanx measurements than females for all variables. These results once again contrast with the chimpanzee phalanges (Table E.2, Appendix E) where no significant effects were found, but are in keeping with the Écija phalanges (Table 5.5) which also found a strong sex effect. The variables for which sex was non-significant in the Écija analysis were predominantly for the distal phalanges, which were not available for study in the gorilla analysis.

Table 7.16. One-way ANOVA for the effect of sex on gorilla phalanx length variables.

Measurement	Side	Sex	N	Mean	F	Sig. (2-tailed)
pp1L	L	male	10	28.24	16.58	**$p < 0.01$**
		female	11	23.78		
	R	male	10	27.71	11.79	**$p < 0.01$**
		female	10	23.77		
pp2L	L	male	10	54.16	48.22	**$p < 0.01$**
		female	11	45.84		
	R	male	10	54.16	53.75	**$p < 0.01$**
		female	11	45.69		
pp3L	L	male	10	61.77	76.61	**$p < 0.01$**
		female	11	51.78		
	R	male	10	61.33	49.80	**$p < 0.01$**
		female	11	51.64		
pp4L	L	male	10	58.67	61.02	**$p < 0.01$**
		female	11	49.14		
	R	male	10	58.58	42.71	**$p < 0.01$**
		female	10	49.65		
pp5L	L	male	10	48.87	43.88	**$p < 0.01$**
		female	11	40.83		
	R	male	10	48.71	32.82	**$p < 0.01$**
		female	11	40.93		
ip2L	L	male	10	34.88	22.61	**$p < 0.01$**
		female	10	29.49		
	R	male	10	34.42	39.28	**$p < 0.01$**
		female	9	29.32		

Measurement	Side	Sex	N	Mean	F	Sig. (2-tailed)
ip3L	L	male	10	42.82	54.27	**$p < 0.01$**
		female	10	36.16		
	R	male	10	42.76	37.45	**$p < 0.01$**
		female	9	36.63		
ip4L	L	male	10	41.16	34.20	**$p < 0.01$**
		female	10	34.63		
	R	male	10	40.63	15.37	**$p < 0.01$**
		female	9	34.78		
ip5L	L	male	10	31.19	8.05	**$p = 0.01$**
		female	10	26.45		
	R	male	10	31.86	19.81	**$p < 0.01$**
		female	10	25.93		

Mean values rounded to two decimal places. Significant p-values highlighted in bold. No distal phalanges were available for study. Abbreviations used: pp*L = proximal phalanx length, ip*L = intermediate phalanx length. Asterisk (*) denotes phalanx number.

7.5.3. Asymmetry in the metacarpals and phalanges

Few statistically significant size differences were identified between the gorilla left and right hands (section 7.5.1). To assess whether this trend extends to a lack of size-independent asymmetry in the gorilla hands, directional asymmetry (i.e. whether measurements are left-side or right-side dominant) and absolute asymmetry (i.e. the magnitude of the asymmetry) were calculated for each individual measurement of the hand. Figures 7.18 to 7.22 (below) present the results of this analysis for the gorilla metacarpals. Each graph represents the percentage of individuals that are left-side dominant, right-side dominant and symmetrical for each metacarpal variable. Data from this analysis can be found in Table E.18 (Appendix E).

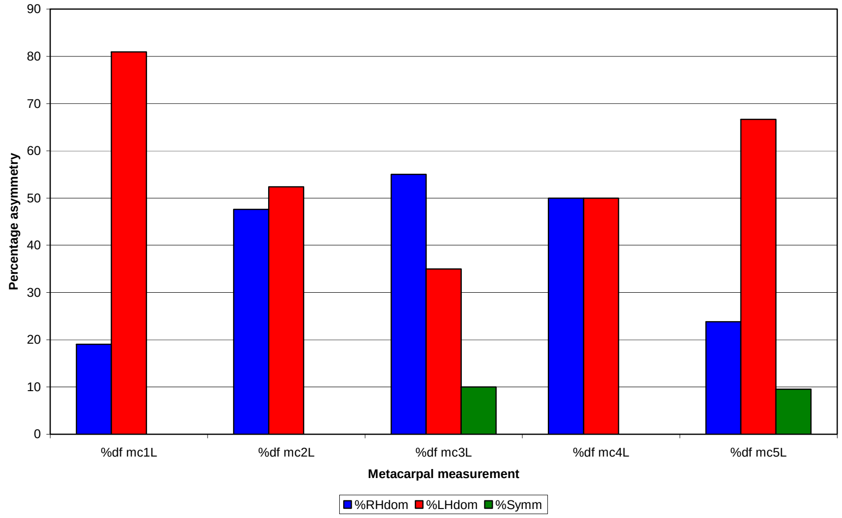


Figure 7.18.Percentage of right- and left-side dominant and symmetric individuals for gorilla metacarpal length (mc*L).

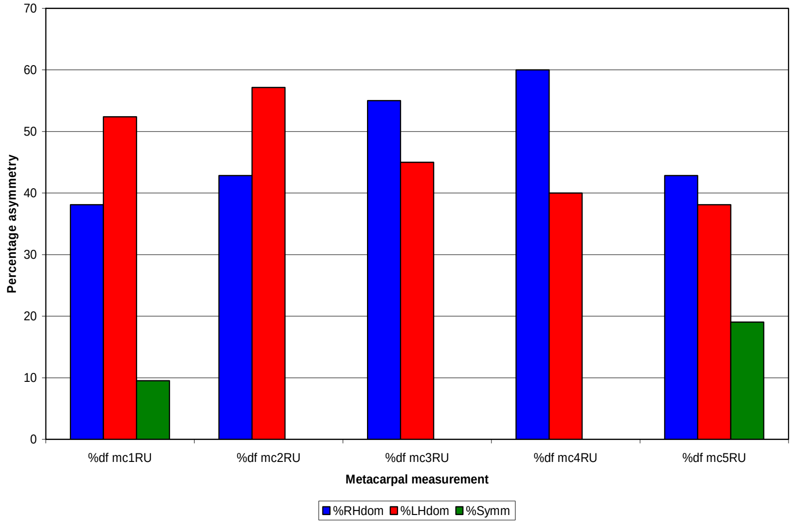


Figure 7.19.Percentage of right- and left-side dominant and symmetric individuals for gorilla metacarpal radio-ulnar diameter (mc*RU).

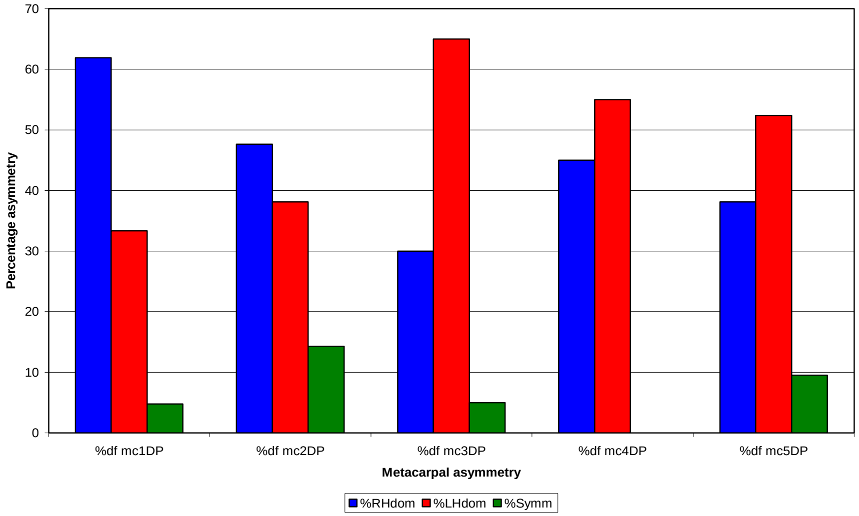


Figure 7.20. Percentage of right- and left-side dominant and symmetric individuals for gorilla metacarpal dorso-palmar diameter (mc*DP).

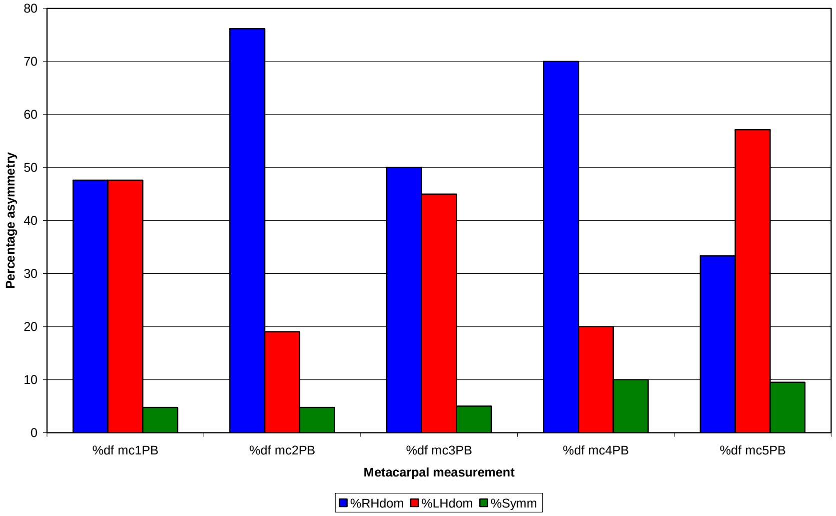


Figure 7.21. Percentage of right- and left-side dominant and symmetric individuals for gorilla metacarpal proximal breadth (mc*PB).

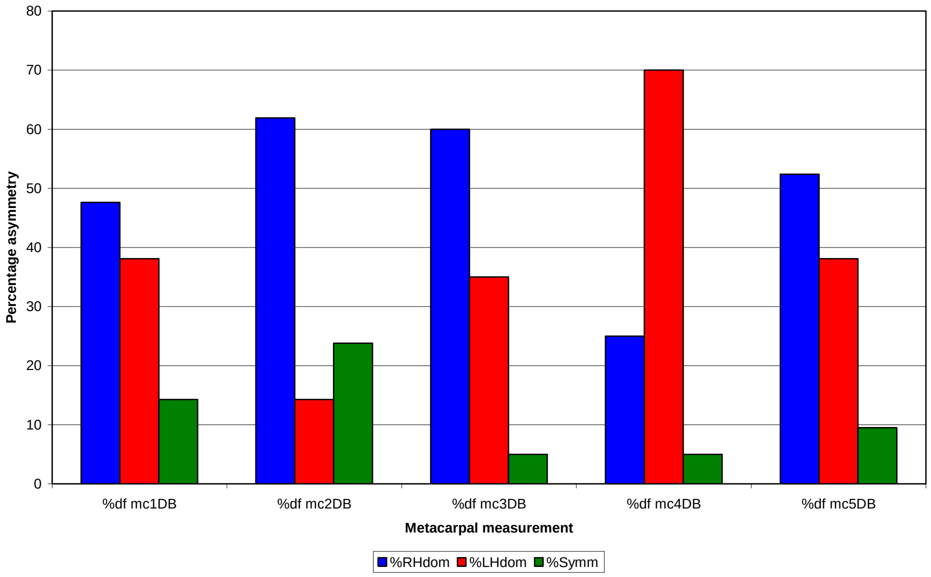


Figure 7.22. Percentage of right- and left-side dominant and symmetric individuals for gorilla metacarpal distal breadth (mc*DB). Further data available in Table E.18, Appendix E.

Figures 7.18 to 7.22 indicate that there is no clear asymmetry profile linking the metacarpal variables. As was seen with chimpanzee metacarpal asymmetry (section 7.1.3), there is a certain amount of variation in the magnitude of gorilla metacarpal asymmetry, with dominant asymmetry values ranging from 42.9% (for mc5RU) to 81% (for mc1L). The majority of variables show dominant asymmetry less than 70%, with only two variables (mc1L and mc2PB) having a percentage value greater than 70%. There is an almost equal distribution of right-side dominant and left-side dominant variables in this analysis, with 13 of the 25 measurements showing a right-side dominance and 10 of 25 showing a left-side dominance. The remaining 2 variables have the same percentage of left-side and right-side dominant individuals. The variables that show a left-side dominant asymmetry appear to be randomly spread between the metacarpals and between measurement types, which is perhaps a reflection of the influence of fluctuating rather than directional asymmetry. The overall asymmetry pattern clearly contrasts with the human metacarpal samples studied (sections 5.1.3 and 6.1.3), where strong right-side dominant asymmetry was identified. Perhaps most interestingly, the pattern in the gorilla metacarpals also contrasts with the trend for right-side dominant asymmetry in the chimpanzee metacarpals (20/25 variables). While the reduced levels and relatively equal distribution of asymmetry in the gorilla metacarpals are consistent with the notion of more symmetrical loading of the gorilla upper limb relative to the human pattern, it is unclear at this why they should tend more towards symmetry than the chimpanzee metacarpals.

From Figures 7.18 to 7.22 it was not possible to identify any clear trends within or between metacarpal measurements. The asymmetry data were therefore re-plotted to represent the asymmetry profile of each individual metacarpal. The results of this analysis are presented in Figures 7.23 to 7.27 (below).

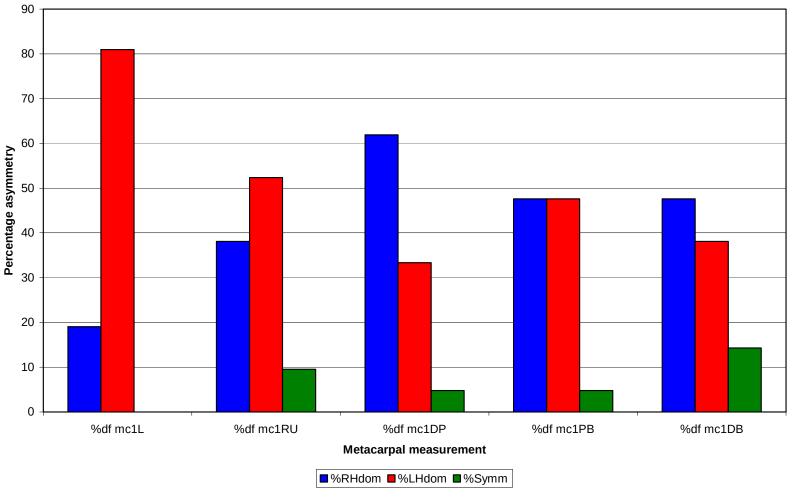


Figure 7.23. Asymmetry values for each gorilla metacarpal 1 measurement (length, radio-ulnar diameter, dorso-palmar diameter, proximal breadth and distal breadth).

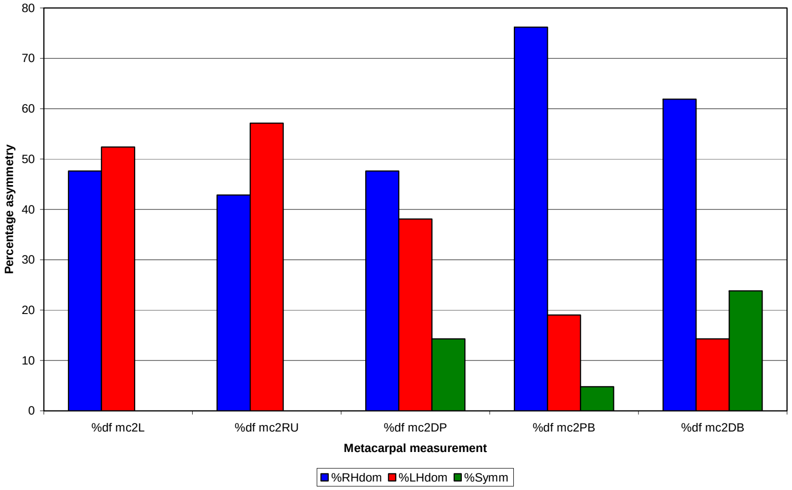


Figure 7.24. Asymmetry values for each gorilla metacarpal 2 measurement (length, radio-ulnar diameter, dorso-palmar diameter, proximal breadth and distal breadth).

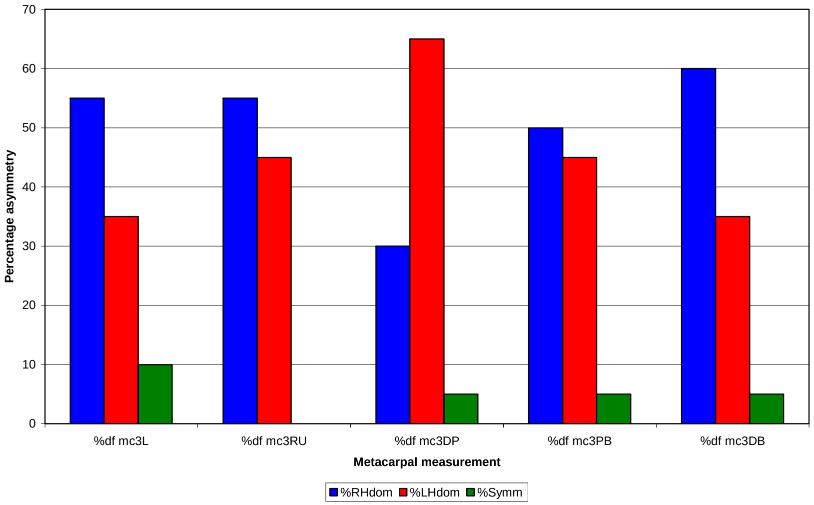


Figure 7.25. Asymmetry values for each gorilla metacarpal 3 measurement (length, radio-ulnar diameter, dorso-palmar diameter, proximal breadth and distal breadth).

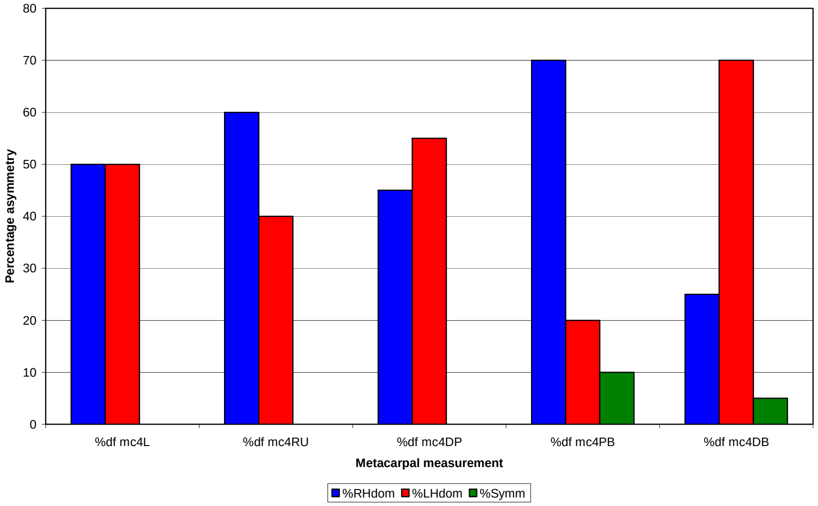


Figure 7.26. Asymmetry values for each gorilla metacarpal 4 measurement (length, radio-ulnar diameter, dorso-palmar diameter, proximal breadth and distal breadth).

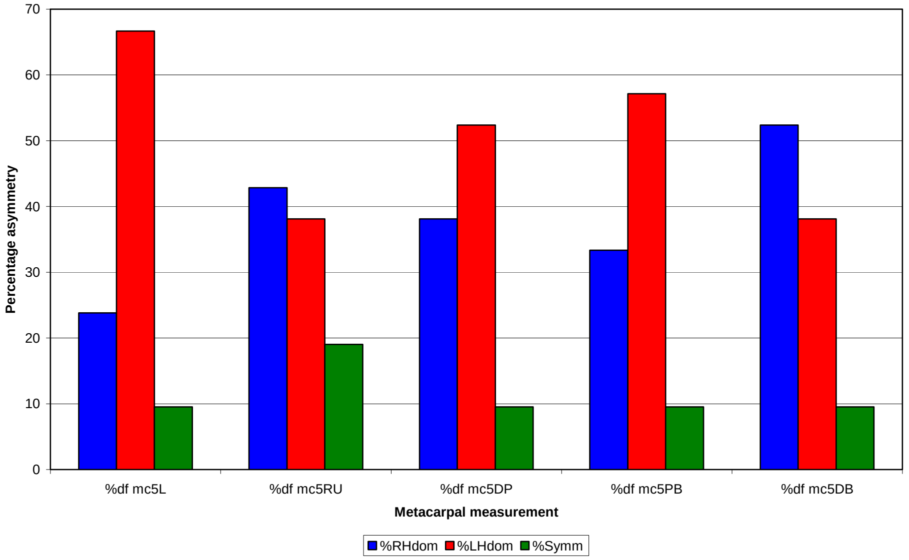


Figure 7.27. Asymmetry values for each gorilla metacarpal 5 measurement (length, radio-ulnar diameter, dorso-palmar diameter, proximal breadth and distal breadth). Further data available in Table E.18, Appendix E.

Figure 7.23 to 7.27 confirm the conclusions drawn from Figures 7.18 to 7.22, namely that there is no clear, discernible pattern in the distribution of asymmetry in the gorilla metacarpals. Each metacarpal shows a mix of right-side and left-side dominant measurements and varying magnitudes of asymmetry. As suggested above, this trend mostly likely reflects fluctuating asymmetry influences in the absence of strong directional loading on the hands. More symmetrical loading of the metacarpals may reflect recruitment of the hands in knuckle-walking, during which considerable strain is transmitted through the hand and wrist region. The hands of chimpanzees and the gorillas are both engaged in digitigrade knuckle-walking (Tuttle, 1967), yet there are clear differences between these metacarpal samples in terms of the direction of the asymmetry they express. Due to the relatively low levels of asymmetry seen in these primate samples, it is possible that the trends identified merely reflect statistical variation across a large number of metacarpal variables. However, a very tentative conclusion could be drawn that differences in object manipulation between the species, with chimpanzees more frequently engaging in certain object manipulations than gorillas (see Breuer *et al.*, 2005), could potentially lead to a move towards a clearer asymmetry, as seen in the chimpanzee sample.

The earlier analysis of chimpanzee hand (section 7.1.3) highlighted differences in asymmetry between the metacarpals and phalanges. To understand whether this was also true for the gorilla sample, percentage asymmetry was calculated for each phalanx length variable. The results of this analysis are presented in Figure 7.28 (below). Data from this analysis can be found in Table E.19 (Appendix E). Figure 7.28 confirms that as with the gorilla metacarpals, there are generally low levels of asymmetry present in the gorilla phalanges. This is in keeping with the trends identified for both the human phalanx samples (Figs 5.11 and 6.11). None of the gorilla phalanx length measurements has a dominant asymmetry score greater than 70%, and only three have greater than 60% dominant asymmetry. The overall trend for the gorilla phalanges is for left-side dominance with 6 of the 9 measurements exhibiting asymmetry in this direction. This is similar to the distribution found for the chimpanzee and Greenwich phalanges, although the asymmetry is in the opposite direction to the right-side dominant asymmetry identified in the Écija phalanx sample. The gorilla phalanges, as with the chimpanzee phalanges in Figure 7.11, show a degree of 'reversal' in the direction of dominant asymmetry between the proximal and intermediate rows. For example, pp2L is right-side dominant, but ip2L is left-side dominant. This pattern should be treated with caution however, due to the low levels of asymmetry present in these measurements. The relatively small degree of asymmetry in the sample can be interpreted as reflecting a certain amount of random and fluctuating influences on asymmetry expression, as a consequence of more symmetrical loading of the phalanges resulting from knuckle-walking. Alternatively, it is possible that the trend towards left-side dominant asymmetry reflects a preference for using the left hand in postural support (e.g. Sarringhaus *et al.*, 2005). The small sizes of the asymmetries however, make such functional interpretations problematic.

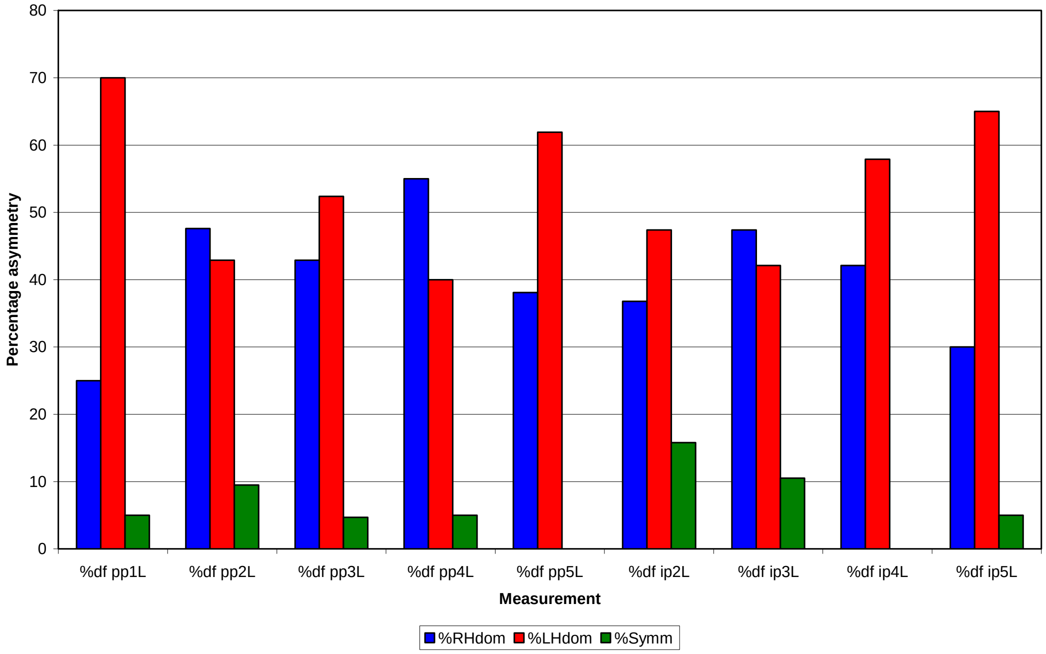


Figure 7.28. Percentage asymmetry values for each phalanx length measurement. No distal phalanges were available for study. Further data available in Table E.19, Appendix E.

7.5.4. Sex effects on asymmetry in the metacarpals and phalanges

The substantial sexual dimorphism observed in gorillas (Fleagle, 1998) was expressed in the strong sex effects identified in gorilla metacarpal dimensions in section 7.5.2. It was unclear however, whether this sexual dimorphism would be represented in asymmetry expression, particularly as the degree of asymmetry previously found in the metacarpals and phalanges was relatively low. A Mann-Whitney U test was performed to assess the effect of sex on both directional and absolute asymmetry, using the asymmetry data from section 7.5.3. The results of this analysis for the gorilla metacarpals are presented in Table 7.17 (below).

Table 7.17. A Mann-Whitney U test of the effects of sex on directional and absolute asymmetry for each of the gorilla metacarpal measurements.

Measurement	N	Directional asymmetry (cf. Steele & Mays, 1995)				Absolute asymmetry (cf. Trinkaus *et al.*, 1994)			
		mean	std dev.	U	Sig. (2-tailed)	mean	std dev.	U	Sig. (2-tailed)
mc1L	21	-0.26	3.90	39.0	p = 0.28	2.00	3.34	39.0	p = 0.28
mc2L	21	0.10	1.41	39.0	p = 0.28	1.07	0.90	32.0	p = 0.11
mc3L	20	0.09	1.11	46.0	p = 0.78	0.93	0.57	48.0	p = 0.90
mc4L	20	0.08	1.25	42.0	p = 0.57	0.97	0.77	45.0	p = 0.74
mc5L	21	-0.64	2.81	49.5	p = 0.72	2.03	2.14	41.5	p = 0.36
mc1RU	21	-1.26	5.99	34.0	p = 0.15	5.32	3.67	27.0	**p = 0.05**
mc2RU	21	-0.98	5.38	33.0	p = 0.13	4.03	4.10	51.5	p = 0.82
mc3RU	20	1.19	5.29	46.0	p = 0.78	4.60	2.92	26.0	*p = 0.07*
mc4RU	20	1.61	5.59	48.0	p = 0.91	5.00	3.11	38.0	p = 0.39
mc5RU	21	1.24	6.65	14.0	**p < 0.01**	4.71	4.90	50.0	p = 0.74
mc1DP	21	3.52	8.32	54.0	p = 0.97	7.85	4.59	52.0	p = 0.85
mc2DP	21	1.03	4.96	51.0	p = 0.81	3.60	3.78	49.0	p = 0.70
mc3DP	20	-0.72	3.54	35.0	p = 0.28	2.87	2.25	35.0	p = 0.27
mc4DP	20	-1.27	5.64	43.0	p = 0.63	4.94	3.42	26.0	*p = 0.08*
mc5DP	21	2.12	13.60	31.0	*p = 0.10*	8.64	10.80	54.5	p = 0.99
mc1PB	21	-0.64	4.14	42.0	p = 0.39	3.32	2.77	53.5	p = 0.93
mc2PB	21	3.43	3.91	30.0	*p = 0.08*	4.33	2.84	32.0	p = 0.11
mc3PB	20	0.15	2.39	47.0	p = 0.84	2.09	1.14	46.0	p = 0.78
mc4PB	20	1.16	3.68	41.0	p = 0.52	2.91	2.53	39.0	p = 0.43
mc5PB	21	-1.02	7.06	41.0	p = 0.34	4.79	5.62	46.0	p = 0.54
mc1DB	21	0.06	6.60	41.0	p = 0.35	5.08	4.91	49.0	p = 0.70
mc2DB	21	1.23	1.74	40.0	p = 0.31	1.54	1.46	51.0	p = 0.79
mc3DB	20	-0.01	2.15	41.0	p = 0.52	1.70	1.34	30.0	p = 0.14
mc4DB	20	-1.22	3.29	34.0	p = 0.25	2.67	2.65	26.0	*p = 0.08*
mc5DB	21	0.88	3.12	36.5	p = 0.20	2.58	1.95	46.5	p = 0.57

Minus values for directional asymmetry means reflects the equation used to calculate asymmetry, in which a left-side dominant individual will have a minus score. Mean and standard deviation values rounded to two decimal places. Significant p-values highlighted in bold. P-values approaching significance (between 0.055 and 0.1) highlighted in italics. Abbreviations used: mc*L = metacarpal length, mc*RU = radio-ulnar midshaft diameter, mc*DP = dorso-palmar midshaft diameter, mc*PB = proximal breadth, mc*DB = distal breadth. Asterisk (*) denotes metacarpal number.

From Table 7.17 it can be seen that there is a very limited effect of sex on either directional or absolute asymmetry in the gorilla metacarpals. There is only one statistically significant effect of sex on directional asymmetry (for mc5RU), and a further significant effect for absolute asymmetry (for mc1RU). In addition, a small number of measurements have p-values approaching significance for both directional and absolute asymmetry. The general lack of significant sexual dimorphism in metacarpal asymmetry is in stark contrast to the strong sexual dimorphism identified in metacarpal size (section 7.5.2). However, the paucity of sex effects in Table 7.17 is in keeping with the results of the corresponding analyses for the chimpanzee and Écija samples (sections 7.1.4 and 5.1.4, respectively). A comparison of mean rank values for both directional and absolute asymmetry analyses (Tables E.20 and E.21, Appendix E) found that males were more likely to be right-side dominant than females (for 16 of 25 directional asymmetry mean rank values, including mc5RU) and also to have larger asymmetry values than females (for 13 of the 25 variables, including mc1RU).

To identify whether the trends identified in Table 7.17 also extended to gorilla phalanx asymmetry, a Mann-Whitney U test was performed on directional and absolute asymmetry data for the gorilla phalanges. The results of this analysis are presented in Table 7.18.

Table 7.18. A Mann-Whitney U test of the effects of sex on directional and absolute asymmetry for each of the gorilla phalanx measurements.

Measurement	N	Directional asymmetry (cf. Auerbach & Ruff, 2006)				Absolute asymmetry (cf. Trinkaus et al., 1994)			
		mean	std dev.	U	Sig. (2-tailed)	mean	std dev.	U	Sig. (2-tailed)
pp1L	20	-0.99	2.69	35.0	p = 0.27	2.10	2.07	49.0	p = 0.96
pp2L	21	-0.14	1.69	38.0	p = 0.24	1.08	1.34	51.0	p = 0.80
pp3L	21	-0.51	1.89	46.0	p = 0.56	1.52	1.29	36.0	p = 0.19
pp4L	20	0.17	1.66	37.0	p = 0.34	1.22	1.12	34.0	p = 0.24
pp5L	21	-0.05	2.41	52.0	p = 0.86	1.74	1.66	29.0	*p = 0.07*
ip2L	19	-1.08	6.11	41.0	p = 0.78	4.01	5.74	33.0	p = 0.36
ip3L	19	0.19	2.16	35.5	p = 0.46	1.60	1.47	35.5	p = 0.46
ip4L	19	-0.96	3.13	42.0	p = 0.84	1.97	3.03	19.0	**p = 0.04**
ip5L	20	1.13	14.48	43.0	p = 0.63	6.14	13.45	42.0	p = 0.58

Minus values for directional asymmetry means reflects the equation used to calculate asymmetry, in which a left-side dominant individual will have a minus score. Mean and standard deviation values rounded to two decimal places. Significant p-values highlighted in bold. P-values approaching significance (between 0.055 and 0.1) highlighted in italics. Abbreviations used: pp*L = proximal phalanx length, ip*L = intermediate phalanx length. No distal phalanges were available for study. Asterisk (*) denotes phalanx number.

The results in Table 7.18 indicate that there is a very limited effect of sex on asymmetry in the gorilla phalanges, as was the case for the gorilla metacarpals. There are no statistically significant effects of sex on directional asymmetry, and for absolute asymmetry only ip4L shows a significant effect (p = 0.04). These results are in keeping with those identified for the same analyses of chimpanzee (Table 7.6) and Écija (Table 5.7) phalanges. When male and female mean rank values are compared (Tables E.22 and E.23, Appendix E), it can be seen that females tend to be right-side dominant more frequently than males (for 6 of 9 directional asymmetry mean rank values) and also exhibit larger asymmetry values (for 6 of 9 absolute asymmetry mean rank values). This pattern of female-dominant asymmetry contrasts with the pattern of male-dominant asymmetry seen for the gorilla metacarpals. The directional asymmetry trend for mean rank values is similar between the gorillas, chimpanzees and Écija phalanges, but the gorilla phalanx trend in absolute asymmetry differs from the other samples.

Together these results lend further (albeit tentative) support to the notion that the metacarpals and phalanges exhibit differing asymmetry profiles, in both the human and non-human primate samples.

7.5.5. Individual asymmetry

The analysis of individual asymmetry in the chimpanzee hands (section 7.1.5) found roughly equal numbers of right- and left-side dominant individuals. This suggested that while individuals may exhibit a certain degree of directional asymmetry, there is no clear trend for group-level asymmetry. This was in keeping with some areas of research into great ape hand preferences (e.g. McGrew & Marchant, 1997). To assess the extent to which this trend holds for individual asymmetry in gorilla hand bones, individual asymmetry was calculated using the method outlined in section 5.1.6. The results of this analysis are presented in Figure 7.29.

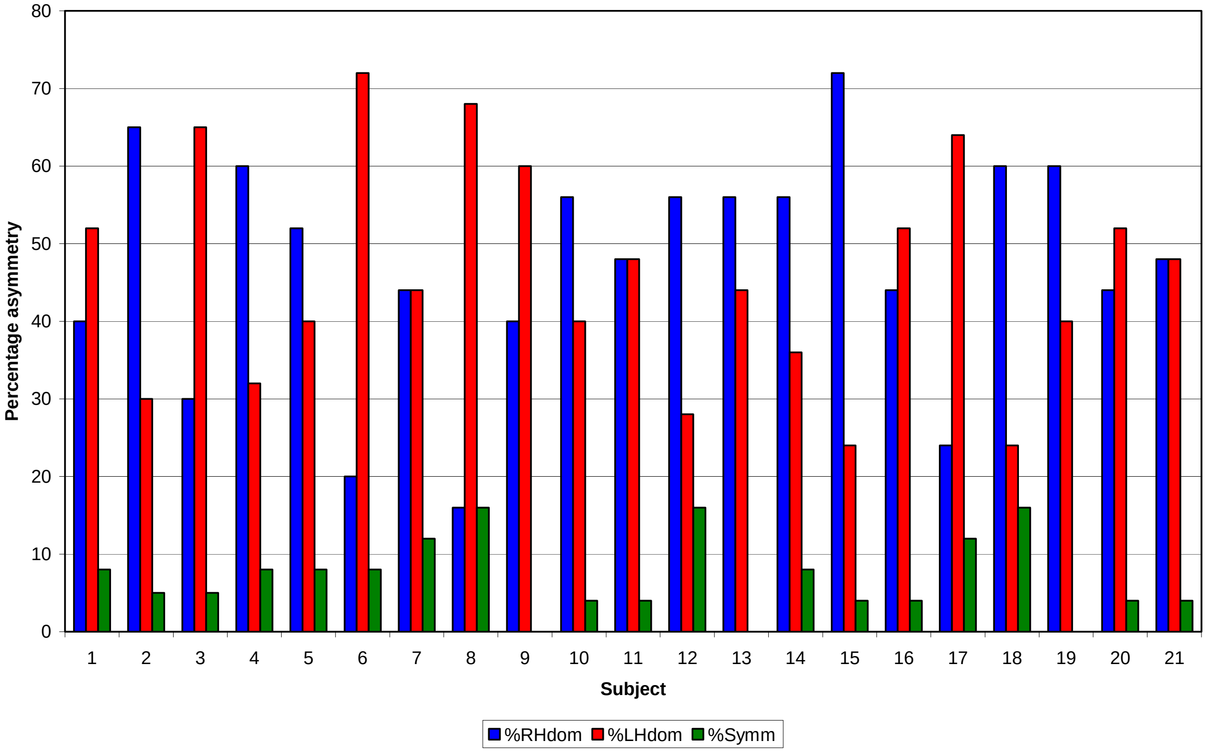


Figure 7.29. For each individual in the gorilla sample, the percentage of right-side dominant, left-side dominant and symmetric scores for all metacarpal measurements.

From Figure 7.29 it can be seen that there is a relatively even distribution of asymmetry between individuals with 10 of the 21 individuals (47.6%) displaying an overall right-side dominance for metacarpal measurements, compared to 8 of the 21 individuals (38.1%) who are left-side dominant. The remaining three individuals show equal numbers of left-side and right-side dominant measurements. This indicates that the gorilla metacarpal sample shows more group-level 'symmetry' than either the chimpanzee or human samples. This also supports the trend for the gorilla hand bones to exhibit on the whole, less directional (i.e. clearly left-side or right-side) asymmetry than the chimpanzee hand bones. As might be expected given the asymmetry analysis in section 7.5.3, the general degree of asymmetry across individuals is low with only two subjects displaying a dominant asymmetry greater than 70%.

Figure 7.30 presents the results of the analysis of individual asymmetry in the gorilla phalanx sample and indicates that there is a general trend of left-side dominance, with 10 of 21 individuals showing a left-side dominant asymmetry for phalanx length measurements. In comparison, six individuals show right-side dominant asymmetry and five show equal numbers of left-side and right-side dominant phalanx variables. Although the Écija individual sample were predominantly right-side dominant for phalanx variables (Fig. 5.13), the results of the gorilla phalanx analysis are similar to those found in both the chimpanzee and Greenwich phalanges (Figs 7.13 and 6.13, respectively). It is interesting to note that a number of individuals in Figure 7.30 show greater than 70% left-side dominant asymmetry. However, due to the small number of phalanx length measurements contributing to individual asymmetry profiles, caution must be taken in order to avoid over-interpretation of this finding.

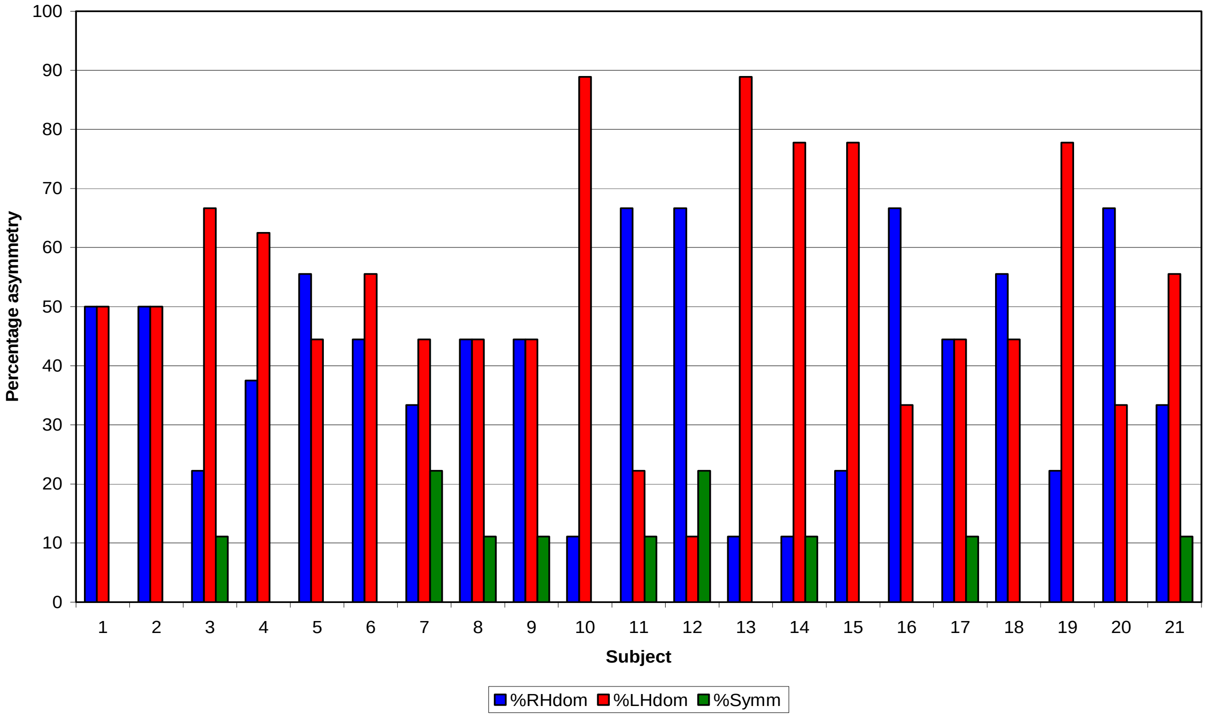


Figure 7.30. For each individual in the gorilla sample, the percentage of right-side dominant, left-side dominant and symmetric scores for all phalanx measurements.

7.5.6. Summary of gorilla metacarpal and phalanx metric analysis

The analyses in the sections above highlight a number of ways in which the asymmetry profiles of the gorilla hand bone sample is similar to that of the chimpanzee sample. The most striking similarity is the relatively low levels of left/right differences present in both samples. The Wilcoxon tests in section 7.5.1 found very few statistically significant size differences between left and right gorilla metacarpal and phalanx measurements. This general lack of size differences is reflected in low levels of size-independent asymmetry in the hands, relative to the human samples (see Figs 7.18 to 7.27). Low levels of asymmetry were also found in the analyses of individual asymmetry in gorilla hand variables (section 7.5.5). Both the gorilla and chimpanzee exhibit variation in asymmetry magnitude between the metacarpal measurements.

One of the areas where the gorilla hands differ most clearly from the chimpanzee sample is in terms of sexual dimorphism. Both the gorilla metacarpal and phalanx variables (section 7.5.2) show statistically significant size differences between males and females (a relationship also identified in the Écija hands). This finding is to be expected, given the relative differences in sexual dimorphism identified in these two non-human primate species (Fleagle, 1998). This sexual dimorphism in gorilla hand bone dimensions did not translate, however, into differences in the magnitude of direction of asymmetry, where few significant sex effects were found (section 7.5.4). The gorilla metacarpals differ from the chimpanzee and human samples in the direction of the asymmetry they display. While the human and chimpanzee samples show predominantly right-side dominant asymmetry in their metacarpal properties, the gorilla metacarpals display an almost equal distribution of left-side and right-side dominant asymmetry. In comparison, the left-side dominant asymmetry exhibited by the gorilla phalanges is in line with the pattern found in the chimpanzee and Greenwich phalanges (the Écija phalanges were found to be right-side dominant).

Interpreting the patterns and trends identified in the analyses that comprise section 7.5 is difficult when asymmetries are generally small in size and sample sizes are also low. The generally low level of asymmetry is most likely to be a result of symmetrical loading in the gorilla hands due to the locomotor functions of this region. Therefore, the presence of left/right differences in this sample may reflect the more ‘random’ influence of fluctuating asymmetry on these bones.

7.6. Gorilla humerus metric analysis

Data were collected on gorilla humeral material for the purposes of comparison with the gorilla metacarpal and phalanx data described in section 7.5. With contrasting patterns of metric bilateral asymmetry identified in the chimpanzee humeri and hands, and the lack of a clear direction to asymmetry in the gorilla metacarpals, exploring asymmetry in the gorilla humerus will hopefully be informative regarding the overall pattern of upper limb asymmetry in this gorilla sample. Descriptive statistics for this sample are reported in Table E.24 (Appendix E). Box-and-whisker plots identified a number of outliers in the data set. As per previous analyses, where outliers were identified they were checked for error. If an error in data collection and processing was found then the data point was excluded from analysis. If no error was found then the value was not removed and non-parametric tests were selected. Histograms and p-p plots (plotted for males and females separately) confirmed the overall normal distribution of the data. The structure of this data analysis follows that of the chimpanzee humeri, described in section 7.2.

7.6.1. Significance testing

To identify the presence of statistically significant size differences between left and right humerus measurements, a Wilcoxon test was performed on the data. This test was chosen as the non-parametric equivalent to the t-test. The results of this analysis are presented in Table 7.19 (below) and indicate that only two variables (MxTDm and MxSDm) show a statistically significant size difference between the left and right measurements, with another two variables (MxDm and MnCir) approaching significance. This finding follows the same pattern seen for the chimpanzee humeri (section 7.2.1) and also the gorilla metacarpals and phalanges (section 7.5.1). Both the significant size differences in this analysis are for humeral head dimensions. Articular dimensions were also found to show significant left/right size differences in the chimpanzee samples. This lends further support to the notion that there are certain differences in joint mobility between the left and right arms (see Rafferty & Ruff, 1994), possibly reflecting differences in bilateral recruitment.

Table 7.19. Wilcoxon test results for the combined-sex gorilla humerus sample.

Measurement	Side	N	Mean	Std dev.	Sig. (2-tailed)
MxL	L	21	422.14	48.99	$p = 0.97$
	R	21	422.05	49.61	
MxDm	L	21	33.34	3.93	*$p = 0.08$*
	R	21	33.17	3.77	
MnDm	L	21	28.25	3.05	$p = 0.52$
	R	21	28.22	3.18	
MnCir	L	21	93.71	11.10	*$p = 0.08$*
	R	21	93.14	10.77	
CirHd	L	21	176.14	23.28	$p = 0.36$
	R	21	175.43	23.86	
MxTDm	L	21	57.84	7.88	**$p = 0.03$**
	R	21	58.21	8.09	
MxSDm	L	21	55.59	7.98	**$p < 0.01$**
	R	21	54.43	7.37	
EpBr	L	21	91.77	13.71	$p = 0.51$
	R	21	92.10	14.42	
TCBr	L	21	64.50	9.51	$p = 0.39$
	R	21	64.41	9.35	

Mean and standard deviation values rounded to two decimal places. Significant p-values highlighted in bold. P-values approaching significance (between 0.055 and 0.1) highlighted in italics. Abbreviations used: MxL = maximum length, MxDm = maximum midshaft diameter, MnDm = minimum midshaft diameter, MnCir = minimum shaft circumference, CirHd = circumference of head, MxTDm = maximum transverse diameter of head, MxSDm = maximum sagittal diameter of head, EpBr = epicondylar breadth, TCBr = trochlea-capitulum breadth.

Comparing mean values for the left and right measurements indicates a trend for left-side humerus measurements to be larger than right-side measurements with 7 of the 9 variables having larger mean values on the left side. The chimpanzee humerus sample also showed a similar but smaller trend towards larger left humerus measurements, but both the Écija and Greenwich humeri were clearly larger on the right-side.

7.6.2. Analysis of Variance (ANOVA)

Given the strong sexual dimorphism identified in gorilla metacarpal and phalanx measurements (section 7.5.1) it was predicted that the same trend would also be found for the gorilla humerus measurements. To test this prediction a one-way ANOVA was performed on the data. The results of this analysis are presented in Table 7.20 (below). As expected, Table 7.20 identifies a strong, statistically significant effect of sex on all humerus measurements. This result contrasts with the chimpanzee humeri which showed only a few significant sex effects (section 7.2.2). It is similar to the Écija humeri however, which displayed clear sexual dimorphism (section 5.2.2). When the mean values in Table 7.20 are compared it can be seen that males are larger than females, as would be expected given the nature of sexual dimorphism in this species.

Table 7.20. One-way ANOVA for the effect of sex on gorilla humerus variables.

Measurement	Side	Sex	N	Mean	F	Sig. (2-tailed)
MxL	L	male	10	468.90	126.61	**$p < 0.01$**
		female	11	379.64		
	R	male	10	469.10	115.33	**$p < 0.01$**
		female	11	379.27		
MxDm	L	male	10	36.66	40.58	**$p < 0.01$**
		female	11	30.33		
	R	male	10	36.41	45.03	**$p < 0.01$**
		female	11	30.23		
MnDm	L	male	10	30.86	44.44	**$p < 0.01$**
		female	11	25.87		
	R	male	10	30.91	40.44	**$p < 0.01$**
		female	11	25.78		
MnCir	L	male	10	103.80	70.37	**$p < 0.01$**
		female	11	84.55		
	R	male	10	102.90	68.92	**$p < 0.01$**
		female	11	84.27		
CirHd	L	male	10	198.90	196.57	**$p < 0.01$**
		female	11	155.45		
	R	male	10	198.60	171.60	**$p < 0.01$**
		female	11	154.36		

Measurement	Side	Sex	N	Mean	F	Sig. (2-tailed)
MxTDm	L	male	10	65.46	158.29	**$p < 0.01$**
		female	11	50.92		
	R	male	10	66.01	148.92	**$p < 0.01$**
		female	11	51.12		
MxSDm	L	male	10	63.25	140.32	**$p < 0.01$**
		female	11	48.62		
	R	male	10	61.45	124.35	**$p < 0.01$**
		female	11	48.05		
EpBr	L	male	10	104.86	127.63	**$p < 0.01$**
		female	11	79.87		
	R	male	10	105.72	108.02	**$p < 0.01$**
		female	11	79.73		
TCBr	L	male	10	72.97	58.85	**$p < 0.01$**
		female	11	56.81		
	R	male	10	73.27	114.46	**$p < 0.01$**
		female	11	56.35		

Mean values rounded to two decimal places. Significant p values highlighted in bold. Abbreviations used: MxL = maximum length, MxDm = maximum midshaft diameter, MnDm = minimum midshaft diameter, MnCir = minimum shaft circumference, CirHd = circumference of head, MxTDm = maximum transverse diameter of head, MxSDm = maximum sagittal diameter of head, EpBr = epicondylar breadth, TCBr = trochlea-capitulum breadth.

7.6.3. Asymmetry in the humerus

The analysis of chimpanzee humeral asymmetry (section 7.2.3) identified a trend towards left-side dominant asymmetry, in comparison to the clear right-side dominant pattern found in the human samples. To test whether left-side dominant asymmetry was the predominant asymmetry pattern for the gorilla humerus sample, size-independent asymmetry was calculated using the equations described in section 5.1.3. Figure 7.31 (below) plots the percentage of individuals that are right-side dominant, left-side dominant and symmetrical for each humerus measurement. The data from this analysis are provided in Table E.25 (Appendix E).

Figure 7.31 indicates that there is little variation between dominant asymmetry scores in the gorilla humerus variables, with scores ranging from 52.4% (for MxL, MnDm and MnCir) to 76.2% (for MxSDm). This range of variation is reduced relative to that seen in the chimpanzee humerus, although most of this difference is accounted for by the strong asymmetry displayed by the chimpanzee TCBr variable. A similar degree of variation is found for the modern human humerus samples (Figs 5.14 and 6.14) and also the gorilla metacarpal and phalanx samples (section 7.5.3). It is worth noting that some of the largest asymmetry values in the gorilla humerus are found for articular surface dimensions, supporting earlier observations that these measurements show the highest degree of asymmetry in the non-human primate samples.

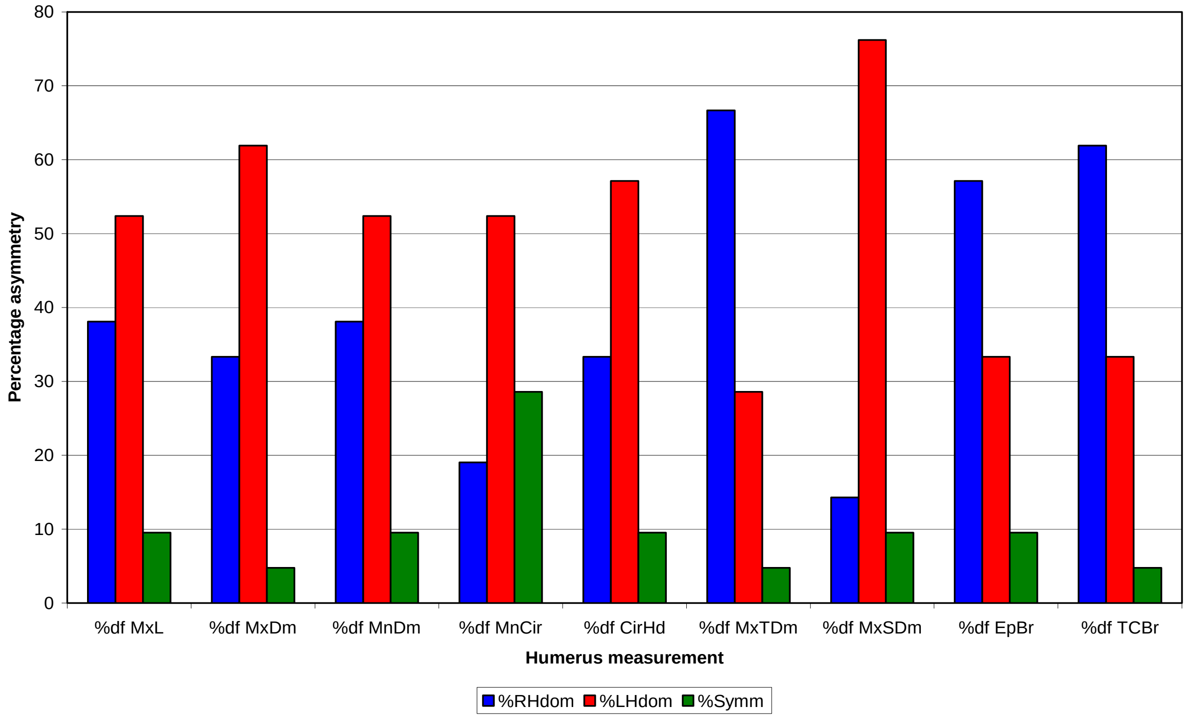


Figure 7.31. Percentage of right- and left-side dominant and symmetrical individuals for gorilla humerus measurements. Further data available in Table E.25, Appendix E.

The pattern in gorilla humerus asymmetry is towards left-side dominant asymmetry, with 6 of the 9 measurements exhibiting asymmetry in this direction. The chimpanzee humeri also displayed a tendency for left-side dominance, although the magnitude of asymmetry appears to be greater for the gorillas than the chimpanzees. The left-side dominance in both these samples contrasts with the clear right-side dominance exhibited by both the modern human humerus samples and lends further support to the conclusion that reduced functional asymmetric loading of the non-human primate upper limb allows for more expression of the influence of fluctuating asymmetry, reflected in increased numbers of left-side dominant measurements.

7.6.4. Sex effects on asymmetry in the humerus

Despite the strong sexual size dimorphism identified in the gorilla metacarpals and phalanges (section 7.5.2), this did not translate into observable sexual dimorphism in hand bone asymmetry (section 7.5.4). Therefore, given the clear sexual dimorphism also identified in gorilla humerus dimensions (section 7.6.2), it was not clear whether these male and female differences would be reflected in dimorphism in humeral asymmetry. To test this, a Mann-Whitney U test was performed on both directional and absolute asymmetry data for the gorilla humeri. The results of this analysis are presented in Table 7.21 (below), and indicate that sex has only a negligible effect on both directional and absolute asymmetry in the gorilla humerus. No sex effect was found for directional asymmetry (although MxSDm was found to be approaching significance), and for absolute asymmetry only MxSDm exhibited a statistically significant effect. This finding follows from previous analyses, which failed to identify substantial sexual dimorphism in either the chimpanzee (section 7.2.4) or modern human samples (sections 5.2.4 and 6.2.4), or the gorilla hands. Comparison of the mean rank values for this analysis (Tables E.26 and E.27, Appendix E) indicates that males are more likely to be right-side dominant than females (for 5 of 9 measurements), and also to have larger asymmetry scores (for 5 of 9 measurements). This was found to be true for MxSDm (which displayed a significant effect for absolute asymmetry), indicating that males are more asymmetric than females. This is an interesting finding given the strong left-side dominant asymmetry profile for this measurement in Figure 7.31. The reasons behind this trend are unclear, but again suggest differences in the expression of asymmetry between the articular surfaces and diaphyses in these non-human primate samples.

Table 7.21. Mann-Whitney U test of the effects of sex on directional asymmetry and absolute asymmetry values for each of the gorilla humerus measurements.

Measurement	N	Directional asymmetry (cf. Steele & Mays, 1995)				Absolute asymmetry (cf. Trinkaus *et al.*, 1994)			
		mean	std dev.	U	Sig. (2-tailed)	mean	std dev.	U	Sig. (2-tailed)
MxL	21	-0.04	0.89	40.5	p = 0.32	0.67	0.58	54.0	p = 0.96
MxDm	21	-0.46	1.41	44.5	p = 0.48	1.26	0.79	51.0	p = 0.80
MnDm	21	-0.11	2.45	52.5	p = 0.88	1.70	1.78	54.5	p = 0.99
MnCir	21	-0.57	1.31	48.0	p = 0.64	1.10	0.92	55.0	p = 1.00
CirHd	21	-0.43	1.88	43.5	p = 0.44	1.49	1.25	50.5	p = 0.77
MxTDm	21	0.60	1.29	44.0	p = 0.47	1.14	0.82	46.5	p = 0.57
MxSDm	21	-1.96	2.03	30.0	*p = 0.08*	2.20	1.96	19.0	**p = 0.01**
EpBr	21	0.27	1.82	40.5	p = 0.32	1.44	1.12	44.5	p = 0.48
TCBr	21	-0.02	4.25	49.0	p = 0.71	2.72	3.91	50.0	p = 0.76

Mean and standard deviation values rounded to two decimal places. Significant p-values highlighted in bold. P-values approaching significance (between 0.055 and 0.1) highlighted in italics. Abbreviations used: MxL = maximum length, MxDm = maximum midshaft diameter, MnDm = minimum midshaft diameter, MnCir = minimum shaft circumference, CirHd = circumference of head, MxTDm = maximum transverse diameter of head, MxSDm = maximum sagittal diameter of head, EpBr = epicondylar breadth, TCBr = trochlea-capitulum breadth.

7.6.5. Individual asymmetry

The asymmetry profile of each individual in the gorilla sample was calculated for their humerus measurements, using the asymmetry data from section 7.6.3. The results of this analysis are presented in Figure 7.32 (below), indicating the percentage of left-side dominant, right-side dominant and symmetrical humerus measurements for each individual. It can be seen from Figure 7.32 that there is no clear trend in humerus asymmetry across the individuals in the gorilla sample, with 11 of the 21 individuals displaying predominantly right-side dominant asymmetries, compared with 10 individuals who display left-side dominant asymmetry. The relatively equal distribution of dominant asymmetry across the individuals is similar to that identified in both the hands and humeri of the chimpanzee sample (section 7.1.5 and 7.2.5, respectively) and the gorilla hands (section 7.5.5). However, it is worth bearing in mind the relatively small sample sizes in question, and the small number of humerus measurements from which the individual asymmetry profile is generated. Despite these considerations, the findings of this analysis suggest a lack of clear group-level humeral asymmetry in this sample, although clear individual asymmetries are present in some instances. Although some studies of gorilla behavioural lateralisation have indicated group-level hand preferences (e.g. Shafer, 1993; Vauclair & Fagot, 1993), studies of wild gorilla groups have not drawn the same conclusions (Byrne & Byrne, 1991). As the gorilla sample from the current study was taken from a wild-shot population, this analysis supports the existing data on wild gorilla behavioural lateralisation.

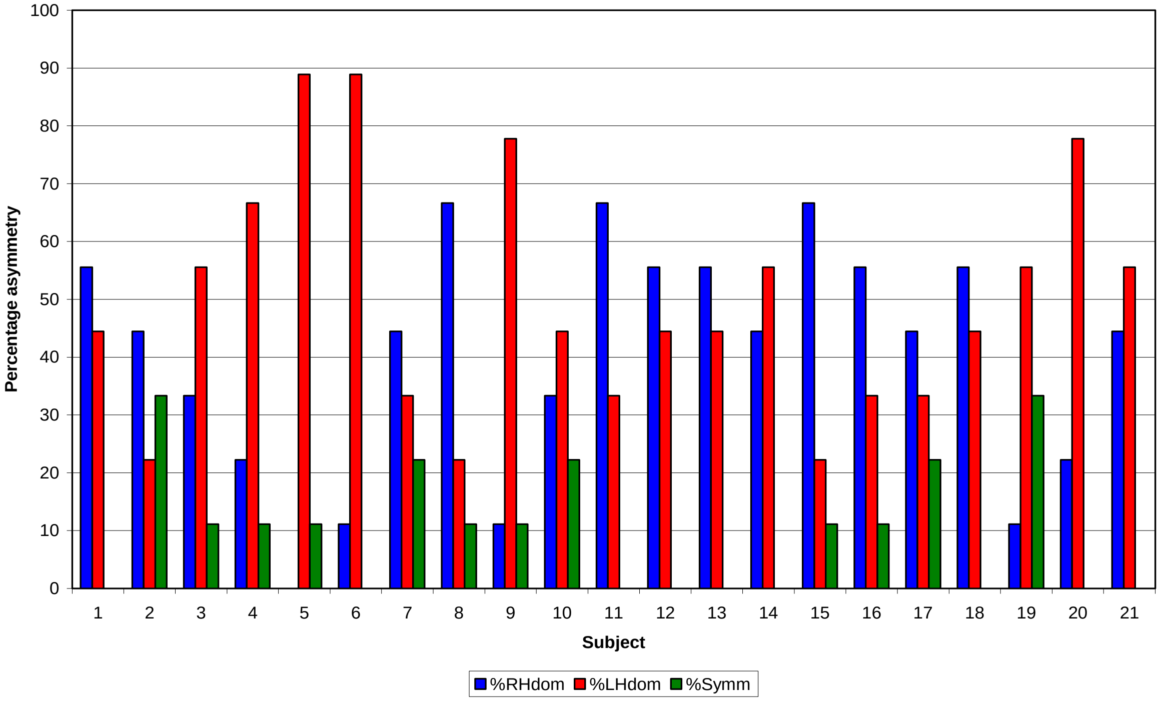


Figure 7.32. For each individual, the percentage of right-side dominant, left-side dominant and symmetric scores for all gorilla humeral measurements.

7.6.6. Summary of gorilla humerus metric analysis

The analysis of the gorilla humeri highlights the low levels of bilateral asymmetry observable in the gorilla upper limb relative to that seen in the Écija humeri (section 5.2), and to a lesser extent, the Greenwich humeri (section 6.2). A Wilcoxon test (section 7.6.1) identified a dearth of statistically significant size differences between left and right gorilla humerus measurements. This trend was reflected in the size-independent asymmetry profile of the humerus represented in Figure 7.31, which found only one variable with a dominant asymmetry score greater than 70%. This is compared to seven variables with greater than 70% dominant asymmetry values in the Écija humerus sample (Fig. 5.14). This reduction in humeral asymmetry is likely to be linked to the observed increase in left-side dominant asymmetries in the gorilla humerus, which were found for 6 of the 9 humerus measurements in Figure 7.31. The symmetrical recruitment of the primate upper limbs in locomotor-directed activities will promote symmetry in the arms and hands and may over-shadow any potential effects of hand preferences for non-locomotor behaviours. With no directional asymmetry at work, fluctuating asymmetry is likely to be influential and this could account for the increase in the number of left-side dominant asymmetries recorded. Due to the small sample sizes and generally low levels of asymmetry present in the gorilla humerus, it is not possible to speculate on functional reasons for the trend towards left-side dominance. However, it is possible that the left-side dominant humeral asymmetry reflects a preference for the use of the left-arm in postural support (Sarringhaus *et al.*, 2005), although the left-side dominant pattern of gorilla metacarpal asymmetry does not support the notion of the corresponding preferential use of the right hand for manipulative tasks.

The analyses in section 7.6 also indicate that the trend for greater asymmetry in articular surface dimensions identified in the chimpanzee humerus analysis (section 7.2) continues to be one of the identifying features of upper limb asymmetry in these non-human primate samples. While it is expected that long bone diaphyses would display more bilateral asymmetry than articular surfaces in human skeletal material (Ruff, 2000), it is possible that differences in joint mobility in primates would affect asymmetry in the articular surfaces in non-human primates (Rafferty & Ruff, 1994). Interestingly, in the analysis of sex differences in humerus asymmetry scores (section 7.6.4), males were found to have statistically significantly larger MxSDm dimensions than females. No significant sexual dimorphism was found for any other humerus measurements. Clear sexual dimorphism was found in humerus size (section 7.6.2) as expected, given the degree of sexual dimorphism observed in live gorilla groups (Fleagle, 1998).

Finally, it was observed that, as with the chimpanzee sample and the gorilla hands, individual asymmetry profiles for the gorilla humeri identified no clear directional trend in group-level asymmetry (Fig. 7.32), although a number of individual showed clear left-side and right-side dominant asymmetry. This lends support to the observation that group-level hand preferences are not present in wild great ape populations, even when individual hand preferences are apparent (McGrew & Marchant, 1997).

7.7. Musculoskeletal stress markers (MSM) in the gorilla hand

The analysis of asymmetry in chimpanzee MSM development (sections 7.3 and 7.4) concluded that asymmetry in that sample followed a broadly similar pattern to that found in the Écija and Greenwich samples, i.e. very little difference between right and left MSM expression, some differences in frequency of expression, and a limited association of MSM with sex. Drapeau (2008) found that gorilla MSM were similar to those of chimpanzees with regards to having a reduced degree of asymmetry relative to her sample of human humerus MSM. Drapeau also found that gorillas were similar to chimpanzees in terms of the direction of MSM asymmetry. However, chimpanzee humerus MSM were significantly more rugose than those of gorillas. To explore this relationship further, and to identify whether these patterns were also present in the gorilla hand, comparative MSM data from the gorilla upper limb was analysed. The structure of the gorilla analyses follows that of the chimpanzee analyses in sections 7.3 and 7.4.

7.7.1. Asymmetry in hand MSM

As with the chimpanzee hand MSM sample, the *flexor digitorum profundus* could not be included in this analysis as the distal phalanges were not available for study. The *flexor pollicis longus* MSM is not present on the gorilla pollical distal phalanx (Aiello & Dean, 1990; Hamrick e*t al.*, 1998). Data from the *flexor digitorum superficialis* 2 to 5 MSM were once again analysed as one data point. Figure 7.33 presents the results of the asymmetry analysis for the gorilla hand MSM. Data from this analysis can be found in Table E.28 (Appendix E).

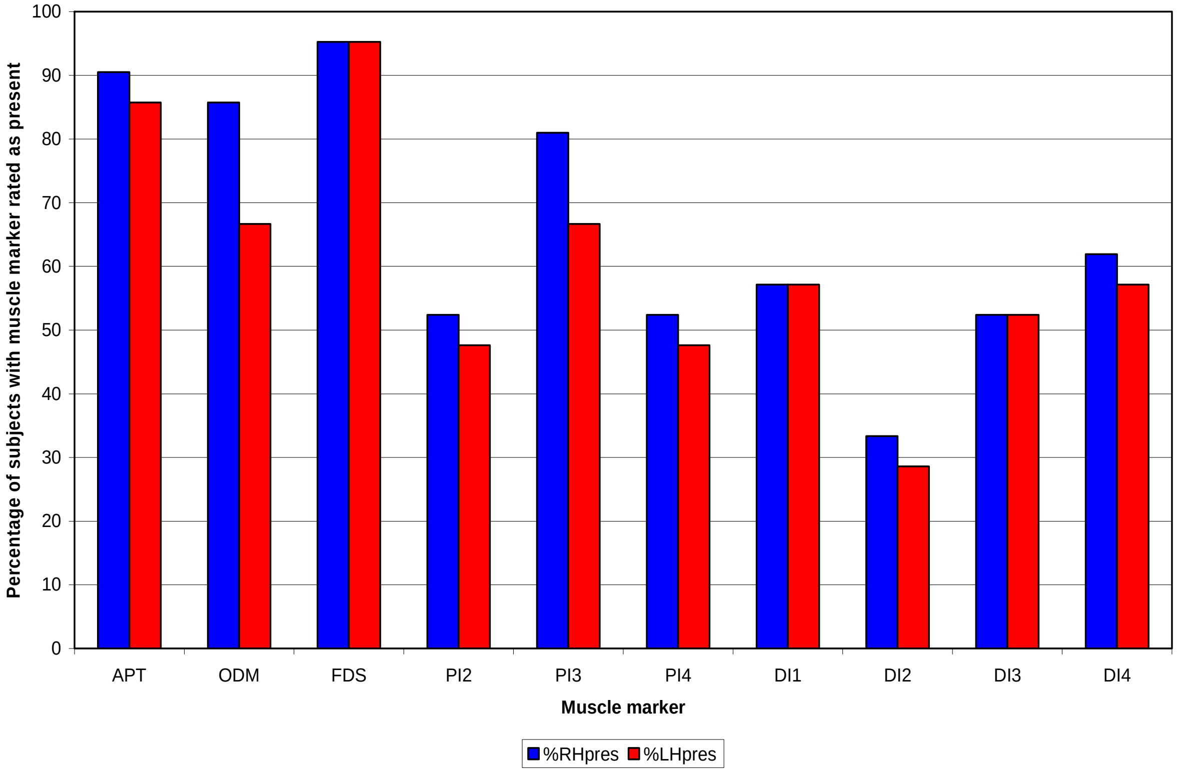


Figure 7.33. For each of the 10 gorilla hand MSM, the percentage scored as ‘present’ for the left hand (red) and the right hand (blue). Abbreviations used: APT = adductor pollicis (transverse head), ODM = oppenens digiti minimi, FDS = flexor digitorum superficialis (2-5), PI = palmar interosseous, DI = dorsal interosseous. Due to the absence of distal phalanges in the gorilla sample, it was not possible to score the flexor digitorum profundus MSM. Further data available in Table E.28, Appendix E.

From Figure 7.33 it can be seen that the general level of asymmetry in this sample is low, with only ODM (19%) and PI3 (14.3%) displaying left/right asymmetries greater than 10%. The level of asymmetry identified in Figure 7.33 is, on the whole, similar to that displayed by the chimpanzee hand MSM (section 7.3.1), where only three MSM (ODM, DI1 and DI3) showed percentage asymmetry differences greater than 10%. This low level of asymmetry in the gorilla hand MSM reflects the generally low levels of asymmetry identified in the gorilla metric analyses (sections 7.5 and 7.6). Across all the samples studied, the ODM has consistently exhibited the highest levels of asymmetry. The muscle is involved in the rotation of the mc5 into opposition with the thumb, as well as flexing the 5th carpometacarpal joint (Table 3.4), suggesting possible differences between the left and right hands in activities including this action. Due to the availability of MSM for study, it was not possible to compare the expression of the MSM of prime movers with their corresponding synergists and antagonists (see Table 5.14).

With regards to the direction of asymmetry displayed in the gorilla hands, 7 MSM display right-side dominant asymmetry while 2 MSM have equal numbers of left and right ‘present’ scores. No MSM in this analysis were found to be left-side dominant. This pattern of right-side dominant asymmetry follows the pattern seen in the Écija and Greenwich hand MSM (sections 5.3.1 and 6.3.1, respectively), but differs from the left-side dominant trend seen in the chimpanzee hand data. This level of right-side dominance is greater than that found in the metric analysis of the gorilla metacarpals (which showed only slightly more right-side dominant measurements that left-side dominant) and phalanges (which tended towards left-side dominant values) (section 7.5.3). Why the gorilla and chimpanzee had MSM should differ in the direction of asymmetry is unclear, although it is worth considering the relatively low levels of asymmetry between the MSM scores when interpreting these results.

As with previous samples, Figure 7.33 highlights the degree of variation that occurs between the asymmetry profiles of the different MSM. For the most part, gorilla hand MSM are more frequently scored as ‘present’ than the chimpanzee hand MSM. This may in part be due to the overall larger size of the gorilla skeletons studied, as it was noted during data collection that MSM were easier to identify in larger individuals. There were, however, differences between the gorilla MSM in terms of how frequently they were scored as ‘present’. The *palmar interossei* were more readily observable in the gorilla sample than was the case for either the chimpanzee or modern human samples. There was also less difference between the frequency of ‘present’ scored for the FDS and the rest of the MSM, as had been seen previously for the chimpanzees. While this may reflect increased use of the muscles in the gorilla hand, and the PI in particular, relative to the chimpanzee hand, it may also reflect the likely increased ease with which gorilla MSM can be identified.

7.7.2. Significance testing

Given the low levels of asymmetry identified in Figure 7.33, it was not expected that any of these differences would be found to be statistically significant, particularly as few significant differences had been indentified in the chimpanzee, Écija and Greenwich hand MSM analyses (sections 7.3.2, 5.3.2 and 6.3.2, respectively). To test this assumption a McNemar test was performed on the gorilla hand

MSM data. The results of this test are reported in Table E.29 (Appendix E). This analysis found no statistically significant differences between any of the left and right MSM pairs, including ODM which displayed the largest amount of asymmetry. This finding is in keeping with the results of previous analyses and suggests that there is a certain asymmetry 'threshold' that must be crossed before observable asymmetries become statistically significant.

7.7.3. Sex and hand MSM

Although previous analyses of the hand MSM in the chimpanzee and Écija samples found only very limited associations between sex and MSM expression, it was not clear whether the same trend would be present in the gorilla hand MSM given the clear sexual dimorphism present in this species. To address this issue a chi-squared test of association was performed on the hand MSM data. Table 7.22 provides the results of this analysis.

Table 7.22. Chi-squared (χ^2) test of association between sex and gorilla hand MSM.

MSM	Side	χ^2 value	Sig. (2-tailed)	φ value
APT	L	0.29	p = 1.00*	0.12
	R	1.05	p = 1.00*	0.23
ODM	L	1.53	p = 0.36*	0.27
	R	3.18	p = 0.21*	0.40
FDS	L	-	-	-
	R	-	-	-
PI2	L	0.44	p = 0.67*	0.15
	R	1.17	p = 0.40*	0.24
PI3	L	0.38	p = 0.66*	0.14
	R	0.39	p = 1.00*	0.14
PI4	L	0.04	p = 1.00*	0.05
	R	0.04	p = 1.00*	0.05
DI1	L	0.40	p = 0.67*	0.14
	R	0.40	p = 0.67*	0.14
DI2	L	9.24	**p < 0.01***	0.66
	R	5.50	*p = 0.06**	0.52
DI3	L	5.84	**p = 0.03***	0.53
	R	8.93	**p < 0.01***	0.69
DI4	L	4.07	*p = 0.08**	0.44
	R	0.53	p = 0.66*	0.16

Significant p-values in bold. P-values approaching significance (between 0.055 and 0.1) highlighted in italics. FDS was not included in analysis as no individuals changed score between 'present' and 'absent' categories. Values marked with an asterisk (*) indicate those comparisons where the Fisher's Exact Test p-value was used due to low cell counts (in most instances, this test provides the same results as the standard χ^2). A phi (φ) value indicates the strength of the χ^2 association. Abbreviations used: APT = adductor pollicis (transverse head), ODM = oppenens digiti minimi, FDS = flexor digitorum superficialis (2-5), PI = palmar interosseous, DI = dorsal interosseous.

It can be seen from Table 7.22 that there is only a limited association between sex and MSM score with three variables, left DI2, left DI3 and right DI3, showing statistically significant p-values. In addition right DI2 and left DI4 have p-values approaching significance. The clear finding of these results is that it is the *dorsal interossei* that differ in their expression between males and females in this sample. The phi values for the significant associations are all above 0.50, indicating that the association between these MSM and sex is relatively strong, particularly when compared to the phi values found for the other samples. Interestingly, DI4 was also found to have a significant association with sex in both the chimpanzee and Écija samples. The role of the *dorsal interossei* muscles is to abduct the digits from the midline of the hand (Table 3.4). Why this group of MSM should differ between males and females in all samples is unclear. This analysis also proves that, in keeping with the results of the metric analyses, male and female gorillas show little asymmetry dimorphism despite their pronounced sexual size dimorphism.

7.8. MSM in the gorilla humerus

The analysis of chimpanzee humerus MSM asymmetry (section 7.4) found a number of differences compared to the chimpanzee hand MSM in terms of the direction and magnitude of asymmetry. In turn, differences were also identified between the results of the MSM analysis compared with the metric analysis and also between the chimpanzee and the modern human samples. Analysis of gorilla humerus MSM asymmetry will help to put the chimpanzee data in context, as well as aiding in understanding the pattern of gorilla upper limb asymmetry.

7.8.1. Asymmetry in gorilla humerus MSM

Asymmetry in gorilla humerus MSM was assessed by comparing the percentage of subjects scored as ‘present’ for each MSM on both the left and right humerus. The results of this analysis are presented in Figure 7.34 (below). Data from this analysis can be found in Table E.30 (Appendix E).

The data presented in Figure 7.34 support the findings of previous MSM analyses, highlighting the generally low levels of asymmetry between left and right MSM. None of the MSM pairs in Figure 7.34 displays substantial asymmetry greater than 10% asymmetry (although LD, TMn, SSc and CEO show differences of 9.5 – 9.6%). This level of asymmetry is slightly less than that seen in the gorilla hands (Fig. 7.33) and the Écija humeri (Fig. 5.17), but similar to that found for the chimpanzee humeri (Fig. 7.17) and the Greenwich humeri (Fig. 6.17).

Figure 7.34 indicates that 4 of the 11 humerus MSM display right-side dominance, compared with 3 that are left-side dominant and 4 MSM that show no difference between left and right expression. The presence of symmetry in MSM expression may reflect the more symmetrical use of the upper limb in the gorilla sample compared to the human samples. The particular pattern of asymmetry found in this analysis tends more towards symmetry than the corresponding analysis of the gorilla hand MSM (which were clearly right-side dominant), but is similar to that found for the chimpanzee humerus MSM. Drapeau (2008) found no significant differences between gorilla and chimpanzee humerus MSM in terms of the direction of their asymmetry, and this finding is supported by the results of the current analysis.

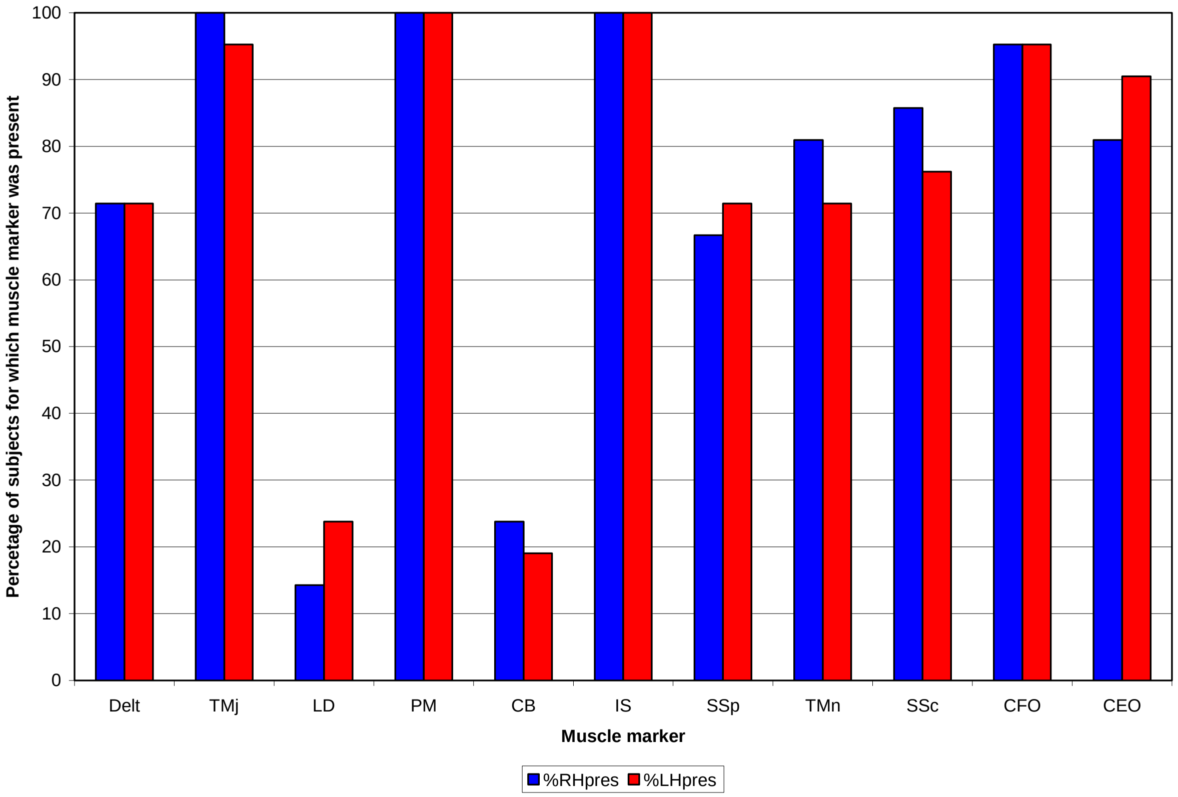


Figure 7.34. For each of the 11 gorilla humerus MSM, the percentage scored as ‘present’ for the left humerus (red) and the right humerus (blue). Abbreviations used: Delt = deltoid, TMj = teres major, LD = latissimus dorsi, PM = pectoralis major, CB = coracobrachialis, IS = infraspinatus, SSp = supraspinatus, TMn = teres minor, SSc = subscapularis, CFO = common flexor origin, CEO = common extensor origin. Further data available in Table E.30, Appendix E.

The gorilla humeral MSM in Figure 7.34 and the chimpanzee humeral MSM in Figure 7.17 both follow a similar pattern of MSM expression. For example, in both groups the TMj, PM, IS and CFO are scored as ‘present’ on more than 90% of occasions and the LD less than 30%. The samples differ, however, for the CB and SSp. The CB is rarely scored as ‘present’ for the gorillas compared to chimpanzees, with the reverse being true for the SSp which is more common in gorillas than chimpanzees. Despite these similarities the great ape samples do not show corresponding patterns for those MSM found to be left-side dominant, right-side dominant and symmetrical. In contrast to the findings of Drapeau (2008), there do not appear to be substantial differences between the gorilla and chimpanzee humerus MSM data in terms of the magnitude of asymmetry expressed in each sample.

7.8.2. Significance testing

Comparison of MSM expression in the gorilla hands found no statistically significant differences between MSM scores in the left and right hands (section 7.7.2) similar to the trend identified in the other samples. To test whether this trend also holds for the gorilla humerus MSM, a McNemar test was performed on the data (see Table E.31, Appendix E). The results of this test show that there were no statistically significant differences between left and right humerus MSM scores. This result is in keeping with the results of this analysis for both the chimpanzee (section 7.4.2) and the modern human (sections 5.4.2 and 6.4.2) humerus MSM.

7.8.3. Sex and humerus MSM

Previous analyses of association between sex and MSM score in both the non-human primate and modern human samples have found few statistically significant associations. The chi-squared (χ^2) test performed for sex and gorilla hand MSM scores (section 7.7.3) found only a few significant associations. To test whether this is also the case for the gorilla humerus MSM a χ^2 test was performed on the data. The results of this analysis are presented in Table 7.23 and show that there are only a limited number of statistically significant associations between sex and MSM score. Left LD, left CB and left SSc show significant p-values, and in addition, right TMn has a p-value approaching significance (p = 0.09). The phi values associated with the significant associations are between 0.50 and 0.60, suggesting that the associations are moderately strong. The χ^2 test performed on the Écija humerus MSM (section 5.4.3) also found significant associations for the LD and SSc, suggesting a general sexual dimorphism in the use of these muscles in both of these samples. Alternatively, the increased size of males relative to females, in both the gorilla and Écija samples, may have increased the ease by which these MSM could be identified. In contrast, there were no statistically significant associations found between sex and MSM score in the chimpanzee humerus MSM data (section 7.4.3).

Table 7.23. Chi-squared (χ^2) test of association between sex and gorilla humerus MSM.

MSM	Side	χ^2 value	Sig. (2-tailed)	φ value
Delt	L	0.69	p = 0.64*	0.18
	R	0.69	p = 0.64*	0.18
TMj	L	1.00	p = 1.00*	0.21
	R	-	-	-
LD	L	7.22	**p = 0.01***	0.59
	R	0.51	p = 0.59*	0.16
PM	L	-	-	-
	R	-	-	-
CB	L	5.44	**p = 0.04***	0.51
	R	0.40	p = 0.64*	0.14
IS	L	-	-	-
	R	-	-	-

MSM	**Side**	**χ^2 value**	**Sig. (2-tailed)**	**φ value**
SSp	L	0.69	p = 0.64*	0.18
	R	1.53	p = 0.36*	0.27
TMn	L	0.69	p = 0.64*	0.18
	R	4.49	*p = 0.09**	0.46
SSc	L	6.00	**p = 0.04***	0.53
	R	3.18	p = 0.21*	0.39
CFO	L	1.00	p = 1.00*	0.21
	R	1.16	p = 0.48*	0.24
CEO	L	0.01	p = 1.00*	0.02
	R	1.01	p = 0.59*	0.22

Significant p-values in bold. P-values approaching significance (between 0.055 and 0.1) highlighted in italics. Right TMj, left and right PM, and left and right IS were not included in the analysis as no individuals changed score between ‘present’ and ‘absent’ categories. Values marked with an asterisk (*) indicate those comparisons where the Fisher’s Exact Test p-value was used due to low cell counts (in most instances, this test provides the same results as the standard χ^2). A phi (φ) value indicates the strength of the χ^2 association. Abbreviations used: Delt = deltoid, TMj = teres major, LD = latissimus dorsi, PM = pectoralis major, CB = coracobrachialis, IS = infraspinatus, SSp = supraspinatus, TMn = teres minor, SSc = subscapularis, CFO = common flexor origin, CEO = common extensor origin.

7.8.4. Summary of gorilla MSM analysis

Similar to the results of the chimpanzee upper limb MSM analysis (sections 7.3 and 7.4), the analysis of the gorilla hand and humerus MSM in the previous sections indicates that there are generally low levels of asymmetry present between left and right MSM, with none of these asymmetries being identified as statistically significant. Despite this, there appears to be a trend for the gorilla humeri to show slightly reduced MSM asymmetry compared to the gorilla hands, similar to the pattern identified in the chimpanzee MSM analyses. The level of asymmetry displayed in the gorilla upper limb MSM appears to be lesser in magnitude than that displayed in the Écija sample (sections 5.3 and 5.4), but generally similar than that seen in both the Greenwich and chimpanzee samples. This finding provides equivocal support to Drapeau’s (2008) observation that humans displayed significantly more upper limb asymmetry than either chimpanzees or gorillas, although the lack of clear differences between the Greenwich sample and the non-human primate samples poses questions about the choice of the most appropriate human sample to compare with the primates. The findings of the current study firmly support Drapeau’s finding that chimpanzees displayed significantly more rugose upper limb MSM than gorillas, although there is a suggestion that the overall trend in the gorilla sample is towards reduced asymmetry relative to the chimpanzees.

The direction of asymmetry in the gorilla MSM analyses shows that, while the humerus MSM do not exhibit a clear asymmetric trend (with equivalent numbers of left-side dominant, right-side dominant and symmetrical MSM), the hand MSM clearly favour right-side dominant asymmetry. This is similar to the patterns of asymmetry identified in the chimpanzee MSM, although the chimpanzee hand MSM tended towards left-side dominant asymmetry. The pattern of gorilla MSM asymmetry appears to contrast with the pattern identified in the gorilla metric analyses (sections 7.5 and 7.6), where the hands showed more symmetry (although the phalanges were left-side dominant) and the humeri were more clearly asymmetric (left-side dominant in this case). This was also the finding of the chimpanzee analyses and highlights a difference between the regions of the upper limb in the nature of their asymmetry profiles in both the non-human primate samples.

Finally, it was observed in the gorilla MSM analyses that sexual size dimorphism does not translate into dimorphism in asymmetry, as was the case in the Écija sample.

Chapter 8. Discussion

8.1. Summary of results

The analyses of both modern human and non-human primate upper limb skeletal material, described in the preceding chapters, have identified a number of interesting findings regarding upper limb bilateral asymmetry in the humerus and the less frequently studied region of the hand. Further comparisons of the metric and musculoskeletal stress marker (MSM) methods used in these analyses highlight differences between the approaches which call into question the appropriateness of using such methods interchangeably. The main features of each skeletal sample will be outlined in this section, followed by a discussion of the over-arching trends found in the bones of the hand relative to the humerus and the application of metric methods relative to MSM methods.

Écija

The metric analysis of the Écija upper limb material (sections 5.1 and 5.2) found that levels of bilateral asymmetry in the humeri and hands appeared to be high, with a large proportion of measurements for the humerus and metacarpals displaying greater than 70% dominant asymmetry. All asymmetries displayed right-side dominance. It was noted that metacarpal 1, in particular, showed reduced levels of asymmetry relative to the other metacarpals. The magnitude of asymmetry in the phalanges was found to be lower than that seen in the metacarpals, with less than 60% dominant asymmetry for all measurements. Analysis of individual asymmetry confirmed that a clear majority of individuals were right-side dominant, although the magnitude of this dominance varied between individuals. Wilcoxon tests identified significant size differences between all left and right humerus measurements, the majority of left and right metacarpal measurements, but very few of the phalanx measurements. Right-side bones were generally larger than left-side bones. Statistically significant sexual dimorphism was identified in the sample, with males being larger than females for the majority of measurements taken. Again, the phalanges showed fewer significant relationships. Conversely, sex was found to have very little effect on either directional or absolute asymmetry for any of the bones studied. Age was also found to have very little effect on size or asymmetry in the Écija sample.

In contrast to the levels of asymmetry displayed in the metric properties of the Écija sample, there were lower levels of identifiable asymmetry in MSM development in the humeri and hands (section 5.3 and 5.4), although as with the metric analyses previously, observable MSM asymmetry was slightly greater in the humeri than the hands. For both anatomical regions, the trend was towards right-side dominant asymmetry. None of the MSM asymmetries was found to be statistically significant, and only limited statistical associations were found between MSM score and both sex and age, although associations were marginally more numerous for sex relative to age.

Greenwich

Compared to the Écija metric analyses, asymmetry was found to be relatively reduced in the metric properties of the Greenwich upper limb as a whole (section 6.1 and 6.2), with fewer measurements displaying greater than 70% asymmetry. This reduction in the magnitude of asymmetry was also reflected in a move towards left-side dominant asymmetry in a number of metacarpal and phalanx variables. Like the Écija metric analyses, general asymmetry patterns followed a similar trend in the Greenwich sample. Metacarpal variables were, on the whole, larger and more right-side dominant than the phalanx variables. Comparing the patterns of asymmetry in the metacarpals and humeri was less straightforward. Humerus measurements were more strongly right-side dominant, although the metacarpals variables had larger dominant asymmetry scores. Wilcoxon tests supported this trend for reduced asymmetry, as they indicated a reduction in the number of significant size differences between left and right measurements, particularly for the phalanges. As the Greenwich sample comprised solely males, sex was not a variable in this analysis, however, age was found to have virtually no effect on either the size of bone properties or their bilateral asymmetry (in terms of magnitude or direction).

Analysis of the Greenwich MSM data (sections 6.3 and 6.4) indicated that the degree of asymmetry observable using this technique was, once more, reduced relative to that seen in the Greenwich metric analyses. In contrast to the Écija MSM, asymmetry was more pronounced in the hand MSM than in the humerus, with asymmetry proving to be statistically significant for the DI1 in the hands. Interestingly, there was a clear move towards left-side dominant asymmetry in the Greenwich MSM data, with this being the dominant pattern for the humerus MSM. No statistically significant associations were found between age and any of the MSM. It is possible that the relatively small sample sizes for each age category mask the true extent of any age differences within the larger Greenwich population.

Together, the results of the Greenwich analysis strongly suggest that the strenuous activities that the individuals were likely to have engaged in over the course of their lives (Boston *et al.*, 2008) have resulted in lower levels of asymmetry in the metric properties of this sample, but an increase in MSM development. The increase in hand asymmetry (both MSM and metric) relative to the humerus is suggestive of heavy bilateral loading of the humeri which reduces their asymmetry while increasing the relative degree of asymmetry observable in the hands. These results should be interpreted within the context of Stirland’s (1993) observation that humeral skeletal asymmetry may decrease with age and therefore the pattern observed in this sample may reflect the influence of a number of factors.

Chimpanzees

Non-human primate samples (chimpanzee and gorilla) were included in the current study to provide control groups for the human samples, as non-human primates should be expected to display a much reduced degree of asymmetry in their upper limb (compared to humans) due to the more symmetrical recruitment of the arms and hands in locomotor activities in these species. Data from the chimpanzee sample (sections 7.1 and 7.2) appear to support this hypothesis, as a relatively low degree of asymmetry was observable in both the hands and humeri, reflected in very few variables showing significant size differences between left and right measurements. The degree of asymmetry seen in the chimpanzee metric properties is therefore more akin to that seen in the Greenwich sample than the Écija sample. It is interesting to note that the chimpanzee metacarpals showed an overall trend towards right-side dominant asymmetry, while both the humeri and phalanges tended towards left-side dominant asymmetry. This supports the 'mixed' pattern of upper limb asymmetry identified by Sarringhaus *et al.* (2005) in their chimpanzee sample. Intriguingly, it was also found that asymmetry was greater in humerus articular surface dimensions than for diaphyseal dimensions, contrary to expectations (e.g. Trinkaus *et al.*, 1994; Ruff, 2000; Auerbach & Ruff, 2006). The relative reduction in magnitude of asymmetry represented in the chimpanzee sample is reflected in relatively few statistically significant size differences between left and right upper limb properties. As with the human samples, male and female chimpanzees displayed very little sexual dimorphism for metric and asymmetry variables. The nature of individual hand preference is of interest in non-human primate groups, particularly chimpanzees, due to the controversial results of such research in living primates (e.g. McGrew & Marchant, 1997). In this study, equivalent proportions of left-side and right-side dominant individuals were identified for the humeri, metacarpals and phalanges suggesting that, while individual asymmetries are present, no sample-level trend is observable. This mirrors the trend identified in many behaviour lateralisation studies (McGrew & Marchant, 1997).

MSM data from the chimpanzee sample (sections 7.3 and 7.4) indicate that the degree of asymmetry is generally low, with no statistically significant differences found between any of the hand and humerus MSM. In contrast to the chimpanzee metric analyses, hand MSM displayed a clear trend towards left-side dominant asymmetry, while the humerus MSM displayed equivalent numbers of left-side and right-side dominant MSM. As with the metric analyses, sex was found to have only a very weak association with MSM expression. There is a suggestion in this sample (and in the human samples also) that the MSM of muscles involved in creating pinch-like grips in the hand, the DI1 and ODM, were more asymmetric than other hand MSM. Overall, these observations support the influence of fluctuating asymmetry on MSM expression, resulting from more symmetrical use of the upper limbs in chimpanzees compared to humans. The identification of asymmetry in chimpanzee MSM, reduced relative to the modern human samples, is in keeping with the findings of Drapeau (2008).

Gorillas

Asymmetry was also measured in the upper limb of a gorilla sample (sections 7.5 and 7.6) and was found to be similar to that of the chimpanzee sample in terms of the magnitude of asymmetry, which was low relative to that observed in the modern human samples. This was reflected in the small numbers of statistically significant size differences found for the hands and humeri. The gorilla sample differed slightly from the chimpanzee sample in terms of the direction of asymmetry. While the gorilla phalanges and humeri also showed left-side dominant asymmetry (in line with the chimpanzee phalanges and humeri), the gorilla metacarpals displayed a mixed pattern of asymmetry, with almost equal numbers of right-side dominant and left-side dominant variables. Patterns of individual asymmetry were equivalent to those found in the chimpanzee sample, i.e. equal proportions of left-side dominant and right-side dominant individuals. The gorilla humerus sample, as with the chimpanzee sample, showed greater asymmetry for articular surface dimensions than diaphyseal dimensions. As might be expected, the two non-human primate samples differed most clearly in terms of sexual dimorphism, with large size differences between male and female upper limb variables for the gorillas. Interestingly however, far fewer significant sex differences were found for directional and absolute asymmetry scores, suggesting that there was no significant sexual dimorphism in the gorilla sample for the use of the arms.

The gorilla MSM data (sections 7.7 and 7.8) showed broad similarities with the pattern of upper limb asymmetry seen in the chimpanzee MSM data. On the whole, while the degree of asymmetry seen between the humerus MSM was similar in the gorillas compared with the chimpanzees, it was slightly reduced in the gorilla hand MSM compared with the chimpanzee hand MSM. None of the gorilla MSM showed significant left/right differences. In Drapeau's (2008) study of non-human primate upper limb MSM she also found that chimpanzees generally displayed more development in MSM than gorillas, although this was only for MSM on the humerus. The gorilla humerus MSM in the current study did not display a clear trend towards side dominance, as seen in the chimpanzee humerus. In the gorilla hands the trend was clearly towards right-side dominant asymmetry, the opposite of the left-side dominant trend identified in the chimpanzee hand MSM. Drapeau (2008) found no significant differences between chimpanzee and gorilla humerus MSM in terms of direction of asymmetry. Despite the striking sexual dimorphism exhibited in gorilla species, there were few statistically significant associations identified between sex and MSM score.

8.2. Discussion of results

The large body of data analysed and described in the preceding chapters leads to a number of possible conclusions regarding the processes of data collection described above. How these results address the two main aims of the thesis, namely the importance of selecting appropriate anatomical markers and understanding differences in methodological approach, will be discussed in more detail below. First, it is useful to summarise some of the key themes that have emerged from the data analysis as they relate to the individual data sets. This will be approached from the perspective of differences and similarities across the samples.

It is clear from the data presented in the previous chapters that there are differences between the metric and MSM methodologies in terms of the asymmetry profiles they produce, with the MSM approach tending to underestimate the degree of asymmetry present relative to the metric approach. Why this should be the case is not clear, but may reflect the difference between the MSM approach which effectively measures single muscle activity and bone robusticity in a small area, and the metric approach which measures larger-scale bone dimensions. It is also possible that the more objective presence/absence scoring system used to categorise MSM development is not as well-suited to reflecting variation in asymmetry as measurements taken on a metric scale. These possible explanations are also echoed by Maggiano *et al.* (2008a), who found differences in the degree of asymmetry measured by geometric and MSM techniques. The comparable findings of the current study, alongside those of Maggiano *et al.* (2008a) (and to an extent, Stirland, 1998) highlight a discernible difference between approaches that determine asymmetry in terms of bone robusticity and those that determine asymmetry from areas of muscle attachment. It is interesting to note that Weiss (2003) only found a correlation between MSM and cross-sectional properties when aggregate muscle markers and geometric scores were compared and not when individual variables were compared. Together, these findings support the adoption of an inclusive approach to the study of upper limb bilateral asymmetry, one that incorporates data from the available methodologies to provide a more comprehensive understand of the expression of asymmetry in the bones of the upper limb.

	METRIC		**MSM**	
	hands	**humerus**	**hands**	**humerus**
Écija	mc: RS phal: RS	RS	RS	RS
Greenwich	mc: RS phal: LS	RS	RS	LS
Chimpanzee	mc: RS phal: LS	LS	LS	Mixed
Gorilla	mc: Mixed phal: LS	LS	RS	Mixed

Table 8.1. Asymmetry profile for each of the samples studied, divided by anatomical region and method. RS = right-side dominant asymmetry, LS = left-side dominant asymmetry, mixed = no clear trend towards right-side or left-side dominant asymmetry, mc = metacarpals, phal = phalanges.

For many of the samples studied there were also observable differences between the metric and MSM methods in the direction of asymmetry reported (see Table 8.1). Although the Écija sample was found to be right-side dominant for humeral and hand asymmetry using both methods, the remaining samples displayed a certain degree of variation between the methods. For example, the chimpanzee hands were right-side dominant for the metacarpals and left-side dominant for the phalanges in the metric analysis, but left-side dominant in the MSM analysis. Chimpanzee humerus properties were left-side dominant in the metric analysis, but displayed a mixed pattern of asymmetry in the MSM analysis. The Greenwich humeri also provide a clear example of a change in asymmetry direction between the measurements, being right-side dominant in the metric analysis, but left-side dominant when analysed using a MSM approach. Exactly why the methods should differ in the direction of asymmetry they record for certain bones is unclear, but as with the differences in the recording of the magnitude of asymmetry between the methods, it is possible that variability in the anatomical markers measured by each approach impact on their respective outcomes.

Table 8.1 highlights differences between the hands and humeri in terms of their asymmetry profiles, reflecting differences in asymmetry between the anatomical regions which persist irrespective of the methodology applied. Again the Écija sample remains clearly right-side dominant in its asymmetry for both the hands and the humeri, but in the other samples it is clear that there is a difference between the metacarpals and phalanges in terms of their directional asymmetry (the metacarpals favour right-side dominant asymmetry while the phalanges tend towards left-side dominant asymmetry). The differences between the hands and humeri are most evident in the non-human primate samples where asymmetry in the metacarpals differs from that of the humerus using both metric and MSM methods. There is also a clear difference in the Greenwich MSM analysis between the right-side dominant asymmetry for the hands, compared to the left-side dominant asymmetry observed in the humeri. These differences may reflect variation between the anatomical regions in terms of their function, suggesting that the bones of the upper limb are morphologically sensitive to variation in mechanical loading. Differences between the hands and the humeri will be discussed in more detail in section 8.2.1.

Care must be taken when interpreting differences in asymmetry between the hands and the humeri, and also between metric and MSM methods. The level of asymmetry identified in some of the samples is low, particularly in the MSM analyses, and this asymmetry is frequently statistically insignificant. Therefore, it is possible that the asymmetry observed in the Greenwich and non-human primate samples represents the effects of fluctuating asymmetry (e.g. ontogenetic and environmental factors which affect symmetric development of an organism) on these samples (e.g. Van Valen, 1962), which is likely to be more readily identifiable when a certain degree of functional symmetry is present. The Écija sample deviates from the other samples studied in that there seems to be clear asymmetry in the mechanical loading of the right and left upper limbs favouring the right-side. The results of the current analysis indicate that there is genuine variation in the asymmetry profiles across the samples, both between the hands and the humeri and between the methods applied to assess asymmetry. This highlights the importance of including a variety of upper limb elements in the study of upper limb asymmetry. In particular, if the purpose of research is to understand hand use and preference, then the bones of the hand should be considered in such analyses.

The current study identifies interesting trends in phalanx asymmetry. Across the majority of the samples (with Écija again proving to be the exception) there are differences in metric asymmetry between the metacarpals and the phalanges with the metacarpals showing right-side dominant asymmetry and the phalanges left-side dominant asymmetry. These opposing trends in asymmetry for the hand bones are found across all the metric samples (although the gorilla metacarpals are considered to have a ‘mixed’ asymmetry pattern, insomuch as there is only a slight preference for right-side dominant asymmetry across the 25 variables measured). While it was suggested for the Écija phalanx analysis that potential uncertainty in phalanx siding may have accounted for the observed variance in asymmetry between the metacarpals and phalanges (section 5.1.3, Fig. 5.11), the observation of this pattern across all samples (included those where phalanx siding was secure) suggests that potential siding problems are not responsible and therefore this pattern represents a genuine difference between the metacarpals and phalanges regarding their expression of asymmetry. It is possible that this contrast emerges from functional differences between the muscles of the metacarpals and phalanges, with the phalanx muscles engaging in flexion and extension of the fingers, and the metacarpal muscles primarily involved in abduction and adduction of the digits (although they also engage in other functions). It is also possible that measuring only phalanx length masks some of the variation present in phalanx asymmetry as measurements are not taken in the axes through which the phalanges are most commonly stressed during muscle activation. For the second metacarpal, Lazenby (2002a) suggests that it is the dorso-palmar plane that is the primary axis of loading and therefore it would be worthwhile in future to measure phalanx dimensions in this plane. Phalanx asymmetry would benefit from research attention to further explore and clarify the nature of asymmetry in this region and the ways in which it differs from that of the metacarpals. Traditionally the hands have been a relatively unstudied region in asymmetry research and the results of the current study suggest that they can provide important information regarding the variation in asymmetry across the upper limb as whole.

8.2.1. Selecting appropriate anatomical measures of asymmetry

One of the key aims of the thesis was to compare the pattern of asymmetry in the well-studied upper arm with that of the less-studied hand region. When conducting asymmetry research, the choice of measurements taken is particularly important, as these have the potential to affect the asymmetry profile generated. With asymmetry data being used to address a variety of research questions including those pertaining to hand preferences and handedness, activity patterns and social organisation, it is crucial that researchers are aware of the level of variation that may be present in data used to answer those questions. The current study has clearly highlighted the degree of variation in asymmetry between the humerus and the bones of the hand, across a number of skeletal samples. As indicated in Table 8.1, the metric properties and MSM of the hand often differ from the humeri in terms of the direction of asymmetry. The anatomical regions also differ in the magnitude of the asymmetry they express, with the hand bones tending to exhibit lower levels of asymmetry relative to the humeri (although the reverse is the case for the Greenwich metacarpals and humeri). In additional, the metacarpals and the phalanges also appear to differ in the direction and magnitude of their respective asymmetry.

This difference in asymmetry profiles identified between the hands and humeri in the current study may reflect different mechanical loading regimes between these anatomical regions, but also disparity in their respective responses to such loading. Differences between hand and humerus asymmetry profiles may result from the humeri engaging in strenuous activities that stress each arm equally, which may not be reflected in the bones of the hand. In the Greenwich sample for example, individuals were likely to have engaged in very strenuous activities related to maritime professions over a substantial proportion of their lifetime, therefore more symmetrical humeri would be expected. However, these strenuous activities appear to have lead to an *increase* in relative asymmetry in the hands. It seems that while the magnitude of the asymmetry between the hands and humeri is in part determined by the level of stress placed upon these regions, differentiation in functional recruitment between the hands and the upper arms is also likely have an impact on both the direction and magnitude of this asymmetry. However, determining the varying influences of activity patterns and stress levels on the nature of asymmetry expressed in the bones of the upper limb is a complicated process.

There are a number of further ways in which these differences can be interpreted. As indicated by Stock & Pfeiffer (2001) and Stock (2006), there appears to be a tendency for bone robusticity to vary throughout the upper limb with variation in robusticity increasing as you move distally through the upper limb. Stock (2006) explains this trend by suggesting that the morphology of the distal elements of the upper limb show a greater influence of mechanical loading than more proximal elements. This could potentially explain why the bones of the hand appear to differ from the humeri in their magnitude of asymmetry, although under this interpretation one would expect to find increased asymmetry in the hands relative to the humeri, which only appeared to be the case for the Greenwich sample. Caution must be used when interpreting the findings of the current study in such a context. The comparisons performed by Stock and colleagues involved cross-sectional long bone properties rather than metric dimensions and they did not incorporate measurements from the bones of the hand. Such research however, highlights the importance of taking into consideration the degree of variation present in upper limb morphology when assessing asymmetry. It also highlights the necessity of including multi-dimensional bone properties in such analyses.

Comparisons were also made *within* anatomical regions to assess whether the various measurements it is possible to take on a particular bone(s) represent asymmetry in the same way. What these comparisons found was that there were indeed observable differences in asymmetry within the anatomical regions studied. Within the humeri metric measurements and, in particular, for the non-human primates, variation was found in asymmetry between the diaphyseal and articular surface dimensions. As indicated by a number of researchers (e.g. Trinkaus *et al.*, 1994; Ruff, 2000; Lieberman *et al.*, 2001; Auerbach & Ruff, 2006; Lazenby *et al.*, 2008), diaphyseal bone dimensions display more plasticity in response to mechanical loading than corresponding articular surface dimensions and therefore are more likely to display a greater degree of asymmetry than the articular surfaces. While there are no clear trends in the modern human humeral samples measured in the current study for such a distribution of asymmetry, the non-human primate samples measured appear to display the reverse trend, i.e. the humeral articular surfaces (both proximal and distal) were more asymmetric than the diaphyses. It is not clear why the non-human primate humeral material in this study should exhibit a pattern of asymmetry that contrasts with the findings of these previous studies. Plochocki *et al.* (2006) suggest that joint size and shape are both influenced by mechanical stress placed upon the joint, and Rafferty & Ruff (1994) and Lieberman *et al.* (2001) suggest that articular surface dimensions are likely to reflect the joint mobility and locomotor strategy of a particular species. Joint morphology will also be related to the body mass of the individual, particularly where a joint is weight-bearing. For the chimpanzee and gorilla individuals measured in the current study it is therefore likely that the asymmetric differences observed between the diaphyseal and articular surface dimensions reflect differences in the weight-bearing strains placed on each arm concomitant with the behaviours engaged in by both species. This explanation supports the observations of Sarringhaus *et al.* (2005), who postulated that asymmetry observed between the humeri and 2nd metacarpals of their chimpanzee sample represented the left arm being used to provide postural support to an individual, while the right hand engaged in manipulative actions. Overall, the analysis of the non-human primate samples asymmetry in the current study sheds interesting light on the nature of asymmetry in the upper limb of chimpanzees and gorillas. The analyses highlight differences between the chimpanzee and gorilla samples in terms of both the magnitude and direction of their various asymmetries, and suggest that it may be possible to identify variation in functional recruitment both between the upper limbs and between the species.

Due to the number of metric measurements taken on the bones of the hand in the current study, interpretation of asymmetry patterns within this region is necessarily more complex. Comparisons of both between-metacarpal and within-metacarpal asymmetry show a high degree of variation between the measurements. For the Écija sample, there is a reduction in asymmetry in the 1st metacarpal relative to the other metacarpals. There are clear differences between asymmetry in metacarpals compared to the phalanges for all the skeletal samples studied. The magnitude of asymmetry was often reduced in the phalanges relative to the metacarpals and the two sets of bones frequently differed in the direction of their asymmetry (see Table 8.1). As discussed above, there are possible methodological reasons why such contrasting asymmetry patterns emerge; however, the systematic nature of these differences indicate that there is a difference either in functional recruitment or response to mechanical loading (or both) between the metacarpals and phalanges that requires further investigation. It is also worth noting the variation in asymmetry between the phalanges themselves. For all the phalanx samples (except Écija) there was a trend for 'reversal' in asymmetry between the proximal phalanges and the intermediate phalanges, i.e. the proximal phalanx from a particular digit was right-side dominant while the corresponding intermediate phalanx from that digit was left-side dominant, and vice versa. Distal phalanges were often not available for study. Although this reversal in asymmetry appears to be quite common in the phalanx samples the nature of the change in direction varies between digits and between samples. Due to the generally small numbers of phalanges available for study further investigation is required to clarify whether this reflects functional differences between the phalanges related to muscle recruitment in the fingers or whether the trend is more reflective of fluctuating asymmetry which is more readily noticeable in small sample displaying relatively low levels of directional asymmetry.

The results of the current study, and those from the hand analyses in particular, emphasise the importance of selecting appropriate measurements to assess asymmetry. Differences in both the magnitude and direction of asymmetry, for example between manual rays or even within the rays themselves, indicate that the measurement selected as a marker of asymmetry will exert a degree of influence over the conclusions of asymmetry analyses. While the norm in asymmetry research has been to use asymmetry in the humerus as a measure of hand preference in a given sample, the results of the current study indicate that such an approach is misleading due to the distinctive asymmetry profile of the hands in this sample relative to their corresponding humeri. Although the precise reasons for the differences observed between the hands and humeri are unclear, it is appears that differences in the actions of the hands and arms are reflected in their respective asymmetries. For these reasons, future research may benefit from clearly delineating between concepts of 'handedness' and 'armedness' when attempting to study asymmetry in the upper limb. It is no longer advisable to use the humerus as a proxy for the upper limb as a whole. It is therefore suggested that a more comprehensive and inclusive approach is taken to determining asymmetry in the upper limb, incorporating data representing a number of skeletal dimensions and properties appropriate to the research questions being asked. As Lazenby highlights, “not all parts of a given element will equally reflect its behavioural environment” (2002c: 134). Such an approach is particularly important for analyses of the hand, a region which comprises a large number of separate structures and functions.

8.2.2. Application of asymmetry assessment methods

Metric

The results of the current study have a number of important implications for the way in which the available methods are applied to the assessment of upper limb asymmetry. While section 2.2 discussed the comparability of metric and geometric approaches to upper limb asymmetry, it also highlighted the potential influences of ontogenetic and environment factors on metric properties, particularly on the humerus (Steele & Mays, 1995). The current study indicates that, despite the undoubted influence of developmental factors on the morphology of the upper limb, the effect of asymmetric mechanical loading can still be detected. While the trend towards right-side dominant asymmetry identified in many human samples may in part be influenced by non-mechanical factors, it appears to be exaggerated by a lifetime of asymmetric mechanical loading (Steele & Mays, 1995). This becomes clear when modern human samples are compared with non-human primate samples, where the upper limbs are subjected to symmetrical loading, as in the current study or in studies such as that carried out by Sarringhaus *et al.* (2005). This relationship is also evidenced by differences in asymmetry between the upper and lower limbs in humans where locomotor activities reduce lower limb asymmetry relative to the upper limb (e.g. Auerbach & Ruff, 2006). The current study therefore supports the continued application of metric techniques to the investigation of asymmetry and activity in past populations, although it also advises caution when interpreting the results of such analyses, favouring the drawing of broader, more general conclusions. Adoption of a more comprehensive approach to asymmetry analyses in terms of the breadth and range of measurements collected may provide opportunities to answer more specific questions regarding variation in the use of the upper limb in skeletal populations.

MSM

The results of the data analysis outlined in Chapters 4 to 7 suggest strongly that caution must be exercised when applying an MSM method and interpreting its results. As such, these data have raised a number of important issues for future research. The lack of significant differences between many of the left and right MSM pairs across the samples questions the usefulness of the MSM method applied here for the assessment of upper limb bilateral asymmetry. Some researchers, including Weiss (2007), have found strong correlations between MSM scores in the left and right upper limbs, often leading to the combination of MSM scores in these studies. This suggests that the differences we are trying to identify in MSM asymmetry research are slight, with the upper limbs likely to be more similar than they are different. Rather than dismissing MSM research, however, investigators should be encouraged to take a more ‘generalised’ approach to MSM interpretation, making only general conclusions regarding activity patterns and resisting the urge to over-interpret data (as advocated by Robb, 1998; Stirland, 1998; Wilczak, 1998, al-Oumaoui *et al.*, 2004). If this is the case then larger sample sizes than are often used will be required. Stirland (1993) advocates a minimum of 30 individuals in order to gain statistically valid mean and standard deviation values.

The results of the current analyses are unusual in identifying few statistically significant effects of sex and age on MSM score. This is in contrast to a number of studies which have found significant differences between the sexes (Peterson, 1998; Robb, 1998; Steen & Lane, 1998; Weiss, 2003; al-Oumaoui *et al.* 2004; Eshed *et al.*, 2004; Molnar, 2006; Weiss, 2007) and between age categories

(Robb, 1998; Stirland, 1998; Weiss, 2003; Molnar, 2006; Weiss, 2007) in terms of MSM development. There are a number of possible explanations for this finding. Weiss (2007) highlights the fact that sex differences in MSM scores can often be as a result of differences in body size, disappearing when body size is controlled for. By only scoring MSM as ‘present’ or ‘absent’, as in the current study, a certain amount of the effect of body size is removed as the ‘present’ category does not carry any further information about the degree of development of the MSM, only that it can be identified visually and or tactilely. Potential methodological problems with accurately sexing and ageing skeletons may mask differences between groups in terms of their MSM score although this is more likely to occur when ageing skeletons. A more likely problem is that the small number of individuals in some of the age categories, combined with missing data for certain subjects, reduces the likelihood of identifying significant differences. For the Greenwich sample in particular, the older age of the sample and the high degree of pathology present may have impeded accurate age assessment.

Remaining with the Greenwich sample, the MSM results do not conclusively support the exclusion of individuals with ‘bone-forming’ diseases, such as DISH and ankylosing spondylitis, from MSM research (Henderson, 2008). However, this is mainly based on the observation that very few individuals in the Greenwich collection were found to be suffering from diseases of this kind (Boston *et al.*, 2008). It therefore appears the increased number of ‘present’ MSM scores in this sample reflects the advanced age of this sample and the strenuous activities engaged in during life and not the presence of bone-forming conditions. Despite this, the role of bone-forming diseases should certainly be considered when interpreting MSM data. This encourages the adoption of a ‘whole body’ approach which is not just focused on the key area of anatomical interest, but incorporates data from across the skeleton.

There are certain issues surrounding the ways in which MSM are scored. The outcomes of the current study encourage the integration of hand MSM into studies of upper limb asymmetry and activity patterns, especially if the purpose of investigation includes the assignment of hand preference to a sample. While the presence/absence approach utilised here appears to identify certain trends in the hand MSM data, it is possible that some patterns are concealed when MSM development is expressed only in a binary state (Benjamin Auerbach, pers. comm.). Anecdotal observations from the data collection process suggest that it may be possible to develop a more detailed scoring system for hand MSM, more akin to that of Hawkey & Merbs (1995) (although this would be in terms of numbers of categories identifiable, rather than types of modifications observable). During the data collection process, certain individuals were noted to have very faint but still observable MSM, while others had extremely prominent sites. This variation could provide the basis for an ordinal scoring system. There would, however, be certain issues that would need to be addressed with such an approach. For example, an ordinal scoring system would require larger sample sizes to make statistical comparisons valid. For that reason a nominal, presence/absence approach may be more appropriate, in a statistical sense, for small sample sizes in order to maximise data potential.

There are factors that must be taken into consideration when applying an MSM methodology to the bones of the hand, particularly when selecting MSM for study. Firstly, due to the small size of hand bones, taphonomic damage may have a proportionally greater effect on MSM preservation in the hands relative to the long bones of the arm. This can make accurate identification of variation in MSM development difficult and therefore tactile verification of MSM presence is often required. For example, the MSM for the *dorsal interossei* are spread between adjacent metacarpals, but are generally more commonly ‘present’ on the medial metacarpal surface than the lateral surface. If the medial metacarpal is missing then it increases the likelihood that the MSM will be scored as ‘absent’. Identification of certain MSM will be easier than others, particularly the ‘larger’ MSM on the metacarpal shafts. For this reason, future studies of hand bone MSM may benefit from continuing to focus on the metacarpals, rather than the carpals. Finally, the phalanges, when recovered, often preserve traces of *flexor digitorum superficialis* and *profundus* attachments. However, the difficulties inherent in accurately siding and ordering phalanx bones makes it problematic to draw conclusions regarding specific digits based on these MSM alone.

The findings of the data analyses discussed above ultimately have implications for the ways in which we investigate and understand asymmetry, for modern human and non-human primate samples, as well as fossil hominin groups. These results suggest that the choice of method used to quantify asymmetry, plus the number and type of measurements taken, are crucial to providing the most comprehensive picture of asymmetry in an individual or across a group as these factors can influence the nature of the asymmetry expressed in a sample. As has been shown, the bones of the hands and the humeri differ in terms of the magnitude and direction asymmetry they convey. The implication of this finding is that the bones of the hand have been unnecessarily neglected from research into upper limb asymmetry and therefore should be reintroduced into such studies, particularly if attempts are being made to determine hand preference in a skeletal sample. It is also appears from these results that activities which predominantly stress the humerus will be reflected in humeral asymmetry, while activities where muscle recruitment is targeted primarily in the hand will change the nature of asymmetry in this region more than the rest of the upper limb. While this may seem intuitive, the trend in asymmetry research has traditionally been to use humeral asymmetry as a proxy for asymmetry across the upper limb. The results of the current study suggest that this should no longer be the case and each anatomical region should be analysed as a separate functional unit. These findings correlate with the findings of an EMG analysis carried out by Marzke *et al.* (1998) into the recruitment of upper limb muscles during the manufacture of Oldowan stone tools. Their analysis found that eight of the ten muscles most active during the manufacturing process were intrinsic to the hand (i.e. they both originate and insert onto bones of the hand) supporting the notion that the hand should be considered as having a certain degree of functional independence from the rest of the upper limb, which appears to be reflected in its relative asymmetry.

The methods by which upper limb asymmetry can be assessed have also been shown to display certain differences, primarily in the magnitude of asymmetry they quantify. On the whole, the MSM method tends to underestimate the magnitude of observable asymmetry relative to the metric methods applied in the current study. The implication of this finding, therefore, is that care must be taken when selecting a method with which to assess asymmetry. Ideally a combination of methods should be used in order to gain the broadest possible picture of asymmetry expression in a sample. If this is not possible then an acknowledgement of the likely influence of the method chosen on asymmetry profiles derived from this method is necessary.

For the reasons above, the reliability of asymmetry research will be improved by the adoption of a more inclusive approach, as suggested by Steele (2000a,b), one which incorporates information from the various methods available and as many anatomical features of the upper limb as possible in order to provide solutions to questions of asymmetry expression.

8.3. General discussion

How we understand the development and distribution of hand use and preference in extinct populations and species is ultimately determined by the methods used to assess asymmetry. As discussed above, the appropriate application of such methodologies is therefore crucial to our understanding of these traits and behaviours. A better understanding of the issues inherent in the application of these methodologies also allows us to better conceptualise and frame the research questions being asked in handedness research. Awareness of the strengths, and perhaps more importantly, the limitations of particular techniques and approaches should encourage the development of research design that makes the most of the available data and has realistic expectations of the level of resolution that can be obtained.

To that end, the results of the current study have a number of implications for our understanding of the expression of handedness in archaeological populations and the evolution of this trait in our hominin ancestors. One of the implications of the results discussed above is that the most accurate picture of asymmetry, and therefore behavioural lateralisation, will come from adopting the most inclusive approach possible which ideally requires large sample sizes, multiple skeletal measurements and a combination of methodological techniques. As highlighted by Cashmore *et al.* (2008), there is a general dearth of suitable skeletal material in the hominin fossil record from which to take appropriate asymmetry measurements. While there are no quick and ready solutions to this problem save further excavations, recently developed methodological advances have the potential to increase the amount of available asymmetry data. Lazenby *et al.* (2008) used CT scanning of the distal head of the second metacarpal to determine the organisation of the bone's underlying trabeculae structure. They identified differences in the structural organisation of the trabeculae between the right and left metacarpals studied (which they interpreted as representing the 'dominant' and 'non-dominant' hands, respectively in their 18th century cemetery sample). As the authors state, assuming that this finding can be replicated; the results of this study highlight a potential method for assessing the presence of 'dominance' and by extension, hand preference in single bones. If this technique holds up to future methodological scrutiny then it will provide an exciting new avenue for increasing our understanding of preferences in functional recruitment in extinct groups.

The paucity of fossil hominin upper limb material has a further implication for hominin handedness research. If we assume 'handedness' (i.e. a strong population level preference for the use of the right hand across tasks) to be an essentially modern human condition (section 1.3.1), then we can venture that it is in fact theoretically impossible to identify 'handedness' in extinct hominin species. This is because we will never be able to identify and measure every member of a 'population' or indeed even a representative sample of that population, even with methodological advances such as those described by Lazenby *et al.* (2008). As Lazenby (2002c) highlights, it is prudent to move away from terminology which relies on large-scale trends. For this reason, it is perhaps more beneficial for continuing hominin 'handedness' research to discuss asymmetry in terms of 'hand preference' and 'hand use', as espoused by Marchant & McGrew (1998).

Questions of terminology lead us to re-evaluate what terms such as 'handedness' actually represent. Much of our understanding of modern human 'handedness' comes from the Psychology literature in which handedness is frequently self-reported or determined from questionnaires of hand preferences for tasks such as writing, drawing, using scissors and so forth (see Oldfield, 1971 for an example). Such specific methods of determining hand-use reflect the cultural nature of such tasks, which is borne out in the many ways that societies across the world differentiate between concepts of 'left' and 'right' (McManus, 2002). Questions must therefore be asked about the suitability of applying such a culturally-influenced concept to the study of hand-use and preference in extinct groups throughout the course of human evolution. As with the example made above, it may be more appropriate to reserve the term 'handedness' to refer only to modern populations in which a clear population-level hand preference can be observed and use the term 'hand preference' to refer to those groups where such trends have not or can not be reliability identified, as per Marchant & McGrew (1998).

Moving away from the use of the term 'handedness' should also be associated with a move away from defining hand-use in terms of culturally specific tasks. Marchant *et al.* (1995) highlight the impact of such an approach in their ethological study of hand-use in ‘traditional’ (i.e. pre-industrialised and pre-literate) cultures where hand preference is not determined by the use of writing and drawing implements. By utilising an approach which assesses laterality across all types of activity engaged in by the hands, Marchant and colleagues could identify variation in asymmetry specific to different classes of activity. From this they noted that, while a weak right-hand preference was present in the three cultures studied for a variety of hand actions, individuals displayed a mostly mixed-pattern of hand preference. The exception to this trend was for tool-use (rather than just object manipulation) and in particular, precision tool-use where clear right-hand preferences were identified. Findings such as these have implications for the study of hand use and preference in hominin species. It suggests that, while low levels of right-side dominant asymmetry are likely to be present in early hominin skeletal samples, it is only with the adoption of tool-use that stronger, that more ‘modern-like’ hand preferences probably emerged. This means an understanding of the behaviours likely to elicit such preferences is necessary in order to accurately interpret skeletal asymmetry data. This also advises us of the importance of asymmetry magnitude, which may be indicative of the strength of behavioural lateralisation.

All of this of course assumes a direct link between asymmetric morphology and lateralised behaviour, which Blackburn & Knüsel (2006) advise may not be a straight-forward relationship. An important future line of research could focus on the better understanding the relationship between ‘real-world’ hand preference and skeletal bilateral asymmetry. At present there is a tacit assumption that a direct and strong correlation between the two factors with the magnitude of skeletal asymmetry directly reflecting the extent of the directional hand preference in a give sample. However, caution must be exercised when making this assumption, as Blackburn & Knüsel’s study of humeral epicondylar breadth asymmetry (palpated in live subjects at the elbow) and self-reported handedness found that the direction of handedness and asymmetry was the same in only 60% of cases. Potential discrepancies between handedness and skeletal asymmetries therefore need to be investigated further and the causes for such discrepancies identified and explored. Until that point, the implications of skeletal asymmetry and hand preference in life will be misinterpreted and erroneous determinations made regarding the strength and direction of these hand preferences.

The concept of ‘handedness’ and its evolution over the course of human history continues to be fascinating, but problematic. Modern notions of handedness cloud the likely nature of hand preference in pre-modern species and groups and must be reviewed in order for us to better understand the evolution of this behaviour and the hows, whens and wheres of its emergence in the genus *Homo*. Before that can be achieved however, the methods by which hand preference is recognised in our hominin ancestors, i.e. through analyses of asymmetry in skeletal material, must be thoroughly investigated and the asymmetry profiles they create interpreted. The results of the current study indicate that this is a valid concern as the various methods available for asymmetry research, as well as the bones from which measures of asymmetry are taken, differ in the magnitude and direction of the asymmetry they express. This study, therefore, supports the adoption of a more comprehensive approach to determining hand preference through skeletal asymmetry. Regardless of the species being studied, the firmest conclusions will be based on the most comprehensive methodological approach, incorporating the largest range of measurements.

Chapter 9. Conclusions and Future Directions

9.1. Conclusions

The current study posed two main questions: 1) What contribution can the bones of the hand make to the understanding of upper limb bilateral asymmetry in humans and non-human primates and how do they compare to asymmetry as derived from the humerus? 2) What are the relative impacts of metric and MSM methods on asymmetry profiles in the hands and the humeri of human and non-human primate samples? The results of the current study have shown that upper limb asymmetry is a complex phenomenon and our understanding of such asymmetry is likely to be highly influenced by the methodological choices we make when designing our research.

Analyses of asymmetry variation between the regions of the upper limb indicate clear differences between the bones of the hand and the humeri. The overall magnitude of asymmetry was found to be variable across the hands and the humeri, although levels of asymmetry generally appear to be higher in the metacarpals compared to the phalanges for all samples. Perhaps the key difference observed in the hands and the humeri was in direction of asymmetry, which fluctuated between the anatomical regions (and also between the metacarpals and phalanges), irrespective of the method used to measure asymmetry. The exception to this pattern was the Écija sample where both the hands and the upper arm exhibited a trend for right-side dominant asymmetry. These findings suggest that the bones of the hand have an important contribution to make to our understanding of upper limb asymmetry and handedness in archaeological populations. Due to the differences in asymmetry profiles between the hands and the humeri in the current study, it may be unwise to continue to consider humerus asymmetry to be representative of asymmetry across the upper limb as a whole. Future studies are likely to benefit from considering each region of the upper limb (hand, lower arm, upper arm) as a separate functional unit liable to specifically reflect asymmetries in the activities performed by that region. These distinctions are crucial if the purpose of such research is to determine hand preference or handedness. However, if the levels of asymmetry are low, as was sometimes the case in the current study, then asymmetry patterns should be interpreted with caution. As these results have shown, the greater the number of measurements that can be included in an analysis, the more comprehensive the understanding of asymmetry in that sample will be.

The second key finding to emerge from the current study is the notable difference between the chosen asymmetry methodologies in terms of the asymmetry profiles they produce. Differences were identified between the metric and MSM methods in terms of the direction of asymmetry they reported for a given anatomical region. This finding must again be interpreted with caution due to the low levels of asymmetry present in some samples which may impact on the observed direction of asymmetry.

Despite this, what is clearly different between these approaches is the magnitude of asymmetry reported by each method. On the whole, the MSM approach appears to underestimated the degree of asymmetry present relative to the metric approach. These findings concur with those of Maggiano *et al.* (2008a) who found that the level of MSM-derived asymmetry in their sample was reduced relative to that determined through cross-sectional analysis. A number of researchers have identified a relative reduction in the asymmetry of metric bone properties compared to corresponding geometric properties (e.g. Roy *et al.*, 1994; Auerbach & Ruff, 2006; Lazenby *et al.*, 2008). This suggests that there is a large amount of variation between these methods and further research is required to clarify the nature of these relationships. The results of the current study indicate that when asymmetry levels are low, such a difference between the methods has the potential to change the overall direction of asymmetry in a sample. For this reason, the choice of method used to assess asymmetry is crucial, as is an understanding of the implications of using a particular methodology. Adoption of more than one approach will ultimately provide a more wide-ranging assessment of the nature of asymmetry in the sample under study.

More generally, the modern human and non-human primate samples selected for study each display a unique pattern of asymmetry which likely reflects specific patterns of functional recruitment within these groups. These patterns may be based on sociocultural differences between the groups, as is the case for the Écija and Greenwich samples, or reflect responses to biomechanical requirements of the environment from which the sample comes, as for the chimpanzee and gorilla groups. Although such differences between the groups were not the primary focus of the current study, the results presented in the preceding chapters highlight a number of further avenues for future research. In particular, the findings of the non-human primate analysis (Ch. 7) highlight certain features of upper limb asymmetry which correlate with other anatomical (Sarringhaus *et al.*, 2005; Drapeau, 2008) and behavioural (McGrew & Marchant, 1997; Hopkins, 2008) studies into the controversial topic of non-human primate hand preference. The results of the current study also indicate the presence of differences in asymmetry between the species which hint at sample-specific mechanical loading patterns. Together, these findings highlight the need for further investigation into the relationship between skeletal asymmetry and behavioural lateralisation in non-human primate species.

In conclusion, to gain the most comprehensive understanding of the asymmetric nature of individual (and group-level) upper limb use, the most inclusive possible approach must be taken, incorporating a wide range of measurements across the arm and hand and preferably applying more than one methodology to the collection of asymmetry data. Adopting a wide-ranging approach will ultimately provide the most informative and accurate picture of asymmetry in the upper limb. Every methodological approach has its limitations but an inclusive approach is a way of addressing these issues. This is particularly important if the goal of the analysis is to understand hand preference and handedness. Despite the limitations and issues surrounding osteological methodologies, skeletal indicators continue to lend themselves more readily to the study of hand preference in archaeological populations than material culture. For this reason it is important to scrutinise the methods by which this trait is identified and interpreted in skeletal material. In future, more focused research questions can be used to determine more precisely those dimensions that are the most informative and the most appropriate to provide answers to these questions.

9.2. Future directions

The outcomes of the current study identify a number of potential avenues through which future research could expand and develop on the results described in the preceding chapters. With regards to the methodological comparisons undertaken in this study it would be now be useful to expand this to incorporate geometric data from both the humeri and the hands into the samples studied. While it was not possible to access the equipment required to measure bone cross-sectional properties as part of the current data collection process, the addition of geometric data would allow for further comparison with the results of the metric and MSM analyses. As suggested by Pearson & Lieberman (2004: 76), “mechanical loads during adulthood have little effect on the external dimensions of long bone diaphyses, but result in greater cross-sectional areas from smaller medullary cavities”. This implies that using cross-sectional properties to derive asymmetry profiles may elicit increased levels of asymmetry relative to metric properties taken from the same bone. This proposed trend is supported by Maggiano *et al.* (2008a), who found that geometric and MSM approaches differed in the degree of asymmetry they identified. Additionally, various researchers (e.g. Roy *et al.*, 1994; Auerbach & Ruff, 2006; Lazenby *et al.*, 2008) indicate that metric dimensions are less asymmetric than geometric ones. By extending the current comparison to include geometric data the hierarchical nature of the relationship between these three approaches could be further clarified.

In terms of the measurements taken in the metric analyses there is scope for adding more measurements to subsequent analyses. In particular, future analyses may benefit from incorporating more phalanx measurements. As highlighted in section 8.2, phalanx length may not be the most appropriate measurement to reflect the mechanical strains placed upon the fingers and therefore, a data set which included a number of different phalanx dimensions could shed light on the intriguing relationship identified between asymmetry in the phalanges compared with the metacarpals. Where available, large collections of hand bones (and especially those which contain large numbers of distal phalanges) would be a useful addition to the body of data collected in the current study. In particular, they would allow future research to focus on understanding asymmetries specific to the hand that result from manipulative tasks which stress the bones and muscles of the hands but are less reliant on upper arm involvement and strength. This would address the observation in the current study that a different pattern of asymmetry appears to be present in the bones of the hand compared to the humerus, suggesting a certain degree of independence in functional asymmetry between the anatomical units (i.e. the hand, the humerus and potentially the radius/ulna).

The MSM analyses undertaken in the current study established conclusively that it is possible to assess MSM development in the hands using a presence/absence approach. This important finding highlights the potential of MSM in the hands to contribute to upper limb asymmetry and handedness research and therefore further research is now required in order to refine and expand the applicability of this technique. As discussed in section 8.2.2, the use of a ‘binary’ approach which scores MSM only in terms of presence and absence may add ‘noise’ to the analysis of MSM and could lead to certain patterns in the data being missed (Benjamin Auerbach, pers. comm.). For that reason, it would now be informative to attempt a more detailed analysis of hand MSM, more similar to that of Hawkey & Merbs (1995). While it is unlikely to be possible to apply an exact Hawkey & Merbs scoring system to the MSM of the hands, further investigation is required to determine which facets of the methodology would be suitable for the hand MSM and in particular, how much variation is observable in these MSM.

As outlined in the methods (section 3.2.2.1) the hand MSM included in the current study were initially selected from those studied by Marzke *et al.* (1998). This selection was later refined due to problems with identifying these MSM on dry bone and expanded to include MSM that were readily identifiable during the early pilot study (see sections 4.2.2 for further discussion of the data from this study). An area of potential further study therefore, could examine more systematically the suitability of all the MSM in the hand for inclusion in future studies. Experience of scoring MSM in the hands may make it possible to successfully identify variation in a wider range of MSM, as evidenced in the current study. During collection of the MSM data analysed herein, it was noted by the author that the insertion site of the *opponens pollicis* on the lateral edge of the 1st metacarpal and the insertion sites for the *extensor carpi radialis longus* and *extensor carpi radialis brevis* on the proximal dorsal surfaces of the 2nd metacarpal and 3rd metacarpal, respectively could be regularly identified in the samples studied (see Figure 3.5 for a diagrammatic representation of the location of these MSM). As it was also possible to identify a degree of variation in the ‘presence’ of these MSM, it highlights the potential for expanding the group of hand MSM available for study in subsequent analyses in this region. This would also serve to provide more information regarding asymmetric uses of the hands.

Studies of hand MSM may also benefit from a comparison of MSM scored at both the origin and insertion sites of a particular muscle. The humerus MSM in the current study were all measured at points of muscle insertion, due to the observation that insertion sites are likely to display more observable variation than origin sites (Marieb, 2004). Due to the nature of selecting MSM in the hand it was necessary to also include MSM from muscle origin sites in the current study. It would therefore be useful to compare MSM in the hand from the origin and insertion sites of the muscle in question to better understand the relationship between muscle origin and insertion sites in terms of their respective developments and asymmetry. As many of the origin sites for muscles of the hand are found in the arm, such a comparison would provide further interesting insight into the relationship between MSM asymmetry in the arms relative to the hands.

While the standard Hawkey & Merbs (1995) approach to scoring MSM development has been widely applied to the MSM of the humeri the presence/absence approach, represented by the methods used in al-Oumaoui *et al.* (2004) and the current study, is not in common use. The presence/absence method was originally selected for use on the humeral material from the current study in order to provide a more direct comparison with the MSM data from the hands. However, it is not clear the extent to which these two methods differ in the asymmetry profiles they generate and the relative conclusions that can be drawn from them. For this reason, a systematic comparison of a presence/absence and ordinal scoring approach to upper limb bilateral MSM asymmetry is required.

All of the samples studied show interesting and individual patterns of MSM development and bone robusticity which encourage more detailed examination of the activity-related trends over and above those pertaining to asymmetry in the sample. In particular, the non-human primate species included in this analysis could benefit from more detailed study to help clarify some of the intriguing trends identified. In the first instance, increased sample sizes would provide a stronger statistical basis to analyses and allow for more in depth investigations of asymmetry patterns. It would also be informative to extend analyses to other ape and monkey species, in order to compare species with differing locomotor strategies; for example, *Hylobates* species would provide a comparison between chimpanzees and gorillas, which spend the majority of their time engaged in knuckle-walking and terrestrial locomotion with gibbon species that primarily brachiate. The findings of the non-human primate analysis lent tentative support to the observation that while individual behavioural lateralisation is common in the hands of non-human primates (and particularly chimpanzees), this does not extend to clear group-level preferences (e.g. McGrew & Marchant, 1997). However, more research is needed to clarify the relationship between skeletal asymmetry and ‘real-world’ hand preference in both humans and non-human primates, particularly as Blackburn & Knüsel (2006) indicate that the correlation between these factors in their sample of modern humans is not as strong as might be expected.

The current study identified many interesting findings which can now be built upon in future research. Further investigation is necessary into the intriguing topic of upper limb asymmetry and its relationship to hand preference and handedness if we are to better understand the evolution of this unique feature of *Homo sapiens*. Only by doing so will we gain increased insight into those traits that make us ‘human’.

Appendix A. Presence/absence criteria for MSM analysis

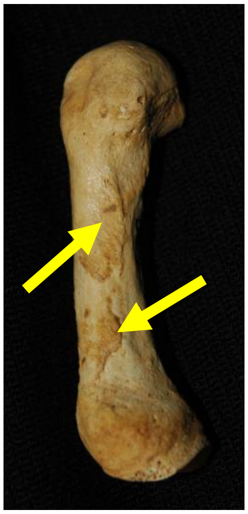
A1. Presence/absence criteria for hand MSM

Present	**Absent**

Flexor pollicis longus (FPL)

Adductor pollicis – transverse head (APT)

Opponens digiti minimi (ODM)

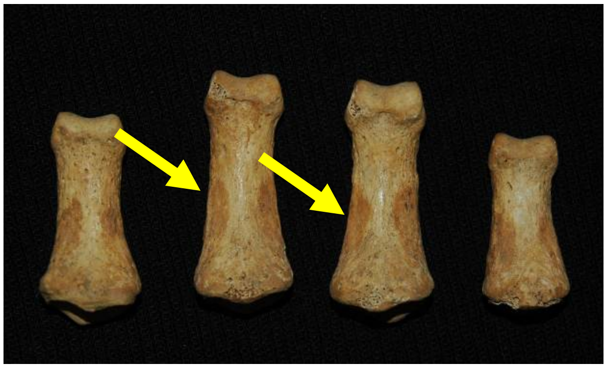


Present

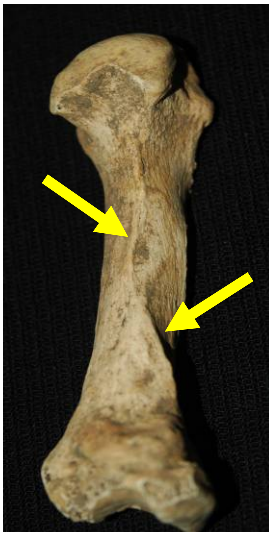
Absent

Flexor digitorum profundus 2 – 5 (FDP)

Flexor digitorum superficialis 2 – 5 (FDS)



Palmar interosseous 2 (PI2)



Present | **Absent**

Palmar interosseous 3 (PI3)

Palmar interosseous 4 (PI4)

Dorsal interosseous 1 (DI1)

Present **Absent**

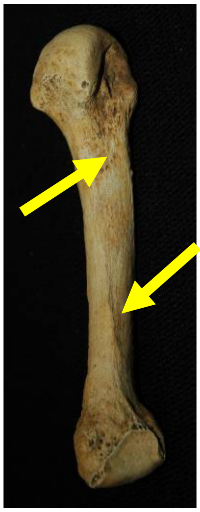
Dorsal interosseous 2 (DI2)



Dorsal interosseous 3 (DI3)



Dorsal interosseous 4 (DI4)




A.2. Presence/absence criteria for humerus MSM

Present	**Absent**

Deltoid (Delt)

Teres major (TMj)

Pectoralis major (PM)

Present	**Absent**

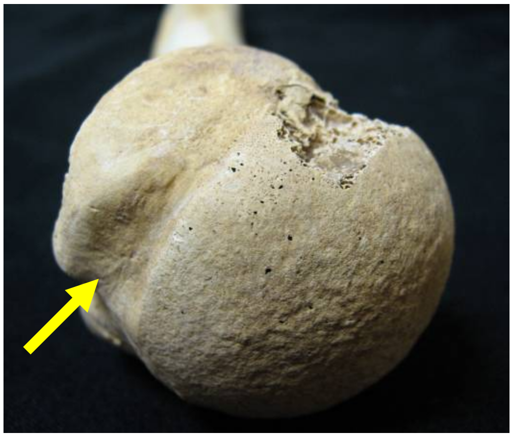
Latissimus dorsi (LD)

Coracobrachialis (CB)

Infraspinatus (IS)

Present | **Absent**

Supraspinatus (SSp)



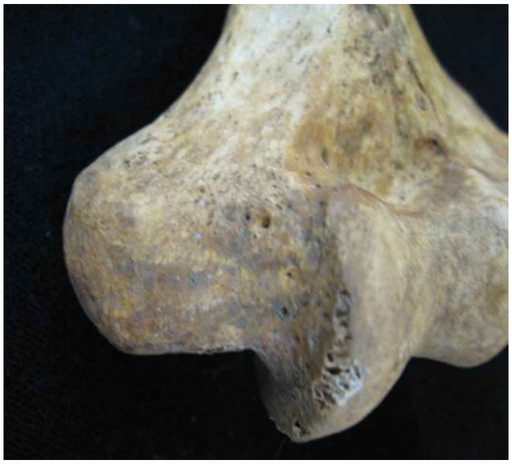
Teres minor (TMn)

Subscapularis (SSc)

Present

Absent

Common flexor origin (CFO)



Common extensor origin (CEO)

Appendix B. Analysis of observer reliability

Table B.1. Data from comparative Great Chesterford humerus MSM analysis (2005 vs 2007).

MSM	Side	N	Percentage present (%) 2005	Percentage present (%) 2007
Delt	L	21	55.6	95.2
	R	20	58.8	95.0
TMj	L	18	27.8	100
	R	20	33.3	75.0
LD	L	17	5.6	58.8
	R	20	16.7	55.0
PM	L	18	66.7	83.3
	R	20	61.1	80.0
CB	L	20	5.3	85.0
	R	18	0	88.9
IS	L	17	18.8	76.5
	R	13	38.5	92.3
SSp	L	16	0	31.3
	R	15	7.7	40.0
TMn	L	15	26.7	86.7
	R	12	50.0	91.7
SSc	L	16	26.7	93.8
	R	18	18.8	83.3
CFO	L	11	8.3	90.9
	R	13	20.0	84.6
CEO	L	14	8.3	78.6
	R	14	15.4	92.9

Abbreviations used: Delt = deltoid, TMj = teres major, LD = latissimus dorsi, PM = pectoralis major, CB = coracobrachialis, IS = infraspinatus, SSp = supraspinatus, TMn = teres minor, SSc = subscapularis, CFO = common flexor origin, CEO = common extensor origin.

Table B.2. Data from comparative Great Chesterford hand MSM analysis (2005 vs 2007).

MSM	Side	N	Percentage present (%) 2005	Percentage present (%) 2007
FPL	L	8	50.0	100.0
	R	10	80.0	90.0
APT	L	20	0	90.0
	R	24	8.3	79.2
ODM	L	16	25.0	50.0
	R	19	25.0	42.1
FDP	L	9	12.5	77.8
	R	10	8.3	90.0
FDS	L	17	36.8	94.1
	R	20	42.1	80.0
PI2	L	24	0	62.5
	R	21	9.1	90.5

MSM	Side	N	Percentage present (%) 2005	Percentage present (%) 2007
PI3	L	20	0	90.0
	R	21	0	100.0
PI4	L	17	11.1	76.5
	R	20	4.8	85.0
DI1	L	24	8.7	66.7
	R	22	18.2	81.8
DI2	L	23	21.7	95.7
	R	24	17.4	87.5
DI3	L	22	0	90.9
	R	24	9.1	87.5
DI4	L	21	9.5	95.2
	R	23	4.5	95.7

Abbreviations used: APT = adductor pollicis (transverse head), ODM = oppenens digiti minimi, FDS = flexor digitorum superficialis (2-5), PI = palmar interosseous, DI = dorsal interosseous.

Table B.3. Data from comparative Great Chesterford hand MSM analysis (2007 vs 2008).

MSM	Side	N	Percentage present (%) 2007	Percentage present (%) 2008
FPL	L	8	100	100
	R	10	90.0	90.0
APT	L	20	90.0	90.0
	R	24	79.2	87.5
ODM	L	16	50.0	50.0
	R	19	42.1	42.1
FDP	L	9	77.8	77.8
	R	10	90.0	90.0
FDS	L	17	94.1	94.1
	R	20	80.0	80.0
PI2	L	24	62.5	79.2
	R	21	90.5	90.5
PI3	L	20	90.0	90.0
	R	21	100	95.5
PI4	L	17	76.5	82.4
	R	20	85.0	85.0
DI1	L	24	66.7	75.0
	R	22	81.8	90.9
DI2	L	23	95.7	95.7
	R	24	87.5	87.5
DI3	L	22	90.9	90.9
	R	24	87.5	91.7
DI4	L	21	95.2	95.2
	R	23	95.7	100

Abbreviations used: APT = adductor pollicis (transverse head), ODM = oppenens digiti minimi, FDS = flexor digitorum superficialis (2-5), PI = palmar interosseous, DI = dorsal interosseous.

Appendix C. Écija data analysis

C.1 Metacarpal and phalanx metric analysis

Table C.1. Summary statistics for Écija metacarpal and phalanx metric data.

Measurement	Side	Male			Female		
		N	Mean	Std dev.	N	Mean	Std dev.
mc1L	L	29	45.10	2.40	26	40.60	2.05
	R	32	45.39	2.57	24	41.62	2.30
mc2L	L	30	66.76	3.56	24	62.70	3.43
	R	29	66.78	3.71	24	63.33	3.52
mc3L	L	31	64.87	3.24	26	59.90	3.50
	R	32	64.72	3.72	27	60.23	3.31
mc4L	L	31	57.56	2.94	21	53.11	3.34
	R	33	57.75	3.01	29	53.67	2.98
mc5L	L	33	53.46	2.88	25	49.46	2.55
	R	33	53.70	2.92	28	49.90	2.84
mc1RU	L	31	12.05	0.97	26	10.95	0.99
	R	33	12.51	0.91	25	11.33	0.82
mc2RU	L	35	8.53	0.63	27	7.52	0.53
	R	35	8.71	0.72	29	7.76	0.62
mc3RU	L	34	8.59	0.60	28	7.87	0.66
	R	33	8.74	0.67	29	8.05	0.62
mc4RU	L	33	6.97	0.56	27	6.26	0.44
	R	35	7.29	0.70	30	6.62	0.54
mc5RU	L	34	7.85	0.61	27	7.19	0.80
	R	34	8.44	0.89	30	7.53	0.77
mc1DP	L	31	9.03	1.04	26	7.65	0.80
	R	33	9.01	0.86	25	7.89	0.67
mc2DP	L	35	9.15	0.81	27	8.17	0.60
	R	35	9.39	0.80	29	8.53	0.67
mc3DP	L	34	9.27	0.82	28	8.32	0.72
	R	33	9.67	0.68	29	8.83	0.70
mc4DP	L	33	7.75	0.67	27	6.78	0.67
	R	35	8.04	0.77	30	7.15	0.69
mc5DP	L	34	7.16	0.82	27	6.35	0.69
	R	33	7.68	0.88	30	6.84	0.69
mc1PB	L	30	15.61	1.59	26	13.97	1.08
	R	33	15.64	1.48	25	14.40	1.03
mc2PB	L	32	17.20	1.23	23	15.59	1.47
	R	31	17.22	1.34	25	15.31	1.33
mc3PB	L	33	14.07	1.00	28	12.83	1.05
	R	30	14.17	0.96	30	12.97	0.83
mc4PB	L	34	12.28	0.91	24	11.15	0.68
	R	34	12.48	0.94	29	11.52	0.79
mc5PB	L	33	11.52	1.16	27	10.77	1.00
	R	34	11.86	1.13	29	11.60	1.03

Measurement	Side	Male			Female		
		N	Mean	Std dev.	N	Mean	Std dev.
mc1DB	L	30	14.57	1.10	27	12.74	0.83
	R	33	14.69	1.06	25	13.11	0.70
mc2DB	L	32	14.07	0.83	26	12.62	0.90
	R	31	14.35	0.97	27	12.83	0.87
mc3DB	L	32	13.92	0.80	26	12.44	0.81
	R	32	14.28	0.84	27	12.79	0.68
mc4DB	L	31	11.82	0.76	24	10.84	0.73
	R	33	12.20	0.83	28	11.19	0.67
mc5DB	L	33	11.33	0.69	25	10.71	0.64
	R	32	11.63	0.81	29	10.82	0.66
pp1L	L	31	29.59	2.05	22	27.02	1.74
	R	31	29.71	2.09	22	27.13	1.71
pp2L	L	31	39.89	1.98	22	36.49	1.84
	R	29	39.80	2.14	25	36.73	1.96
pp3L	L	33	44.12	2.43	24	40.32	2.01
	R	34	44.22	2.38	25	40.89	2.01
pp4L	L	28	41.75	2.14	24	38.50	2.01
	R	32	41.37	2.91	26	38.53	1.82
pp5L	L	29	32.61	1.88	23	30.12	1.40
	R	30	32.88	1.71	22	30.55	1.43
ip2L	L	24	23.75	1.47	21	21.65	1.55
	R	27	23.89	1.41	22	21.90	1.54
ip3L	L	28	28.37	1.65	22	26.14	1.80
	R	29	28.94	2.70	24	26.42	1.60
ip4L	L	24	27.06	1.67	17	25.15	1.75
	R	27	26.91	1.58	21	25.28	1.67
ip5L	L	23	19.14	1.54	18	17.78	1.47
	R	26	18.93	1.81	25	17.82	1.15
dp1L	L	24	22.18	1.68	18	20.65	1.49
	R	27	22.66	1.63	19	20.69	1.43
dp2L	L	8	17.26	1.26	3	16.33	0.76
	R	5	16.98	0.99	9	16.22	1.20
dp3L	L	12	18.39	1.24	6	17.48	1.30
	R	18	18.73	0.95	8	17.06	1.42
dp4L	L	11	18.33	1.36	6	16.35	0.83
	R	11	18.14	0.85	5	16.44	0.90
dp5L	L	8	17.01	1.28	2	14.05	2.62
	R	10	16.63	1.27	7	15.43	1.85

Abbreviations used: mc*L = metacarpal length, mc*RU = radio-ulnar midshaft diameter, mc*DP = dorso-palmar midshaft diameter, mc*PB = proximal breadth, mc*DB = distal breadth, pp*L = proximal phalanx length, ip*L = intermediate phalanx length, dp*L = distal phalanx length. Asterisk (*) denotes metacarpal or phalanx number.

Table C.2. Écija metacarpal asymmetry equation data.

Measurement	N	Percentage right-side dominant (%)	Percentage left-side dominant (%)	Percentage symmetrical (%)
mc1L	47	70.2	27.7	2.1
mc2L	48	62.5	33.3	4.2
mc3L	51	51.0	45.1	3.9
mc4L	50	60.0	34.0	6.0
mc5L	54	57.4	40.7	1.9
mc1RU	50	68.0	28.0	4.0
mc2RU	61	68.9	19.7	11.5
mc3RU	59	64.4	25.4	10.2
mc4RU	60	75.0	16.7	8.3
mc5RU	60	73.3	13.3	13.3
mc1DP	51	66.7	21.6	11.8
mc2DP	61	78.7	19.7	1.6
mc3DP	57	82.5	12.3	10.5
mc4DP	60	80.0	13.3	6.7
mc5DP	59	91.5	5.1	3.4
mc1PB	50	64.0	28.0	8.0
mc2PB	47	53.2	44.7	2.1
mc3PB	57	54.4	40.4	5.3
mc4PB	57	66.7	28.1	5.3
mc5PB	58	77.6	19.0	3.4
mc1DB	50	60.0	34.0	6.0
mc2DB	53	62.3	32.1	5.7
mc3DB	52	78.8	15.4	5.8
mc4DB	52	84.6	9.6	5.8
mc5DB	54	74.1	22.2	3.7

Abbreviations used: mc*L = metacarpal length, mc*RU = radio-ulnar midshaft diameter, mc*DP = dorso-palmar midshaft diameter, mc*PB = proximal breadth, mc*DB = distal breadth. Asterisk (*) denotes metacarpal number.

Table C.3. Écija phalanx asymmetry equation data.

Measurement	N	Percentage right-side dominant (%)	Percentage left-side dominant (%)	Percentage symmetrical (%)
pp1L	48	50.0	41.7	8.3
pp2L	49	59.2	32.7	8.2
pp3L	53	52.8	32.1	15.1
pp4L	48	58.3	35.4	6.3
pp5L	45	53.3	31.1	15.6
ip2L	39	51.3	28.2	20.5
ip3L	46	52.2	41.3	6.5
ip4L	38	47.4	42.1	10.5
ip5L	35	48.6	37.1	14.3
dp1L	34	50.0	38.2	11.8
dp2L	5	60.0	40.0	0.0
dp3L	14	42.9	42.9	14.3
dp4L	10	30.0	60.0	10.0
dp5L	6	50.0	33.3	16.7
Abbreviations used: pp*L = proximal phalanx length, ip*L = intermediate phalanx length, dp*L = distal phalanx length. Asterisk (*) denotes phalanx number.				

Table C.4. Mann-Whitney U test mean rank values for the effect of sex on directional asymmetry in the Écija metacarpals.

Measurement	Sex	N	Mean Rank
mc1L	male	27	22.80
	female	20	25.63
mc2L	male	28	23.63
	female	20	25.73
mc3L	male	28	23.68
	female	20	28.83
mc4L	male	29	22.22
	female	21	30.02
mc5L	male	31	24.76
	female	23	31.20
mc1RU	male	29	28.33
	female	21	21.60
mc2RU	male	35	29.84
	female	26	32.56
mc3RU	male	32	27.98
	female	27	32.39
mc4RU	male	33	29.65
	female	27	31.54
mc5RU	male	33	33.85
	female	27	26.41
mc1DP	male	29	24.14
	female	22	28.45
mc2DP	male	35	28.07
	female	26	34.94

Measurement	Sex	N	Mean Rank
mc3DP	male	32	25.06
	female	27	35.85
mc4DP	male	33	29.91
	female	27	31.22
mc5DP	male	32	29.63
	female	27	30.44
mc1PB	male	29	23.33
	female	21	28.50
mc2PB	male	29	26.09
	female	18	20.64
mc3DP	male	29	26.52
	female	28	31.57
mc4PB	male	33	25.89
	female	24	33.27
mc5PB	male	32	24.77
	female	26	35.33
mc1DB	male	28	23.54
	female	22	28.00
mc2DB	male	30	28.30
	female	23	25.30
mc3DB	male	29	25.88
	female	23	27.28
mc4DB	male	29	26.74
	female	23	26.20
mc5DB	male	30	30.15
	female	24	24.19

Abbreviations used: mc*L = metacarpal length, mc*RU = radio-ulnar midshaft diameter, mc*DP = dorso-palmar midshaft diameter, mc*PB = proximal breadth, mc*DB = distal breadth. Asterisk (*) denotes metacarpal number.

Table C.5. Mann-Whitney U test mean rank values for the effect of sex on absolute asymmetry in the Écija metacarpals.

Measurement	Sex	N	Mean Rank
mc1L	male	27	21.89
	female	20	26.85
mc2L	male	28	23.43
	female	20	26.00
mc3L	male	28	25.88
	female	23	26.15
mc4L	male	29	24.16
	female	21	27.36
mc5L	male	31	26.98
	female	23	28.20
mc1RU	male	29	28.09
	female	21	21.93
mc2RU	male	35	26.76
	female	26	36.71

Measurement	Sex	N	Mean Rank
mc3RU	male	32	24.72
	female	27	36.26
mc4RU	male	33	30.23
	female	27	30.83
mc5RU	male	33	33.70
	female	27	26.59
mc1DP	male	29	23.03
	female	22	29.91
mc2DP	male	35	29.80
	female	26	32.62
mc3DP	male	33	26.48
	female	27	35.41
mc4DP	male	33	30.06
	female	27	31.04
mc5DP	male	32	29.56
	female	27	30.52
mc1PB	male	29	23.59
	female	21	28.14
mc2PB	male	29	24.12
	female	18	23.81
mc3DP	male	29	27.34
	female	28	30.71
mc4PB	male	33	24.50
	female	24	35.19
mc5PB	male	32	26.23
	female	26	33.52
mc1DB	male	28	25.13
	female	22	25.98
mc2DB	male	30	29.20
	female	23	24.13
mc3DB	male	29	26.09
	female	23	27.02
mc4DB	male	29	27.67
	female	23	25.02
mc5DB	male	30	29.62
	female	24	24.85

Abbreviations used: mc*L = metacarpal length, mc*RU = radio-ulnar midshaft diameter, mc*DP = dorso-palmar midshaft diameter, mc*PB = proximal breadth, mc*DB = distal breadth. Asterisk (*) denotes metacarpal number.

Table C.6. Mann-Whitney U test mean rank values for the effect of sex on directional asymmetry in the Écija phalanges.

Measurement	Sex	N	Mean Rank
pp1L	male	28	23.45
	female	20	25.98
pp2L	male	27	20.76
	female	22	30.20
pp3L	male	32	25.58
	female	21	29.17
pp4L	male	26	24.38
	female	22	24.64
pp5L	male	26	22.15
	female	19	24.16
ip2L	male	21	21.62
	female	18	18.11
ip3L	male	26	23.62
	female	20	23.35
ip4L	male	23	17.28
	female	15	22.90
ip5L	male	18	13.78
	female	17	22.47
dp1L	male	21	16.02
	female	13	19.88
dp2L	male	2	3.50
	female	3	2.67
dp3L	male	9	9.50
	female	5	3.90
dp4L	male	6	5.50
	female	4	5.50
dp5L	male	4	3.75
	female	2	3.00

Abbreviations used: pp*L = proximal phalanx length, ip*L = intermediate phalanx length, dp*L = distal phalanx length. Asterisk (*) denotes phalanx number.

Table C.7. Mann-Whitney U test mean rank values for the effect of sex on absolute asymmetry in the Écija phalanges.

Measurement	Sex	N	Mean Rank
pp1L	male	24	21.52
	female	21	24.69
pp2L	male	27	26.39
	female	17	16.32
pp3L	male	27	25.44
	female	21	23.29
pp4L	male	24	22.17
	female	20	22.90
pp5L	male	23	23.61
	female	20	20.15
ip2L	male	17	17.76
	female	19	19.16
ip3L	male	22	21.52
	female	21	22.50
ip4L	male	18	17.81
	female	18	19.19
ip5L	male	15	17.13
	female	17	15.94
dp1L	male	19	20.95
	female	13	10.00
dp2L	male	1	3.00
	female	3	2.33
dp3L	male	7	8.21
	female	6	5.58
dp4L	male	3	6.00
	female	6	4.50
dp5L	male	4	3.00
	female	2	4.50

Abbreviations used: pp*L = proximal phalanx length, ip*L = intermediate phalanx length, dp*L = distal phalanx length. Asterisk (*) denotes phalanx number.

Table C.8. Mann-Whitney U test mean rank values for the effect of age on directional asymmetry in the Écija metacarpals.

Measurement	Age	N	Mean Rank
mc1L	young adult	27	21.87
	middle adult	18	24.69
mc2L	young adult	30	23.03
	middle adult	17	25.71
mc3L	young adult	31	24.89
	middle adult	17	23.79
mc4L	young adult	24	25.38
	middle adult	22	21.45

Measurement	Age	N	Mean Rank
mc5L	young adult	30	25.00
	middle adult	20	26.25
mc1RU	young adult	28	23.95
	middle adult	19	24.08
mc2RU	young adult	35	28.39
	middle adult	22	29.98
mc3RU	young adult	34	27.01
	middle adult	21	29.60
mc4RU	young adult	32	27.86
	middle adult	24	29.35
mc5RU	young adult	31	22.21
	middle adult	25	36.30
mc1DP	young adult	28	24.93
	middle adult	20	23.90
mc2DP	young adult	35	31.59
	middle adult	22	24.89
mc3DP	young adult	34	29.87
	middle adult	21	24.98
mc4DP	young adult	32	25.50
	middle adult	24	32.50
mc5DP	young adult	30	26.45
	middle adult	25	29.86
mc1PB	young adult	28	25.04
	middle adult	19	22.47
mc2PB	young adult	27	22.33
	middle adult	18	24.00
mc3DP	young adult	32	26.47
	middle adult	21	27.81
mc4PB	young adult	29	26.57
	middle adult	24	27.52
mc5PB	young adult	29	27.28
	middle adult	25	27.76
mc1DB	young adult	27	21.69
	middle adult	20	27.13
mc2DB	young adult	33	25.03
	middle adult	19	29.05
mc3DB	young adult	32	25.56
	middle adult	18	25.39
mc4DB	young adult	27	23.63
	middle adult	21	25.62
mc5DB	young adult	30	24.65
	middle adult	20	26.78

Abbreviations used: mc*L = metacarpal length, mc*RU = radio-ulnar midshaft diameter, mc*DP = dorso-palmar midshaft diameter, mc*PB = proximal breadth, mc*DB = distal breadth. Asterisk (*) denotes metacarpal number.

Table C.9. Mann-Whitney U test mean rank values for the effect of age on absolute asymmetry in the Écija metacarpals.

Measurement	Age	N	Mean Rank
mc1L	young adult	27	24.43
	middle adult	20	20.86
mc2L	young adult	28	23.98
	middle adult	20	24.03
mc3L	young adult	28	23.26
	middle adult	23	26.76
mc4L	young adult	29	24.00
	middle adult	21	22.95
mc5L	young adult	31	26.98
	middle adult	23	23.28
mc1RU	young adult	29	25.05
	middle adult	21	22.45
mc2RU	young adult	35	30.47
	middle adult	26	26.66
mc3RU	young adult	32	28.13
	middle adult	27	27.79
mc4RU	young adult	33	28.36
	middle adult	27	28.69
mc5RU	young adult	33	23.76
	middle adult	27	34.38
mc1DP	young adult	29	27.23
	middle adult	22	20.68
mc2DP	young adult	35	30.87
	middle adult	26	26.02
mc3DP	young adult	33	28.59
	middle adult	27	28.36
mc4DP	young adult	33	26.77
	middle adult	27	30.81
mc5DP	young adult	32	27.65
	middle adult	27	28.42
mc1PB	young adult	29	27.32
	middle adult	21	19.11
mc2PB	young adult	29	25.11
	middle adult	18	19.83
mc3DP	young adult	29	31.42
	middle adult	28	20.26
mc4PB	young adult	33	26.48
	middle adult	24	27.63
mc5PB	young adult	32	28.59
	middle adult	26	26.24
mc1DB	young adult	28	21.54
	middle adult	22	27.33
mc2DB	young adult	30	25.36
	middle adult	23	28.47
mc3DB	young adult	29	24.56
	middle adult	23	27.17
mc4DB	young adult	29	23.20
	middle adult	23	26.17

Measurement	Age	N	Mean Rank
mc5DB	young adult	30	23.18
	middle adult	24	28.98
Abbreviations used: mc*L = metacarpal length, mc*RU = radio-ulnar midshaft diameter, mc*DP = dorso-palmar midshaft diameter, mc*PB = proximal breadth, mc*DB = distal breadth. Asterisk (*) denotes metacarpal number.			

Table C.10. Mann-Whitney U test mean rank values for the effect of age on directional asymmetry in the Écija phalanges.

Measurement	Age	N	Mean Rank
pp1L	young adult	24	21.52
	middle adult	21	24.69
pp2L	young adult	27	26.39
	middle adult	17	16.32
pp3L	young adult	27	25.44
	middle adult	21	23.29
pp4L	young adult	24	22.17
	middle adult	20	22.90
pp5L	young adult	23	23.61
	middle adult	20	20.15
ip2L	young adult	17	17.76
	middle adult	19	19.16
ip3L	young adult	22	21.52
	middle adult	21	22.50
ip4L	young adult	18	17.81
	middle adult	18	19.19
ip5L	young adult	15	17.13
	middle adult	17	15.94
dp1L	young adult	19	20.95
	middle adult	13	10.00
dp2L	young adult	1	3.00
	middle adult	3	2.33
dp3L	young adult	7	8.21
	middle adult	6	5.58
dp4L	young adult	3	6.00
	middle adult	6	4.50
dp5L	young adult	4	3.00
	middle adult	2	4.50
Abbreviations used: pp*L = proximal phalanx length, ip*L = intermediate phalanx length, dp*L = distal phalanx length. Asterisk (*) denotes phalanx number.			

Table C.11. Mann-Whitney U test mean rank values for the effect of age on absolute asymmetry in the Écija phalanges.

Measurement	Age	N	Mean Rank
pp1L	young adult	24	23.21
	middle adult	21	22.76
pp2L	young adult	27	25.17
	middle adult	17	18.26
pp3L	young adult	27	24.28
	middle adult	21	24.79
pp4L	young adult	24	23.88
	middle adult	20	20.85
pp5L	young adult	23	23.65
	middle adult	20	20.10
ip2L	young adult	17	15.29
	middle adult	19	21.37
ip3L	young adult	22	21.86
	middle adult	21	22.14
ip4L	young adult	18	15.81
	middle adult	18	21.19
ip5L	young adult	15	14.87
	middle adult	17	17.94
dp1L	young adult	19	17.47
	middle adult	13	15.08
dp2L	young adult	1	2.00
	middle adult	3	2.67
dp3L	young adult	7	6.07
	middle adult	6	8.08
dp4L	young adult	3	4.00
	middle adult	6	5.50
dp5L	young adult	4	3.50
	middle adult	2	3.50

Abbreviations used: pp*L = proximal phalanx length, ip*L = intermediate phalanx length, dp*L = distal phalanx length. Asterisk (*) denotes phalanx number.

C.2. Humerus metric analysis

Table C.12. Summary statistics for Écija humerus metric data.

Measurement	Side	Male			Female		
		N	Mean	Std dev.	N	Mean	Std dev.
MxL	L	19	310.74	17.18	15	289.20	16.12
	R	27	322.59	16.64	25	294.36	14.78
MxDm	L	22	22.43	1.31	24	20.13	1.20
	R	32	23.00	1.66	27	20.84	1.38
MnDm	L	22	17.54	1.39	23	15.44	1.44
	R	32	18.02	1.54	28	15.44	1.51
MnCir	L	19	63.58	3.32	17	54.53	3.17
	R	20	65.15	3.30	18	55.89	3.12
CirHd	L	13	137.69	5.71	14	121.43	6.84
	R	18	142.11	7.25	18	122.39	7.36
MxTDm	L	22	41.84	2.17	19	37.63	1.86
	R	26	43.00	2.20	24	38.36	2.02
MxSDm	L	23	44.84	2.67	20	39.76	2.62
	R	27	46.22	2.60	25	40.86	3.23
EpBr	L	24	64.24	4.96	26	55.54	2.41
	R	31	63.82	4.83	26	56.29	2.36
TCBr	L	25	45.62	3.45	26	39.67	1.44
	R	30	46.30	3.01	28	40.86	1.97

Abbreviations used: MxL = maximum length, MxDm = maximum midshaft diameter, MnDm = minimum midshaft diameter, MnCir = minimum shaft circumference, CirHd = circumference of head, MxTDm = maximum transverse diameter of head, MxSDm = maximum sagittal diameter of head, EpBr = epicondylar breadth, TCBr = trochlea-capitulum breadth.

Table C.13. Écija humerus asymmetry equation data.

Measurement	N	Percentage right-side dominant (%)	Percentage left-side dominant (%)	Percentage symmetrical (%)
MxL	29	93.1	3.4	3.4
MxDm	43	79.1	14.0	7.0
MnDm	43	65.1	34.9	0
MnCir	35	77.1	2.9	20.0
CirHd	25	80.0	16.0	4.0
MxTDm	32	87.5	9.4	3.1
MxSDm	36	75.0	19.4	5.6
EpBr	43	67.4	27.9	4.7
TCBr	45	84.4	13.3	2.2

Abbreviations used: MxL = maximum length, MxDm = maximum midshaft diameter, MnDm = minimum midshaft diameter, MnCir = minimum shaft circumference, CirHd = circumference of head, MxTDm = maximum transverse diameter of head, MxSDm = maximum sagittal diameter of head, EpBr = epicondylar breadth, TCBr = trochlea-capitulum breadth.

Table C.14. Mann-Whitney U test mean rank values for the effect of sex on directional asymmetry in the Écija humeri.

Measurement	Sex	N	Mean Rank
MxL	male	15	13.63
	female	14	16.46
MxDm	male	20	23.18
	female	23	20.98
MnDm	male	20	28.03
	female	23	16.76
MnCir	male	18	18.33
	female	17	17.65
CirHd	male	11	17.27
	female	14	9.64
MxTDm	male	16	18.75
	female	16	14.25
MxSDm	male	18	20.08
	female	18	16.92
EpBr	male	20	18.08
	female	23	25.41
TCBr	male	20	22.93
	female	25	23.06

Abbreviations used: MxL = maximum length, MxDm = maximum midshaft diameter, MnDm = minimum midshaft diameter, MnCir = minimum shaft circumference, CirHd = circumference of head, MxTDm = maximum transverse diameter of head, MxSDm = maximum sagittal diameter of head, EpBr = epicondylar breadth, TCBr = trochlea-capitulum breadth.

Table C.15. Mann-Whitney U test mean rank values for the effect of sex on absolute asymmetry in the Écija humeri.

Measurement	Sex	N	Mean Rank
MxL	male	15	12.90
	female	14	17.25
MxDm	male	20	20.73
	female	23	23.11
MnDm	male	20	23.08
	female	23	21.07
MnCir	male	18	17.78
	female	17	18.24
CirHd	male	11	16.36
	female	14	10.36
MxTDm	male	16	18.94
	female	16	14.06
MxSDm	male	18	19.75
	female	18	17.25

Measurement	Sex	N	Mean Rank
EpBr	male	20	19.28
	female	23	24.37
TCBr	male	20	22.88
	female	25	23.10
Abbreviations used: MxL = maximum length, MxDm = maximum midshaft diameter, MnDm = minimum midshaft diameter, MnCir = minimum shaft circumference, CirHd = circumference of head, MxTDm = maximum transverse diameter of head, MxSDm = maximum sagittal diameter of head, EpBr = epicondylar breadth, TCBr = trochlea-capitulum breadth.			

Table C.16. Mann-Whitney U test mean rank values for the effect of age on directional asymmetry in the Écija humeri.

Measurement	Age	N	Mean Rank
MxL	young adult	14	13.14
	middle adult	13	14.92
MxDm	young adult	22	17.27
	middle adult	18	24.44
MnDm	young adult	23	16.76
	middle adult	17	25.56
MnCir	young adult	18	15.36
	middle adult	16	19.91
CirHd	young adult	16	11.41
	middle adult	8	14.69
MxTDm	young adult	21	16.10
	middle adult	10	15.80
MxSDm	young adult	22	16.11
	middle adult	12	20.04
EpBr	young adult	24	20.60
	middle adult	16	20.34
TCBr	young adult	26	19.12
	middle adult	15	24.27
Abbreviations used: MxL = maximum length, MxDm = maximum midshaft diameter, MnDm = minimum midshaft diameter, MnCir = minimum shaft circumference, CirHd = circumference of head, MxTDm = maximum transverse diameter of head, MxSDm = maximum sagittal diameter of head, EpBr = epicondylar breadth, TCBr = trochlea-capitulum breadth.			

Table C.17. Mann-Whitney U test mean rank values for the effect of age on absolute asymmetry in the Écija humeri.

Measurement	Age	N	Mean Rank
MxL	young adult	14	13.71
	middle adult	13	14.31
MxDm	young adult	22	18.14
	middle adult	18	23.39
MnDm	young adult	23	19.52
	middle adult	17	21.82
MnCir	young adult	18	15.75
	middle adult	16	19.47
CirHd	young adult	16	12.16
	middle adult	8	13.19
MxTDm	young adult	21	14.43
	middle adult	10	19.30
MxSDm	young adult	22	17.16
	middle adult	12	18.13
EpBr	young adult	24	20.63
	middle adult	16	20.31
TCBr	young adult	26	19.83
	middle adult	15	23.03

Abbreviations used: MxL = maximum length, MxDm = maximum midshaft diameter, MnDm = minimum midshaft diameter, MnCir = minimum shaft circumference, CirHd = circumference of head, MxTDm = maximum transverse diameter of head, MxSDm = maximum sagittal diameter of head, EpBr = epicondylar breadth, TCBr = trochlea-capitulum breadth.

C.3. Musculoskeletal stress markers in the hand

Table C.18. Data from Écija hand MSM presence/absence analysis.

MSM	Side	N	Percentage present (%)	Percentage absent (%)
FPL	L	42	97.6	2.4
	R	48	97.9	2.1
APT	L	62	72.6	27.4
	R	60	81.7	18.3
ODM	L	60	78.3	21.7
	R	63	65.1	34.9
FDP	L	23	72.7	27.3
	R	31	72.4	27.6
FDS	L	56	80.4	19.6
	R	60	86.7	13.3
PI2	L	62	58.1	41.9
	R	64	57.8	42.2
PI3	L	60	48.3	51.7
	R	64	56.3	43.7
PI4	L	61	52.5	47.5
	R	64	59.4	40.6
DI1	L	65	63.1	36.9
	R	65	72.3	27.7
DI2	L	65	80.0	20.0
	R	65	90.8	9.2
DI3	L	65	70.8	29.2
	R	64	64.1	35.9
DI4	L	63	92.1	7.9
	R	65	90.8	9.2

Abbreviations used: FPL = flexor pollicis longus, APT = adductor pollicis (transverse head), ODM = oppenens digiti minimi, FDP = flexor digitorum profundus (2-5), FDS = flexor digitorum superficialis (2-5), PI = palmar interosseous, DI = dorsal interosseous.

Table C.19. McNemar test of association between Écija left- and right-hand MSM.

MSM	N	Sig. (2-tailed)
FPL	35	p = 1.00
APT	57	p = 0.15
ODM	58	p = 0.18
FDP	19	p = 0.25
FDS	56	p = 0.29
PI2	61	p = 1.00
PI3	60	p = 0.15
PI4	60	p = 0.33
DI1	65	p = 0.24
DI2	65	*p = 0.07*
DI3	64	p = 0.45
DI4	63	p =1.00

N = number of comparisons performed. P-values approaching significance (between 0.055 and 0.1) highlighted in italics. Due to the low number of instances where score changed between categories, binomial distribution was used instead of chi-squared statistic. Abbreviations used: FPL = flexor pollicis longus, APT = adductor pollicis (transverse head), ODM = oppenens digiti minimi, FDP = flexor digitorum profundus (2-5), FDS = flexor digitorum superficialis (2-5), PI = palmar interosseous, DI = dorsal interosseous.

C.4. Musculoskeletal stress markers in the humerus

Table C.20. Data from Écija humerus MSM presence/absence analysis.

MSM	Side	N	Percentage present (%)	Percentage absent (%)
Delt	L	61	68.9	21.1
	R	63	85.7	14.3
TMj	L	59	71.2	28.8
	R	65	73.8	26.2
LD	L	58	43.1	56.9
	R	65	53.8	46.2
PM	L	59	74.6	25.4
	R	65	84.6	15.4
CB	L	58	46.6	53.4
	R	62	53.2	46.8
IS	L	53	58.5	41.5
	R	59	66.1	33.9
SSp	L	53	22.6	77.4
	R	58	22.4	77.6
TMn	L	51	56.9	43.1
	R	61	77.0	23.0

MSM	Side	N	Percentage present (%)	Percentage absent (%)
SSc	L	54	57.4	42.6
	R	61	59.0	41.0
CFO	L	61	63.9	36.1
	R	61	72.1	27.9
CEO	L	60	65.0	35.0
	R	64	82.8	17.2

Abbreviations used: Delt = deltoid, TMj = teres major, LD = latissimus dorsi, PM = pectoralis major, CB coracobrachialis, IS = infraspinatus, SSp = supraspinatus, TMn = teres minor, SSc = subscapularis, CFO = common flexor origin, CEO = common extensor origin.

Table C.21. McNemar test of association between Écija left- and right-humerus MSM.

MSM	N	Sig. (2-tailed)
Delt	46	p = 1.00
TMj	44	p = 0.51
LD	44	p = 1.00
PM	45	p = 1.00
CB	39	p = 1.00
IS	31	p = 0.50
SSp	29	p = 1.00
TMn	30	p = 0.25
SSc	31	p = 1.00
CFO	49	p = 0.38
CEO	47	*p = 0.07*

N = number of comparisons performed. P-values approaching significance (between 0.055 and 0.1) highlighted in italics. Due to the low number of instances where score changed between categories, binomial distribution was used instead of chi-squared statistic. Abbreviations used: Delt = deltoid, TMj = teres major, LD = latissimus dorsi, PM = pectoralis major, CB coracobrachialis, IS = infraspinatus, SSp = supraspinatus, TMn = teres minor, SSc = subscapularis, CFO = common flexor origin, CEO = common extensor origin.

Appendix D. Greenwich data analysis

D.1 Metacarpal and phalanx metric analysis

Table D.1. Summary statistics for Greenwich metacarpal and phalanx metric data.

Measurement	Side	Middle adult			Old adult		
		N	Mean	Std dev.	N	Mean	Std dev.
mc1L	L	12	43.16	2.65	12	43.78	2.07
	R	11	43.05	2.86	14	44.42	2.19
mc2L	L	13	66.29	2.66	15	64.55	3.16
	R	13	65.85	2.34	16	65.59	3.07
mc3L	L	13	64.02	2.48	14	63.31	2.99
	R	12	63.90	2.37	15	62.38	3.22
mc4L	L	12	57.11	2.23	11	55.04	2.22
	R	13	56.29	1.06	15	55.92	2.14
mc5L	L	12	53.08	1.92	9	53.47	2.68
	R	10	53.25	2.21	14	51.95	2.58
mc1RU	L	11	12.02	1.08	12	12.45	0.64
	R	13	12.55	1.24	14	12.86	0.98
mc2RU	L	14	8.39	0.54	16	8.57	0.74
	R	14	8.67	0.49	17	8.95	0.65
mc3RU	L	14	8.42	0.58	16	8.60	0.72
	R	12	8.62	0.57	16	8.75	0.48
mc4RU	L	14	6.93	0.69	12	6.80	0.58
	R	14	7.31	0.63	16	7.36	0.58
mc5RU	L	13	7.84	0.71	10	7.97	0.85
	R	10	8.27	0.70	14	8.24	0.70
mc1DP	L	11	8.75	0.89	12	9.22	0.98
	R	13	8.96	0.83	15	9.33	1.03
mc2DP	L	14	9.46	0.80	16	9.84	0.98
	R	14	9.71	0.78	17	9.82	0.85
mc3DP	L	14	9.24	0.69	16	9.81	0.90
	R	13	9.59	0.76	16	9.98	0.67
mc4DP	L	14	7.76	0.60	12	7.80	0.67
	R	14	8.04	0.47	16	8.14	0.63
mc5DP	L	13	7.04	0.82	12	7.18	0.72
	R	10	7.31	0.77	15	7.57	0.84
mc1PB	L	10	15.51	1.15	12	16.10	0.72
	R	11	15.80	1.00	13	16.34	1.16
mc2PB	L	14	17.71	0.79	15	17.65	0.87
	R	13	17.28	1.18	16	17.37	1.00
mc3PB	L	13	14.35	0.55	13	14.52	0.92
	R	13	14.20	0.70	15	14.37	0.83
mc4PB	L	11	12.93	0.93	10	12.47	1.12
	R	13	12.86	1.02	16	13.01	1.14
mc5PB	L	12	12.79	1.19	10	13.21	1.23
	R	9	13.07	1.19	12	13.43	1.28

Measurement	Side	Middle adult			Old adult		
		N	Mean	Std dev.	N	Mean	Std dev.
mc1DB	L	9	15.07	0.60	12	15.17	0.90
	R	11	15.45	0.62	12	15.44	0.88
mc2DB	L	12	14.54	0.67	13	14.38	1.07
	R	13	14.79	0.89	14	14.81	0.77
mc3DB	L	12	14.03	0.97	13	14.22	0.94
	R	11	14.55	0.61	12	14.33	0.76
mc4DB	L	12	12.37	0.94	9	11.91	0.80
	R	12	12.62	0.76	11	11.95	0.95
mc5DB	L	12	11.84	0.91	10	11.95	0.62
	R	10	12.38	0.79	10	11.84	1.14
pp1L	L	12	29.52	1.46	12	29.36	1.63
	R	11	29.00	1.76	12	29.31	1.43
pp2L	L	14	39.07	1.07	14	39.19	1.66
	R	14	39.04	1.52	13	39.08	1.82
pp3L	L	13	43.18	1.47	12	43.33	2.19
	R	14	43.24	1.39	15	43.34	1.72
pp4L	L	13	40.83	1.26	12	41.23	1.86
	R	14	40.61	1.41	13	40.45	2.13
pp5L	L	14	32.11	2.15	9	32.99	1.46
	R	13	32.61	1.15	9	32.83	2.24
ip2L	L	8	23.56	0.99	8	23.08	1.31
	R	9	23.77	1.41	9	23.76	1.56
ip3L	L	9	28.74	1.48	9	27.83	1.57
	R	10	28.18	1.61	10	28.69	1.74
ip4L	L	9	27.51	1.41	6	26.78	2.23
	R	8	27.21	1.26	10	26.93	1.37
ip5L	L	8	19.46	1.16	3	20.03	1.27
	R	7	19.30	1.33	9	19.22	1.38

Abbreviations used: mc*L = metacarpal length, mc*RU = radio-ulnar midshaft diameter, mc*DP = dorso-palmar midshaft diameter, mc*PB = proximal breadth, mc*DB = distal breadth, pp*L = proximal phalanx length, ip*L = intermediate phalanx length. Asterisk (*) denotes metacarpal or phalanx number.

Table D.2. Greenwich metacarpal asymmetry data.

Measurement	N	Percentage right-side dominant (%)	Percentage left-side dominant (%)	Percentage symmetrical (%)
mc1L	22	59.1	36.4	4.5
mc2L	26	57.7	42.3	0
mc3L	24	25.0	66.7	8.3
mc4L	20	30.0	65.0	5.0
mc5L	15	53.3	46.7	0
mc1RU	22	54.6	36.3	9.1
mc2RU	30	76.7	23.3	0
mc3RU	27	55.6	18.5	25.9
mc4RU	25	72.0	8.0	20.0

Measurement	N	Percentage right-side dominant (%)	Percentage left-side dominant (%)	Percentage symmetrical (%)
mc5RU	20	65.0	20.0	15.0
mc1DP	23	56.5	21.8	21.8
mc2DP	30	63.3	26.7	10.0
mc3DP	28	71.4	21.5	7.2
mc4DP	25	60.0	24.0	16.0
mc5DP	21	71.4	28.6	0
mc1PB	20	75.0	20.0	5.0
mc2PB	27	40.8	44.4	14.8
mc3PB	23	39.1	47.8	13.1
mc4PB	20	40.0	55.0	5.0
mc5PB	15	66.7	33.3	0
mc1DB	18	61.1	33.3	5.6
mc2DB	22	77.3	18.2	4.5
mc3DB	18	72.2	22.2	5.6
mc4DB	17	47.1	35.3	17.6
mc5DB	15	66.7	20.0	13.3

Abbreviations used: mc*L = metacarpal length, mc*RU = radio-ulnar midshaft diameter, mc*DP = dorso-palmar midshaft diameter, mc*PB = proximal breadth, mc*DB = distal breadth. Asterisk (*) denotes metacarpal number.

Table D.3. Greenwich phalanx asymmetry data.

Measurement	N	Percentage right-side dominant (%)	Percentage left-side dominant (%)	Percentage symmetrical (%)
pp1L	18	38.9	61.1	0
pp2L	26	42.3	53.9	3.9
pp3L	25	52.0	36.0	12.0
pp4L	24	45.8	54.2	0
pp5L	18	55.6	33.3	11.1
ip2L	9	66.7	33.3	0
ip3L	14	64.3	28.6	7.1
ip4L	13	38.5	61.5	0
ip5L	8	25.0	75.0	0

Abbreviations used: pp*L = proximal phalanx length, ip*L = intermediate phalanx length. Asterisk (*) denotes phalanx number.

Table D.4. Mann-Whitney U test mean rank values for the effect of age on directional asymmetry in the Greenwich metacarpals.

Measurement	Age	N	Mean Rank
mc1L	middle adult	11	11.00
	old adult	11	12.00
mc2L	middle adult	12	10.67
	old adult	14	15.93
mc3L	middle adult	11	12.73
	old adult	12	11.33

Measurement	Age	N	Mean Rank
mc4L	middle adult	11	9.50
	old adult	9	11.72
mc5L	middle adult	9	8.56
	old adult	6	7.17
mc1RU	middle adult	11	10.45
	old adult	10	11.60
mc2RU	middle adult	14	14.36
	old adult	16	16.50
mc3RU	middle adult	12	12.92
	old adult	15	14.87
mc4RU	middle adult	14	12.79
	old adult	11	13.27
mc5RU	middle adult	10	10.85
	old adult	9	9.06
mc1DP	middle adult	11	12.50
	old adult	11	10.50
mc2DP	middle adult	14	17.71
	old adult	16	13.56
mc3DP	middle adult	13	14.12
	old adult	15	14.83
mc4DP	middle adult	14	13.68
	old adult	11	12.14
mc5DP	middle adult	10	11.40
	old adult	11	10.64
mc1PB	middle adult	9	10.67
	old adult	11	10.36
mc2PB	middle adult	13	13.69
	old adult	14	14.29
mc3DP	middle adult	12	10.33
	old adult	11	13.82
mc4PB	middle adult	11	10.45
	old adult	9	10.56
mc5PB	middle adult	8	8.81
	old adult	7	7.07
mc1DB	middle adult	9	10.22
	old adult	9	8.78
mc2DB	middle adult	12	10.83
	old adult	10	12.30
mc3DB	middle adult	10	10.70
	old adult	8	8.00
mc4DB	middle adult	11	10.82
	old adult	6	5.67
mc5DB	middle adult	10	9.25
	old adult	5	5.50

Abbreviations used: mc*L = metacarpal length, mc*RU = radio-ulnar midshaft diameter, mc*DP = dorso-palmar midshaft diameter, mc*PB = proximal breadth, mc*DB = distal breadth. Asterisk (*) denotes metacarpal number.

Table D.5. Mann-Whitney U test mean rank values for the effect of age on absolute asymmetry in the Greenwich metacarpals.

Measurement	Age	N	Mean Rank
mc1L	middle adult	11	11.73
	old adult	11	11.27
mc2L	middle adult	12	10.58
	old adult	14	16.00
mc3L	middle adult	11	13.95
	old adult	13	11.27
mc4L	middle adult	11	9.59
	old adult	9	11.61
mc5L	middle adult	9	9.22
	old adult	6	6.17
mc1RU	middle adult	11	12.86
	old adult	11	10.14
mc2RU	middle adult	14	14.68
	old adult	16	16.22
mc3RU	middle adult	12	11.13
	old adult	15	16.30
mc4RU	middle adult	14	12.14
	old adult	11	14.09
mc5RU	middle adult	10	11.90
	old adult	10	9.10
mc1DP	middle adult	11	14.36
	old adult	12	9.83
mc2DP	middle adult	14	15.54
	old adult	16	15.47
mc3DP	middle adult	13	12.50
	old adult	15	16.23
mc4DP	middle adult	14	11.68
	old adult	11	14.68
mc5DP	middle adult	10	11.85
	old adult	11	10.23
mc1PB	middle adult	9	11.56
	old adult	11	9.64
mc2PB	middle adult	13	15.73
	old adult	14	12.39
mc3DP	middle adult	12	11.50
	old adult	11	12.55
mc4PB	middle adult	11	9.82
	old adult	9	11.33
mc5PB	middle adult	8	8.31
	old adult	7	7.64
mc1DB	middle adult	9	9.00
	old adult	9	10.00
mc2DB	middle adult	12	10.50
	old adult	10	12.70
mc3DB	middle adult	10	10.90
	old adult	8	7.75
mc4DB	middle adult	11	9.64
	old adult	6	7.83

Measurement	Age	N	Mean Rank
mc5DB	middle adult	10	8.45
	old adult	5	7.10
Abbreviations used: mc*L = metacarpal length, mc*RU = radio-ulnar midshaft diameter, mc*DP = dorso-palmar midshaft diameter, mc*PB = proximal breadth, mc*DB = distal breadth. Asterisk (*) denotes metacarpal number.			

Table D.6. Mann-Whitney U test mean rank values for the effect of age on directional asymmetry in the Greenwich phalanges.

Measurement	Age	N	Mean Rank
pp1L	middle adult	10	9.95
	old adult	8	8.94
pp2L	middle adult	14	14.75
	old adult	12	12.04
pp3L	middle adult	13	13.69
	old adult	12	12.25
pp4L	middle adult	13	14.69
	old adult	11	9.91
pp5L	middle adult	13	10.35
	old adult	5	7.30
ip2L	middle adult	5	5.20
	old adult	4	4.75
ip3L	middle adult	8	6.31
	old adult	6	9.08
ip4L	middle adult	8	6.38
	old adult	5	8.00
ip5L	middle adult	6	4.50
	old adult	2	4.50
Abbreviations used: pp*L = proximal phalanx length, ip*L = intermediate phalanx length, dp*L = distal phalanx length. Asterisk (*) denotes phalanx number.			

Table D.7. Mann-Whitney U test mean rank values for the effect of age on absolute asymmetry in the Greenwich phalanges.

Measurement	Age	N	Mean Rank
pp1L	middle adult	10	8.35
	old adult	8	10.94
pp2L	middle adult	14	11.68
	old adult	12	15.63
pp3L	middle adult	13	13.46
	old adult	12	12.50
pp4L	middle adult	13	11.00
	old adult	11	14.27
pp5L	middle adult	13	9.92
	old adult	5	8.40
ip2L	middle adult	5	5.00
	old adult	4	5.00

Measurement	Age	N	Mean Rank
ip3L	middle adult	8	7.19
	old adult	6	7.92
ip4L	middle adult	8	7.88
	old adult	5	5.60
ip5L	middle adult	6	4.50
	old adult	2	4.50

Abbreviations used: pp*L = proximal phalanx length, ip*L = intermediate phalanx length, dp*L = distal phalanx length. Asterisk (*) denotes phalanx number.

D.2. Humerus metric analysis

Table D.8. Summary statistics for Greenwich humerus metric data.

Measurement	Side	Middle adult			Old adult		
		N	Mean	Std dev.	N	Mean	Std dev.
MxL	L	13	319.15	15.74	16	319.56	11.66
	R	13	323.69	13.62	17	320.29	11.28
MxDm	L	14	22.94	1.05	17	23.55	2.01
	R	14	23.77	1.42	17	24.06	1.72
MnDm	L	14	18.59	1.66	17	19.09	1.57
	R	14	18.69	1.55	17	19.14	1.07
MnCir	L	14	65.00	3.68	17	66.59	4.44
	R	14	65.43	3.27	17	67.12	3.72
CirHd	L	9	145.11	7.80	9	146.11	5.09
	R	12	146.67	6.83	12	142.50	5.20
MxTDm	L	10	42.99	1.67	9	43.94	1.68
	R	12	43.93	1.42	11	44.01	1.65
MxSDm	L	12	46.39	2.78	16	47.46	1.87
	R	13	47.68	2.15	16	47.21	1.84
EpBr	L	12	62.25	2.65	13	64.57	2.85
	R	10	62.61	3.51	14	65.18	2.70
TCBr	L	6	47.05	3.23	10	47.53	2.14
	R	12	48.38	2.54	13	47.58	1.53

Abbreviations used: MxL = maximum length, MxDm = maximum midshaft diameter, MnDm = minimum midshaft diameter, MnCir = minimum shaft circumference, CirHd = circumference of head, MxTDm = maximum transverse diameter of head, MxSDm = maximum sagittal diameter of head, EpBr = epicondylar breadth, TCBr = trochlea-capitulum breadth.

Table D.9. Greenwich humerus asymmetry data.

Measurement	N	Percentage right-side dominant (%)	Percentage left-side dominant (%)	Percentage symmetrical (%)
MxL	29	93.1	3.4	3.4
MxDm	43	79.1	14.0	7.0
MnDm	43	65.1	34.9	0
MnCir	35	77.1	2.9	20.0
CirHd	25	80.	16.0	4.0
MxTDm	32	87.5	9.4	3.1
MxSDm	36	75.0	19.4	5.6
EpBr	43	67.4	27.9	4.7
TCBr	45	87.4	13.3	2.2

Abbreviations used: MxL = maximum length, MxDm = maximum midshaft diameter, MnDm = minimum midshaft diameter, MnCir = minimum shaft circumference, CirHd = circumference of head, MxTDm = maximum transverse diameter of head, MxSDm = maximum sagittal diameter of head, EpBr = epicondylar breadth, TCBr = trochlea-capitulum breadth.

Table D.10. Mann-Whitney U test mean rank values for the effect of age on directional asymmetry in the Greenwich humeri.

Measurement	Age	N	Mean Rank
MxL	middle adult	12	15.38
	old adult	16	13.84
MxDm	middle adult	14	18.64
	old adult	17	13.82
MnDm	middle adult	14	16.21
	old adult	17	15.82
MnCir	middle adult	14	15.82
	old adult	17	16.15
CirHd	middle adult	9	10.44
	old adult	9	8.56
MxTDm	middle adult	9	9.44
	old adult	7	7.29
MxSDm	middle adult	11	15.18
	old adult	15	12.27
EpBr	middle adult	10	12.05
	old adult	11	10.05
TCBr	middle adult	6	8.00
	old adult	9	8.00

Abbreviations used: MxL = maximum length, MxDm = maximum midshaft diameter, MnDm = minimum midshaft diameter, MnCir = minimum shaft circumference, CirHd = circumference of head, MxTDm = maximum transverse diameter of head, MxSDm = maximum sagittal diameter of head, EpBr = epicondylar breadth, TCBr = trochlea-capitulum breadth.

Table D.11. Mann-Whitney U test mean rank values for the effect of age on absolute asymmetry in the Greenwich humeri.

Measurement	Age	N	Mean Rank
MxL	middle adult	12	13.96
	old adult	16	14.91
MxDm	middle adult	14	17.32
	old adult	17	14.91
MnDm	middle adult	14	12.29
	old adult	17	19.06
MnCir	middle adult	14	15.82
	old adult	17	16.15
CirHd	middle adult	9	8.22
	old adult	9	10.78
MxTDm	middle adult	9	8.00
	old adult	7	9.14
MxSDm	middle adult	11	12.91
	old adult	15	13.93
EpBr	middle adult	10	11.25
	old adult	11	10.77
TCBr	middle adult	6	7.33
	old adult	9	8.44

Abbreviations used: MxL = maximum length, MxDm = maximum midshaft diameter, MnDm = minimum midshaft diameter, MnCir = minimum shaft circumference, CirHd = circumference of head, MxTDm = maximum transverse diameter of head, MxSDm = maximum sagittal diameter of head, EpBr = epicondylar breadth, TCBr = trochlea-capitulum breadth.

D.3. Musculoskeletal stress markers in the hand

Table D.12. Data from Greenwich hand MSM presence/absence analysis.

MSM	Side	N	Percentage present (%)	Percentage absent (%)
FPL	L	8	100	0
	R	13	100	0
APT	L	30	86.7	13.3
	R	27	85.2	14.8
ODM	L	22	59.1	40.9
	R	21	71.4	28.6
FDP	L	7	66.7	33.3
	R	8	87.5	12.5
FDS	L	21	95.2	4.8
	R	25	92.0	8.0
PI2	L	30	80.0	20.0
	R	31	83.9	16.1
PI3	L	26	61.5	38.5
	R	30	60.0	40.0
PI4	L	21	90.5	9.5
	R	23	73.9	26.1

MSM	Side	N	Percentage present (%)	Percentage absent (%)
DI1	L	30	43.3	56.7
	R	31	77.4	22.6
DI2	L	30	93.3	6.7
	R	31	90.3	9.7
DI3	L	28	50.0	50.0
	R	31	54.8	45.2
DI4	L	27	88.9	11.1
	R	29	93.1	6.9

Abbreviations used: FPL = flexor pollicis longus, APT = adductor pollicis (transverse head), ODM = oppenens digiti minimi, FDP = flexor digitorum profundus (2-5), FDS = flexor digitorum superficialis (2-5), PI = palmar interosseous, DI = dorsal interosseous.

Table D.13. Chi-squared (χ^2) test of association between age and Greenwich hand MSM.

MSM	Side	χ^2 value	Sig. (2-tailed)	φ value
FPL	L	-	-	-
	R	-	-	-
APT	L	0.21	p = 1.00*	0.03
	R	0.01	p = 1.00*	0.02
ODM	L	2.20	p = 0.20*	0.32
	R	4.30	*p = 0.06**	0.45
FDP	L	1.22	p = 0.49*	0.42
	R	0.69	p = 1.00*	0.29
FDS	L	0.87	p = 1.00*	0.20
	R	2.36	p = 0.22*	0.31
PI2	L	0.54	p = 0.66*	0.13
	R	0.06	p = 1.00*	0.05
PI3	L	0.25	p = 0.70*	0.10
	R	1.43	p = 0.28	0.22
PI4	L	1.66	p = 0.49*	0.28
	R	0.34	p = 0.66*	0.12
DI1	L	2.04	p = 0.27	0.26
	R	0.02	p = 1.00*	0.03
DI2	L	0.01	p = 1.00*	0.02
	R	0.62	p = 0.58*	0.14
DI3	L	0.57	p = 0.71	0.14
	R	2.84	p = 0.15	0.30
DI4	L	0.46	p = 0.60*	0.13
	R	2.64	p = 0.19*	0.30

P-values approaching significance (between 0.055 and 0.1) highlighted in italics. FPL was not included in the analysis as no individuals changed score between 'present' and 'absent' categories. Values marked with an asterisk (*) indicate where the Fisher's Exact Test p-value was used due to low cell counts (in most instances, this test provides the same results as the standard χ^2). A phi (φ) value indicates the strength of the χ^2 association. Abbreviations used: FPL = flexor pollicis longus, APT = adductor pollicis (transverse head), ODM = oppenens digiti minimi, FDP = flexor digitorum profundus (2-5), FDS = flexor digitorum superficialis (2-5), PI = palmar interosseous, DI = dorsal interosseous.

D.4. Musculoskeletal stress markers in the humerus

Table D.14. Data from Greenwich humerus MSM presence/absence analysis.

MSM	Side	N	Percentage present (%)	Percentage absent (%)
Delt	L	29	93.1	6.9
	R	31	100	0
TMj	L	28	78.6	21.4
	R	29	86.2	13.8
LD	L	28	82.1	17.9
	R	30	76.7	23.3
PM	L	28	96.4	3.6
	R	30	96.7	3.3
CB	L	27	63.0	37.0
	R	29	58.6	41.4
IS	L	23	87.0	13.0
	R	25	84.0	16.0
SSp	L	21	19.0	81.0
	R	23	13.0	87.0
TMn	L	22	95.5	4.5
	R	25	96.0	4.0
SSc	L	25	88.0	12.0
	R	29	82.8	17.2
CFO	L	23	65.2	34.8
	R	23	60.9	39.1
CEO	L	22	72.7	27.3
	R	28	67.9	32.1

Abbreviations used: Delt = deltoid, TMj = teres major, LD = latissimus dorsi, PM = pectoralis major, CB = coracobrachialis, IS = infraspinatus, SSp = supraspinatus, TMn = teres minor, SSc = subscapularis, CFO = common flexor origin, CEO = common extensor origin.

Table D.15. McNemar test of association between left and right Greenwich humerus MSM.

MSM	N	Sig. (2-tailed)
Delt	29	p = 0.50
TMj	27	p = 0.38
LD	28	p = 1.00
PM	28	p = 1.00
CB	26	p = 0.55
IS	20	p = 1.00
SSp	19	p = 1.00
TMn	20	p = 1.00
SSc	25	p = 1.00
CFO	19	p = 0.69
CEO	20	p = 0.75

N = number of comparisons performed. Due to the low number of instances where score changed between categories, binomial distribution was used instead of chi-squared statistic. Abbreviations used: Delt = deltoid, TMj = teres major, LD = latissimus dorsi, PM = pectoralis major, CB = coracobrachialis, IS = infraspinatus, SSp = supraspinatus, TMn = teres minor, SSc = subscapularis, CFO = common flexor origin, CEO = common extensor origin.

Table D.16. Chi-squared (χ^2) test of association between age and Greenwich humerus MSM.

MSM	Side	χ^2 value	Sig. (2-tailed)	φ value
Delt	L	0.003	p = 1.00*	0.01
	R	-	-	-
TMj	L	0.04	p = 1.00*	0.04
	R	0.05	p = 1.00*	0.04
LD	L	0.45	p = 0.64*	0.13
	R	3.14	*p = 0.10**	0.32
PM	L	1.20	p = 0.46*	0.21
	R	1.18	p = 0.47*	0.20
CB	L	2.10	p = 0.24*	0.28
	R	0.63	p = 0.47*	0.15
IS	L	0.49	p = 0.59*	0.15
	R	0.40	*p = 0.10**	0.42
SSp	L	1.49	p = 0.31*	0.27
	R	0.29	p = 1.00*	0.11
TMn	L	1.05	p = 1.00*	0.22
	R	0.96	p = 1.00*	0.20
SSc	L	0.48	p = 0.59*	0.14
	R	2.44	p = 0.17*	0.29
CFO	L	0.52	p = 0.67*	0.15
	R	0.01	p = 1.00*	0.02
CEO	L	0.49	p = 0.65*	0.15
	R	0.87	p = 0.43*	0.18

P-values approaching significance (between 0.55 and 0.1) highlighted in italics. Right Delt was not included in the analysis as no individuals changed score between ‘present’ and ‘absent’ categories. Values marked with an asterisk (*) indicate where the Fisher’s Exact Test p-value was used due to low cell counts (in most instances, this test provides the same results as the standard χ^2). A phi (φ) value indicates the strength of the χ^2 association. Abbreviations used: Delt = deltoid, TMj = teres major, LD = latissimus dorsi, PM = pectoralis major, CB = coracobrachialis, IS = infraspinatus, SSp = supraspinatus, TMn = teres minor, SSc = subscapularis, CFO = common flexor origin, CEO = common extensor origin.

Appendix E. Non-human primate data analysis

E.1 Chimpanzee metacarpal and phalanx metric analysis

Table E.1. Summary statistics for chimpanzee metacarpal and phalanx metric data.

Measurement	Side	Male			Female		
		N	Mean	Std dev.	N	Mean	Std dev.
mc1L	L	8	39.68	2.28	12	39.45	2.70
	R	9	40.01	2.71	12	39.41	2.60
mc2L	L	8	87.63	3.20	12	86.22	4.52
	R	9	88.87	3.91	12	86.14	4.15
mc3L	L	9	87.40	3.10	12	84.73	4.18
	R	9	87.70	2.98	12	84.89	4.03
mc4L	L	8	82.23	3.27	12	79.71	4.46
	R	9	82.87	3.15	12	79.66	4.55
mc5L	L	8	75.56	3.15	12	73.01	4.13
	R	8	75.89	3.01	12	72.74	3.73
mc1RU	L	8	8.78	1.15	12	8.06	0.85
	R	9	8.61	0.87	12	8.15	0.84
mc2RU	L	9	8.33	0.60	12	7.75	0.52
	R	9	8.30	0.60	12	7.63	0.44
mc3RU	L	9	8.87	0.51	12	8.17	0.57
	R	9	8.93	0.38	12	8.33	0.48
mc4RU	L	9	8.16	0.65	12	7.35	0.41
	R	9	8.11	0.64	12	7.33	0.28
mc5RU	L	8	7.83	0.31	12	6.84	0.68
	R	8	7.94	0.50	12	6.97	0.72
mc1DP	L	8	7.11	0.82	12	6.05	0.50
	R	9	7.22	0.99	12	6.23	1.02
mc2DP	L	9	8.61	0.69	12	7.74	0.68
	R	9	8.61	0.88	12	7.98	0.71
mc3DP	L	9	9.21	0.60	12	8.73	0.60
	R	9	9.29	0.71	12	8.93	0.50
mc4DP	L	9	8.00	0.77	12	7.74	0.54
	R	9	8.11	0.61	12	8.09	0.67
mc5DP	L	8	6.35	0.81	12	6.03	0.44
	R	8	6.51	0.76	12	6.25	0.43
mc1PB	L	8	10.80	1.03	12	10.65	0.93
	R	9	10.92	1.03	12	10.69	0.90
mc2PB	L	9	13.33	0.74	12	12.20	0.62
	R	9	13.26	0.69	12	12.48	0.62
mc3PB	L	9	13.76	1.02	12	13.41	0.77
	R	9	13.82	0.95	12	13.27	0.63
mc4PB	L	9	10.78	0.83	12	10.24	0.84
	R	9	10.91	0.87	12	10.58	0.79
mc5PB	L	8	9.68	0.83	12	9.11	1.11
	R	8	9.94	0.81	12	9.30	1.24

Measurement	Side	Male			Female		
		N	Mean	Std dev.	N	Mean	Std dev.
mc1DB	L	8	9.30	0.69	12	9.05	0.72
	R	9	9.57	0.68	12	8.95	0.69
mc2DB	L	8	12.23	0.84	12	11.93	0.45
	R	9	12.56	0.94	12	11.94	0.45
mc3DB	L	9	13.67	0.91	12	12.93	0.80
	R	9	13.81	0.90	12	13.05	0.70
mc4DB	L	8	12.26	0.77	12	11.76	0.75
	R	9	12.43	0.88	12	11.83	0.68
mc5DB	L	8	9.86	0.83	12	9.27	0.74
	R	7	9.74	0.73	12	9.31	0.76
pp1L	L	8	24.41	2.57	12	25.69	2.17
	R	9	24.53	3.42	12	25.12	2.41
pp2L	L	9	48.96	3.33	12	49.32	2.83
	R	9	48.71	3.46	12	49.15	2.84
pp3L	L	8	56.69	3.14	12	57.60	2.50
	R	9	57.47	3.45	12	57.35	2.37
pp4L	L	9	54.40	3.53	12	53.92	2.64
	R	9	54.12	3.57	12	53.86	2.72
pp5L	L	9	42.41	2.57	12	41.74	2.36
	R	9	42.30	2.54	12	41.71	2.75
ip2L	L	8	30.38	2.07	12	30.73	2.20
	R	9	30.84	2.04	12	30.94	2.41
ip3L	L	9	40.89	2.49	12	41.33	2.56
	R	9	40.92	2.37	12	41.32	2.57
ip4L	L	9	37.84	2.52	12	38.20	2.47
	R	8	37.45	2.03	11	38.44	2.47
ip5L	L	8	26.15	2.51	12	27.08	2.30
	R	9	26.81	2.40	12	27.12	2.40

Abbreviations used: mc*L = metacarpal length, mc*RU = radio-ulnar midshaft diameter, mc*DP = dorso-palmar midshaft diameter, mc*PB = proximal breadth, mc*DB = distal breadth, pp*L = proximal phalanx length, ip*L = intermediate phalanx length. Asterisk (*) denotes metacarpal or phalanx number.

Table E.2. One-way ANOVA for the effect of sex on chimpanzee phalanx variables.

Measurement	Side	Sex	N	Mean	F	Sig. (2-tailed)
pp1L	L	male	8	24.41	1.44	p = 0.25
		female	12	25.69		
	R	male	9	24.53	0.07	p = 0.79
		female	12	25.12		
pp2L	L	male	9	48.96	0.52	p = 0.48
		female	12	49.32		
	R	male	9	48.71	0.13	p = 0.72
		female	12	49.15		
pp3L	L	male	8	56.69	0.38	p = 0.54
		female	12	57.60		
	R	male	9	57.47	0.13	p = 0.73
		female	12	57.35		
pp4L	L	male	9	54.40	0.15	p = 0.70
		female	12	53.92		
	R	male	9	54.12	0.11	p = 0.75
		female	12	53.86		
pp5L	L	male	9	42.41	0.74	p = 0.40
		female	12	41.74		
	R	male	9	42.30	0.21	p = 0.65
		female	12	41.71		
ip2L	L	male	8	30.38	0.10	p = 0.75
		female	12	30.73		
	R	male	9	30.84	0.01	p = 0.93
		female	12	30.94		
ip3L	L	male	9	40.89	0.04	p = 0.85
		female	12	41.33		
	R	male	9	40.92	0.25	p = 0.62
		female	12	41.32		
ip4L	L	male	9	37.84	0.01	p = 0.92
		female	12	38.20		
	R	male	8	37.45	0.13	p = 0.72
		female	11	38.44		
ip5L	L	male	8	26.15	0.85	p = 0.37
		female	12	27.08		
	R	male	9	26.81	0.08	p = 0.78
		female	12	27.12		

Mean values rounded to two decimal places. Distal phalanx measurements were not available for inclusion in this analysis.Abbreviations used: pp*L = proximal phalanx length, ip*L = intermediate phalanx length. Asterisk (*) denotes phalanx number.

Table E.3. Chimpanzee metacarpal asymmetry data.

Measurement	N	Percentage right-side dominant (%)	Percentage left-side dominant (%)	Percentage symmetrical (%)
mc1L	20	45.0	50.0	5.0
mc2L	20	50.0	45.0	5.0
mc3L	21	66.7	33.3	0
mc4L	20	55.0	45.0	0
mc5L	19	36.8	63.2	0
mc1RU	20	45.0	50.0	5.0
mc2RU	21	42.9	38.1	19.0
mc3RU	21	71.4	23.8	4.8
mc4RU	21	33.3	57.1	9.5
mc5RU	19	47.4	36.8	15.8
mc1DP	20	50.0	45.0	5.0
mc2DP	21	57.1	33.3	9.5
mc3DP	21	66.7	23.8	9.5
mc4DP	21	61.9	28.6	9.5
mc5DP	19	68.4	21.1	10.5
mc1PB	20	45.0	40.0	15.0
mc2PB	21	52.4	47.6	0
mc3PB	21	38.1	57.1	4.8
mc4PB	21	66.7	19.0	14.3
mc5PB	19	52.6	36.8	10.5
mc1DB	20	45.0	40.0	15.0
mc2DB	20	50.0	30.0	20.0
mc3DB	21	66.7	28.6	4.8
mc4DB	20	45.0	35.0	20.0
mc5DB	18	44.4	27.8	27.8

Abbreviations used: mc*L = metacarpal length, mc*RU = radio-ulnar midshaft diameter, mc*DP = dorso-palmar midshaft diameter, mc*PB = proximal breadth, mc*DB = distal breadth. Asterisk (*) denotes metacarpal number.

Table E.4. Chimpanzee phalanx asymmetry data.

Measurement	N	Percentage right-side dominant (%)	Percentage left-side dominant (%)	Percentage symmetrical (%)
pp1L	20	35.0	60.0	5.0
pp2L	21	33.3	52.4	14.3
pp3L	20	45.0	50.0	5.0
pp4L	21	33.3	47.6	19.0
pp5L	21	52.4	47.6	0
ip2L	20	45.0	40.0	15.0
ip3L	21	47.6	52.4	0
ip4L	19	57.9	31.6	10.5
ip5L	20	40.0	60.0	0

Abbreviations used: pp*L = proximal phalanx length, ip*L = intermediate phalanx length. Asterisk (*) denotes phalanx number.

Table E.5. Mann-Whitney U test mean rank values for the effect of sex on directional asymmetry in the chimpanzee metacarpals.

Measurement	Sex	N	Mean Rank
mc1L	male	8	10.63
	female	12	10.42
mc2L	male	8	11.94
	female	12	9.54
mc3L	male	9	12.56
	female	12	9.83
mc4L	male	8	12.50
	female	12	9.17
mc5L	male	7	10.00
	female	12	10.00
mc1RU	male	8	7.63
	female	12	12.42
mc2RU	male	9	12.00
	female	12	10.25
mc3RU	male	9	9.67
	female	12	12.00
mc4RU	male	9	11.06
	female	12	10.96
mc5RU	male	7	9.64
	female	12	10.21
mc1DP	male	8	9.63
	female	12	11.08
mc2DP	male	9	9.89
	female	12	11.83
mc3DP	male	9	9.00
	female	12	12.50
mc4DP	male	9	8.28
	female	12	13.04
mc5DP	male	7	9.57
	female	12	10.25
mc1PB	male	8	9.50
	female	12	11.17
mc2PB	male	9	8.56
	female	12	12.83
mc3DP	male	9	13.22
	female	12	9.33
mc4PB	male	9	9.00
	female	12	12.50
mc5PB	male	7	9.93
	female	12	10.04
mc1DB	male	8	13.50
	female	12	8.50
mc2DB	male	8	11.31
	female	12	9.96
mc3DB	male	9	11.33
	female	12	10.75
mc4DB	male	8	9.88
	female	12	10.92

Measurement	Sex	N	Mean Rank
mc5DB	male	6	9.33
	female	12	9.58

Abbreviations used: mc*L = metacarpal length, mc*RU = radio-ulnar midshaft diameter, mc*DP = dorso-palmar midshaft diameter, mc*PB = proximal breadth, mc*DB = distal breadth. Asterisk (*) denotes metacarpal number.

Table E.6. Mann-Whitney U test mean rank values for the effect of sex on absolute asymmetry in the chimpanzee metacarpals.

Measurement	Sex	N	Mean Rank
mc1L	male	8	9.00
	female	12	11.50
mc2L	male	8	9.75
	female	12	11.00
mc3L	male	9	16.22
	female	12	7.08
mc4L	male	8	10.81
	female	12	10.29
mc5L	male	7	12.29
	female	12	8.67
mc1RU	male	8	12.44
	female	12	9.21
mc2RU	male	9	11.33
	female	12	10.75
mc3RU	male	9	10.56
	female	12	11.33
mc4RU	male	9	9.78
	female	12	11.92
mc5RU	male	7	7.50
	female	12	11.46
mc1DP	male	8	7.94
	female	12	12.21
mc2DP	male	9	11.11
	female	12	10.92
mc3DP	male	9	7.83
	female	12	13.38
mc4DP	male	9	10.28
	female	12	11.54
mc5DP	male	7	10.86
	female	12	9.50
mc1PB	male	8	12.63
	female	12	9.08
mc2PB	male	9	8.61
	female	12	12.79
mc3PB	male	9	9.78
	female	12	11.92
mc4PB	male	9	10.22
	female	12	11.58
mc5PB	male	7	9.21
	female	12	10.46

Measurement	Sex	N	Mean Rank
mc1DB	male	8	12.25
	female	12	9.33
mc2DB	male	8	12.63
	female	12	9.08
mc3DB	male	9	13.00
	female	12	9.50
mc4DB	male	8	7.63
	female	12	12.42
mc5DB	male	6	6.33
	female	12	11.08
Abbreviations used: mc*L = metacarpal length, mc*RU = radio-ulnar midshaft diameter, mc*DP = dorso-palmar midshaft diameter, mc*PB = proximal breadth, mc*DB = distal breadth. Asterisk (*) denotes metacarpal number.			

Table E.7. Mann-Whitney U test mean rank values for the effect of sex on directional asymmetry in the chimpanzee phalanges.

Measurement	Sex	N	Mean Rank
pp1L	male	8	11.25
	female	12	10.00
pp2L	male	9	9.22
	female	12	12.33
pp3L	male	8	13.00
	female	12	8.83
pp4L	male	9	10.06
	female	12	11.71
pp5L	male	9	10.67
	female	12	11.25
ip2L	male	8	9.88
	female	12	10.92
ip3L	male	9	11.28
	female	12	10.79
ip4L	male	8	11.94
	female	11	8.59
ip5L	male	8	9.25
	female	12	11.33
Abbreviations used: pp*L = proximal phalanx length, ip*L = intermediate phalanx length. Asterisk (*) denotes phalanx number.			

Table E.8. Mann-Whitney U test mean rank values for the effect of sex on absolute asymmetry in the chimpanzee phalanges.

Measurement	Sex	N	Mean Rank
pp1L	male	8	12.00
	female	12	9.50
pp2L	male	9	11.22
	female	12	10.83

Measurement	Sex	N	Mean Rank
pp3L	male	8	11.38
	female	12	9.92
pp4L	male	9	13.11
	female	12	9.42
pp5L	male	9	10.78
	female	12	11.17
ip2L	male	8	10.81
	female	12	10.29
ip3L	male	9	7.78
	female	12	13.42
ip4L	male	8	10.38
	female	11	9.73
ip5L	male	8	11.75
	female	12	9.67

Abbreviations used: pp*L = proximal phalanx length, ip*L = intermediate phalanx length. Asterisk (*) denotes phalanx number.

E.2. Chimpanzee humerus metric analysis

Table E.9. Summary statistics for chimpanzee humerus variables.

Measurement	Side	Male			Female		
		N	Mean	Std dev.	N	Mean	Std dev.
MxL	L	9	300.78	8.97	12	300.67	13.30
	R	9	300.33	10.00	12	301.58	13.08
MxDm	L	9	24.37	1.72	12	24.08	2.10
	R	9	24.20	1.82	12	24.27	2.21
MnDm	L	9	21.76	1.56	12	20.51	1.90
	R	9	21.54	1.60	12	20.50	1.89
MnCir	L	9	72.00	5.29	12	69.33	5.25
	R	9	72.11	5.16	12	69.00	4.99
CirHd	L	9	127.33	7.43	12	121.00	4.97
	R	9	126.44	7.52	12	120.75	4.85
MxTDm	L	9	41.19	3.03	12	39.43	1.86
	R	9	41.51	2.91	12	39.69	1.91
MxSDm	L	9	41.14	2.38	12	38.87	1.50
	R	9	40.58	2.63	12	38.65	1.44
EpBr	L	9	64.69	3.50	12	61.67	3.57
	R	9	64.54	3.20	12	61.27	3.65
TCBr	L	9	46.71	1.73	12	45.33	2.28
	R	9	47.66	1.73	12	45.49	2.23

Abbreviations used: MxL = maximum length, MxDm = maximum midshaft diameter, MnDm = minimum midshaft diameter, MnCir = minimum shaft circumference, CirHd = circumference of head, MxTDm = maximum transverse diameter of head, MxSDm = maximum sagittal diameter of head, EpBr = epicondylar breadth, TCBr = trochlea-capitulum breadth.

Table E.10. Chimpanzee humerus asymmetry data.

Measurement	N	Percentage right-side dominant (%)	Percentage left-side dominant (%)	Percentage symmetrical (%)
MxL	21	28.6	38.1	33.3
MxDm	21	52.4	38.1	9.5
MnDm	21	42.9	47.6	9.5
MnCir	21	19.0	28.6	52.4
CirHd	21	19.0	57.1	23.8
MxTDm	21	52.4	42.9	4.8
MxSDm	21	28.6	66.7	4.8
EpBr	21	33.3	61.9	4.8
TCBr	21	81.0	14.3	4.8

Abbreviations used: MxL = maximum length, MxDm = maximum midshaft diameter, MnDm = minimum midshaft diameter, MnCir = minimum shaft circumference, CirHd = circumference of head, MxTDm = maximum transverse diameter of head, MxSDm = maximum sagittal diameter of head, EpBr = epicondylar breadth, TCBr = trochlea-capitulum breadth.

Table E.11. Mann-Whitney U test mean rank values for the effect of sex on directional asymmetry in the chimpanzee humeri.

Measurement	Sex	N	Mean Rank
MxL	male	9	9.94
	female	12	11.79
MxDm	male	9	7.50
	female	12	13.63
MnDm	male	9	9.67
	female	12	12.00
MnCir	male	9	12.39
	female	12	9.96
CirHd	male	9	10.44
	female	12	11.42
MxTDm	male	9	12.72
	female	12	9.71
MxSDm	male	9	9.94
	female	12	11.79
EpBr	male	9	12.22
	female	12	10.08
TCBr	male	9	15.00
	female	12	8.00

Abbreviations used: MxL = maximum length, MxDm = maximum midshaft diameter, MnDm = minimum midshaft diameter, MnCir = minimum shaft circumference, CirHd = circumference of head, MxTDm = maximum transverse diameter of head, MxSDm = maximum sagittal diameter of head, EpBr = epicondylar breadth, TCBr = trochlea-capitulum breadth.

Table E.12. Mann-Whitney U test mean rank values for the effect of sex on absolute asymmetry in the chimpanzee humeri.

Measurement	Sex	N	Mean Rank
MxL	male	9	9.72
	female	12	11.96
MxDm	male	9	10.89
	female	12	11.08
MnDm	male	9	10.83
	female	12	11.13
MnCir	male	9	11.83
	female	12	10.38
CirHd	male	9	9.33
	female	12	12.25
MxTDm	male	9	10.39
	female	12	11.46
MxSDm	male	9	10.50
	female	12	11.38
EpBr	male	9	12.22
	female	12	10.08
TCBr	male	9	13.56
	female	12	9.08

Abbreviations used: MxL = maximum length, MxDm = maximum midshaft diameter, MnDm = minimum midshaft diameter, MnCir = minimum shaft circumference, CirHd = circumference of head, MxTDm = maximum transverse diameter of head, MxSDm = maximum sagittal diameter of head, EpBr = epicondylar breadth, TCBr = trochlea-capitulum breadth.

E.3. Musculoskeletal stress markers (MSM) in the chimpanzee hand

Table E.13. Data from chimpanzee hand MSM presence/absence analysis.

MSM	Side	N	Percentage present (%)	Percentage absent (%)
APT	L	21	47.6	52.4
	R	21	42.9	57.1
ODM	L	21	23.8	76.2
	R	21	42.9	57.1
FDS	L	21	100	0
	R	21	100	0
PI2	L	21	23.8	76.2
	R	21	33.3	66.7
PI3	L	21	33.3	66.7
	R	21	28.6	71.4
PI4	L	21	14.3	85.7
	R	21	19.0	81.0
DI1	L	21	57.1	42.9
	R	21	28.6	71.4

MSM	Side	N	Percentage present (%)	Percentage absent (%)
DI2	L	21	33.3	66.7
	R	21	23.8	76.2
DI3	L	21	42.9	57.1
	R	21	28.6	71.4
DI4	L	21	61.9	38.1
	R	21	52.4	47.6

Abbreviations used: APT = adductor pollicis (transverse head), ODM = oppenens digiti minimi, FDS = flexor digitorum superficialis (2-5), PI = palmar interosseous, DI = dorsal interosseous.

E.4. Musculoskeletal stress markers (MSM) in the chimpanzee humerus

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Table E.14. Data from chimpanzee humerus MSM presence/absence analysis.

MSM	Side	N	Percentage present (%)	Percentage absent (%)
Delt	L	21	85.7	14.3
	R	21	90.5	9.5
TMj	L	21	95.2	4.8
	R	21	85.7	14.3
LD	L	21	23.8	76.2
	R	21	23.8	76.2
PM	L	21	95.2	4.8
	R	21	100	0
CB	L	21	61.9	38.1
	R	21	52.4	47.6
IS	L	21	95.2	4.8
	R	21	100	0
SSp	L	21	52.4	47.6
	R	21	33.3	66.7
TMn	L	21	71.4	28.6
	R	21	71.4	28.6
SSc	L	21	85.7	14.3
	R	21	85.7	14.3
CFO	L	21	100	0
	R	21	100	0
CEO	L	21	95.2	4.8
	R	21	100	0

Abbreviations used: Delt = deltoid, TMj = teres major, LD = latissimus dorsi, PM = pectoralis major, CB = coracobrachialis, IS = infraspinatus, SSp = supraspinatus, TMn = teres minor, SSc = subscapularis, CFO = common flexor origin, CEO = common extensor origin.

Table E.15. McNemar test of association between left and right chimpanzee humerus MSM.

MSM	N	Sig. (2-tailed)
Delt	21	p = 1.00
TMj	21	p = 0.50
LD	21	p = 1.00
PM	21	p = 1.00
CB	21	p = 0.73

MSM	N	Sig. (2-tailed)
IS	21	p = 1.00
SSp	21	p = 0.13
TMn	21	p = 1.00
SSc	21	p = 1.00
CFO	-	-
CEO	21	p = 1.00

N = number of comparisons performed. CFO not included in analysis as no individuals changed score between ‘present’ and ‘absent’ categories. Due to the low number of cases where score changed between categories, binomial distribution was used in place of the chi-squared statistic. Abbreviations used: Delt = deltoid, TMj = teres major, LD = latissimus dorsi, PM = pectoralis major, CB = coracobrachialis, IS = infraspinatus, SSp = supraspinatus, TMn = teres minor, SSc = subscapularis, CFO = common flexor origin, CEO = common extensor origin.

Table X.16. Chi-squared (χ^2) test of association between age and chimpanzee humerus MSM.

MSM	Side	χ^2 value	Sig. (2-tailed)	φ value
Delt	L	2.63	p = 0.23*	0.35
	R	1.66	p = 0.49*	0.28
TMj	L	0.79	p = 1.00*	0.19
	R	2.63	p = 0.23*	0.35
LD	L	1.40	p = 0.34*	0.26
	R	0.02	p = 1.00*	0.32
PM	L	0.79	p = 1.00*	0.19
	R	-	-	-
CB	L	4.86	*p = 0.07**	0.48
	R	1.29	p = 0.39*	0.25
IS	L	0.79	p = 1.00*	0.19
	R	-	-	-
SSp	L	1.29	p = 0.39*	0.25
	R	3.50	p = 0.16*	0.41
TMn	L	2.35	p = 0.18*	0.34
	R	2.35	p = 0.18*	0.34
SSc	L	2.63	p = 0.23*	0.35
	R	0.13	p = 1.00*	0.08
CFO	L	-	-	-
	R	-	-	-
CEO	L	0.79	p = 1.00*	0.19
	R	-	-	-

P-values approaching significance (between 0.55 and 0.1) highlighted in italics. Right PM, right IS, right CEO and left and right CFO were not included in the analysis as no individuals changed score between ‘present’ and ‘absent’ categories. Values marked with an asterisk (*) indicate where the Fisher’s Exact Test p-value was used due to low cell counts (in most instances, this test provides the same results as the standard χ^2). A phi (φ) value indicates the strength of the χ^2 association. Abbreviations used: Delt = deltoid, TMj = teres major, LD = latissimus dorsi, PM = pectoralis major, CB = coracobrachialis, IS = infraspinatus, SSp = supraspinatus, TMn = teres minor, SSc = subscapularis, CFO = common flexor origin, CEO = common extensor origin.

E.5 Gorilla metacarpal and phalanx metric analysis

Table E.17. Summary statistics for gorilla metacarpal and phalanx metric data.

Measurement	Side	Male			Female		
		N	Mean	Std dev.	N	Mean	Std dev.
mc1L	L	10	51.29	3.24	11	41.51	3.54
	R	10	51.59	2.49	11	41.01	3.52
mc2L	L	10	97.85	4.71	11	81.46	5.22
	R	10	98.32	4.73	11	81.24	5.05
mc3L	L	10	96.33	5.35	11	80.36	5.32
	R	10	96.44	5.29	10	81.16	4.84
mc4L	L	10	94.00	4.85	11	78.09	5.13
	R	10	94.32	4.40	10	78.56	4.90
mc5L	L	10	91.08	4.11	11	74.18	5.88
	R	10	90.43	4.35	11	73.67	5.27
mc1RU	L	10	13.09	1.62	11	9.52	0.79
	R	10	12.62	1.07	11	9.56	1.02
mc2RU	L	10	12.39	1.09	11	10.32	1.05
	R	10	12.53	1.24	11	9.98	0.69
mc3RU	L	10	11.66	0.79	11	9.84	0.69
	R	10	11.81	0.92	10	9.92	0.99
mc4RU	L	10	10.88	1.18	11	8.93	0.97
	R	10	11.02	0.96	10	9.14	0.81
mc5RU	L	10	11.66	1.52	11	8.90	0.74
	R	10	12.27	1.78	11	8.68	0.70
mc1DP	L	10	9.38	1.01	11	7.32	0.68
	R	10	9.68	1.20	11	7.55	0.54
mc2DP	L	10	12.08	0.93	11	9.22	1.10
	R	10	12.26	0.96	11	9.25	1.01
mc3DP	L	10	14.61	0.80	11	11.15	1.28
	R	10	14.36	0.96	10	11.05	1.02
mc4DP	L	10	11.90	0.88	11	9.77	0.94
	R	10	11.84	1.19	10	9.56	0.94
mc5DP	L	10	9.99	0.81	11	8.28	0.85
	R	8	9.70	0.53	11	8.05	0.80
mc1PB	L	10	18.03	0.94	11	13.69	0.93
	R	10	17.75	1.13	11	13.71	1.01
mc2PB	L	10	20.35	1.33	11	15.33	0.69
	R	10	20.71	1.13	11	16.07	1.00
mc3PB	L	10	18.65	1.15	11	14.74	1.10
	R	10	18.70	1.00	10	14.74	1.15
mc4PB	L	10	16.49	0.81	11	13.06	0.77
	R	10	16.80	0.99	10	13.21	0.77
mc5PB	L	10	15.85	1.36	11	12.37	0.98
	R	10	15.91	1.96	11	12.07	0.87
mc1DB	L	10	15.38	1.96	11	11.79	1.02
	R	10	15.17	1.91	11	11.90	0.88
mc2DB	L	10	18.46	1.09	11	14.81	0.87
	R	10	18.74	1.10	11	14.95	0.85

Measurement	Side	Male			Female		
		N	Mean	Std dev.	N	Mean	Std dev.
mc3DB	L	10	19.86	0.82	11	15.58	0.87
	R	10	19.82	0.98	10	15.61	1.16
mc4DB	L	10	18.27	1.15	11	14.29	0.98
	R	10	17.89	1.08	10	14.33	0.94
mc5DB	L	10	15.94	1.22	11	12.46	1.32
	R	10	16.21	1.24	11	12.45	1.12
pp1L	L	10	28.24	2.27	11	23.78	2.70
	R	10	27.71	2.45	10	23.77	2.68
pp2L	L	10	54.16	2.38	11	45.84	3.04
	R	10	54.16	2.53	11	45.69	2.74
pp3L	L	10	61.77	2.67	11	51.78	2.56
	R	10	61.33	3.39	11	51.64	2.91
pp4L	L	10	58.67	3.07	11	49.14	2.52
	R	10	58.58	3.58	10	49.65	2.42
pp5L	L	10	48.87	3.04	11	40.83	2.52
	R	10	48.71	3.17	11	40.93	3.06
ip2L	L	10	34.88	1.43	10	29.49	3.29
	R	10	34.42	1.29	9	29.32	2.19
ip3L	L	10	42.82	1.84	10	36.16	2.19
	R	10	42.76	2.19	9	36.63	2.16
ip4L	L	10	41.16	2.36	10	34.63	2.63
	R	10	40.63	3.42	9	34.78	3.04
ip5L	L	10	31.19	4.17	10	26.45	3.25
	R	10	31.86	2.46	10	25.93	3.42

Abbreviations used: mc*L = metacarpal length, mc*RU = radio-ulnar midshaft diameter, mc*DP = dorso-palmar midshaft diameter, mc*PB = proximal breadth, mc*DB = distal breadth, pp*L = proximal phalanx length, ip*L = intermediate phalanx length. Asterisk (*) denotes metacarpal or phalanx number.

Table E.18. Gorilla metacarpal asymmetry data.

Measurement	N	Percentage right-side dominant (%)	Percentage left-side dominant (%)	Percentage symmetrical (%)
mc1L	21	19.0	81.0	0
mc2L	21	47.6	52.4	0
mc3L	20	55.0	35.0	10.0
mc4L	20	50.0	50.0	0
mc5L	21	23.8	66.7	9.5
mc1RU	21	38.1	52.4	9.5
mc2RU	21	42.9	57.1	0
mc3RU	20	55.0	45.0	0
mc4RU	20	60.0	40.0	0
mc5RU	21	42.9	38.1	19.0
mc1DP	21	61.9	33.3	4.8
mc2DP	21	47.6	38.1	14.3

Measurement	N	Percentage right-side dominant (%)	Percentage left-side dominant (%)	Percentage symmetrical (%)
mc3DP	20	30.0	65.0	5.0
mc4DP	20	45.0	55.0	0
mc5DP	21	38.1	52.4	9.5
mc1PB	21	47.6	47.6	4.8
mc2PB	21	76.2	19.0	4.8
mc3PB	20	50.0	45.0	5.0
mc4PB	20	70.0	20.0	10.0
mc5PB	21	33.3	57.1	9.5
mc1DB	21	47.6	38.1	14.3
mc2DB	21	61.9	14.3	23.8
mc3DB	20	60.0	35.0	5.0
mc4DB	20	25.0	70.0	5.0
mc5DB	21	52.4	38.1	9.5

Abbreviations used: mc*L = metacarpal length, mc*RU = radio-ulnar midshaft diameter, mc*DP = dorso-palmar midshaft diameter, mc*PB = proximal breadth, mc*DB = distal breadth. Asterisk (*) denotes metacarpal number.

Table E.19. Gorilla phalanx asymmetry data.

Measurement	N	Percentage right-side dominant (%)	Percentage left-side dominant (%)	Percentage symmetrical (%)
pp1L	20	25.0	70.0	5.0
pp2L	21	47.6	42.9	9.5
pp3L	21	42.9	52.4	4.7
pp4L	20	55.0	40.0	5.0
pp5L	21	38.1	61.9	0
ip2L	19	36.8	47.4	15.8
ip3L	19	47.4	42.1	10.5
ip4L	19	42.1	57.9	0
ip5L	20	30.0	65.0	5.0

Abbreviations used: pp*L = proximal phalanx length, ip*L = intermediate phalanx length. Asterisk (*) denotes phalanx number.

Table E.20. Mann-Whitney U test mean rank values for the effect of sex on directional asymmetry in the gorilla metacarpals.

Measurement	Sex	N	Mean Rank
mc1L	male	10	12.60
	female	11	9.55
mc2L	male	10	12.60
	female	11	9.55
mc3L	male	10	10.90
	female	10	10.10
mc4L	male	10	11.30
	female	10	9.70
mc5L	male	10	10.45
	female	11	11.50

Measurement	Sex	N	Mean Rank
mc1RU	male	10	8.90
	female	11	12.91
mc2RU	male	10	13.20
	female	11	9.00
mc3RU	male	10	10.90
	female	10	10.10
mc4RU	male	10	10.70
	female	10	10.30
mc5RU	male	10	15.10
	female	11	7.27
mc1DP	male	10	10.90
	female	11	11.09
mc2DP	male	10	11.40
	female	11	10.64
mc3DP	male	10	9.00
	female	10	12.00
mc4DP	male	10	11.20
	female	10	9.80
mc5DP	male	10	13.40
	female	11	8.82
mc1PB	male	10	9.70
	female	11	12.18
mc2PB	male	10	8.50
	female	11	13.27
mc3DP	male	10	10.80
	female	10	10.20
mc4PB	male	10	11.40
	female	10	9.60
mc5PB	male	10	12.40
	female	11	9.73
mc1DB	male	10	9.60
	female	11	12.27
mc2DB	male	10	12.50
	female	11	9.64
mc3DB	male	10	9.60
	female	10	11.40
mc4DB	male	10	8.90
	female	10	12.10
mc5DB	male	10	12.85
	female	11	9.32

Abbreviations used: mc*L = metacarpal length, mc*RU = radio-ulnar midshaft diameter, mc*DP = dorso-palmar midshaft diameter, mc*PB = proximal breadth, mc*DB = distal breadth. Asterisk (*) denotes metacarpal number.

Table E.21. Mann-Whitney U test mean rank values for the effect of sex on absolute asymmetry in the gorilla metacarpals.

Measurement	Sex	N	Mean Rank
mc1L	male	10	9.40
	female	11	12.45
mc2L	male	10	13.30
	female	11	8.91
mc3L	male	10	10.70
	female	10	10.30
mc4L	male	10	11.00
	female	10	10.00
mc5L	male	10	12.35
	female	11	9.77
mc1RU	male	10	13.80
	female	11	8.45
mc2RU	male	10	10.65
	female	11	11.32
mc3RU	male	10	12.90
	female	10	8.10
mc4RU	male	10	9.30
	female	10	11.70
mc5RU	male	10	11.50
	female	11	10.55
mc1DP	male	10	10.70
	female	11	11.27
mc2DP	male	10	10.40
	female	11	11.55
mc3DP	male	10	9.00
	female	10	12.00
mc4DP	male	10	8.10
	female	10	12.90
mc5DP	male	10	11.05
	female	11	10.95
mc1PB	male	10	10.85
	female	11	11.14
mc2PB	male	10	8.70
	female	11	13.09
mc3PB	male	10	10.10
	female	10	10.90
mc4PB	male	10	11.60
	female	10	9.40
mc5PB	male	10	10.10
	female	11	11.82
mc1DB	male	10	11.60
	female	11	10.45
mc2DB	male	10	11.40
	female	11	10.64
mc3DB	male	10	8.50
	female	10	12.50
mc4DB	male	10	12.90
	female	10	8.10

Measurement	Sex	N	Mean Rank
mc5DB	male	10	11.85
	female	11	10.23

Abbreviations used: mc*L = metacarpal length, mc*RU = radio-ulnar midshaft diameter, mc*DP = dorso-palmar midshaft diameter, mc*PB = proximal breadth, mc*DB = distal breadth. Asterisk (*) denotes metacarpal number.

Table E.22. Mann-Whitney U test mean rank values for the effect of sex on directional asymmetry in the gorilla phalanges.

Measurement	Sex	N	Mean Rank
pp1L	male	10	9.00
	female	10	12.00
pp2L	male	10	12.70
	female	11	9.45
pp3L	male	10	10.10
	female	11	11.82
pp4L	male	10	9.20
	female	10	11.80
pp5L	male	10	11.30
	female	11	10.73
ip2L	male	10	9.60
	female	9	10.44
ip3L	male	10	9.05
	female	9	11.06
ip4L	male	10	9.70
	female	9	10.33
ip5L	male	10	11.20
	female	10	9.80

Abbreviations used: pp*L = proximal phalanx length, ip*L = intermediate phalanx length. Asterisk (*) denotes phalanx number.

Table E.23. Mann-Whitney U test mean rank values for the effect of sex on absolute asymmetry in the gorilla phalanges.

Measurement	Sex	N	Mean Rank
pp1L	male	10	10.40
	female	10	10.60
pp2L	male	10	11.40
	female	11	10.64
pp3L	male	10	12.90
	female	11	9.27
pp4L	male	10	12.10
	female	10	8.90
pp5L	male	10	8.40
	female	11	13.36
ip2L	male	10	8.80
	female	9	11.33

Measurement	Sex	N	Mean Rank
ip3L	male	10	9.05
	female	9	11.06
ip4L	male	10	7.40
	female	9	12.89
ip5L	male	10	9.70
	female	10	11.30

Abbreviations used: pp*L = proximal phalanx length, ip*L = intermediate phalanx length. Asterisk (*) denotes phalanx number.

E.6. Gorilla humerus metric analysis

Table E.24. Summary statistics for gorilla humerus metric data.

Measurement	Side	Male			Female		
		N	Mean	Std dev.	N	Mean	Std dev.
MxL	L	10	468.90	16.60	11	379.64	19.45
	R	10	469.10	18.07	11	379.27	20.06
MxDm	L	10	36.66	2.78	11	30.33	1.69
	R	10	36.41	2.51	11	30.23	1.66
MnDm	L	10	30.86	1.76	11	25.87	1.67
	R	10	30.91	2.02	11	25.78	1.68
MnCir	L	10	103.80	5.57	11	84.55	4.95
	R	10	102.90	5.30	11	84.27	4.98
CirHd	L	10	198.90	5.57	11	155.45	8.23
	R	10	198.60	7.69	11	154.36	7.76
MxTDm	L	10	65.46	2.67	11	50.92	2.62
	R	10	66.01	2.89	11	51.12	2.70
MxSDm	L	10	63.25	2.47	11	48.62	3.12
	R	10	61.45	2.11	11	48.05	3.22
EpBr	L	10	104.86	5.10	11	79.87	5.03
	R	10	105.72	5.93	11	79.73	5.53
TCBr	L	10	72.97	3.87	11	56.81	5.54
	R	10	73.27	3.20	11	56.35	3.96

Abbreviations used: MxL = maximum length, MxDm = maximum midshaft diameter, MnDm = minimum midshaft diameter, MnCir = minimum shaft circumference, CirHd = circumference of head, MxTDm = maximum transverse diameter of head, MxSDm = maximum sagittal diameter of head, EpBr = epicondylar breadth, TCBr = trochlea-capitulum breadth.

Table E.25. Gorilla humerus asymmetry data.

Measurement	N	Percentage right-side dominant (%)	Percentage left-side dominant (%)	Percentage symmetrical (%)
MxL	21	38.1	52.4	9.5
MxDm	21	33.3	61.9	4.8
MnDm	21	38.1	52.4	9.5
MnCir	21	19.0	52.4	28.6
CirHd	21	33.3	57.1	9.5
MxTDm	21	66.7	28.6	4.8
MxSDm	21	14.3	76.2	9.5
EpBr	21	57.1	33.3	9.5
TCBr	21	61.9	33.3	4.8

Abbreviations used: MxL = maximum length, MxDm = maximum midshaft diameter, MnDm = minimum midshaft diameter, MnCir = minimum shaft circumference, CirHd = circumference of head, MxTDm = maximum transverse diameter of head, MxSDm = maximum sagittal diameter of head, EpBr = epicondylar breadth, TCBr = trochlea-capitulum breadth.

Table E.26. Mann-Whitney U test mean rank values for the effect of sex on directional asymmetry in the gorilla humerus.

Measurements	Sex	N	Mean Rank
MxL	male	10	12.45
	female	11	9.68
MxDm	male	10	9.95
	female	11	11.95
MnDm	male	10	11.25
	female	11	10.77
MnCir	male	10	10.30
	female	11	11.64
CirHd	male	10	12.15
	female	11	9.95
MxTDm	male	10	12.10
	female	11	10.00
MxSDm	male	10	8.50
	female	11	13.27
EpBr	male	10	12.45
	female	11	9.68
TCBr	male	10	11.60
	female	11	10.45

Abbreviations used: MxL = maximum length, MxDm = maximum midshaft diameter, MnDm = minimum midshaft diameter, MnCir = minimum shaft circumference, CirHd = circumference of head, MxTDm = maximum transverse diameter of head, MxSDm = maximum sagittal diameter of head, EpBr = epicondylar breadth, TCBr = trochlea-capitulum breadth.

Table E.27. Mann-Whitney U test mean rank values for the effect of sex on absolute asymmetry in the gorilla humerus.

Measurement	Sex	N	Mean Rank
MxL	male	10	10.90
	female	11	11.09
MxDm	male	10	11.40
	female	11	10.64
MnDm	male	10	11.05
	female	11	10.95
MnCir	male	10	11.00
	female	11	11.00
CirHd	male	10	10.55
	female	11	11.41
MxTDm	male	10	10.15
	female	11	11.77
MxSDm	male	10	14.60
	female	11	7.73
EpBr	male	10	12.05
	female	11	10.05
TCBr	male	10	11.50
	female	11	10.55

Abbreviations used: MxL = maximum length, MxDm = maximum midshaft diameter, MnDm = minimum midshaft diameter, MnCir = minimum shaft circumference, CirHd = circumference of head, MxTDm = maximum transverse diameter of head, MxSDm = maximum sagittal diameter of head, EpBr = epicondylar breadth, TCBr = trochlea-capitulum breadth.

E.7. Musculoskeletal stress markers (MSM) in the gorilla hand

Table E.28. Data from gorilla hand MSM presence/absence analysis.

MSM	Side	N	Percentage present (%)	Percentage absent (%)
APT	L	21	85.7	14.3
	R	21	90.5	9.5
ODM	L	21	66.7	33.3
	R	21	85.7	14.3
FDS	L	21	95.2	4.8
	R	21	95.2	4.8
PI2	L	21	47.6	52.4
	R	21	52.4	47.6
PI3	L	21	66.7	33.3
	R	21	81.0	19.0
PI4	L	21	47.6	52.4
	R	21	52.4	47.6
DI1	L	21	57.1	42.9
	R	21	57.1	42.9
DI2	L	21	28.6	71.4
	R	21	33.3	66.7
DI3	L	21	52.4	47.6
	R	21	52.4	47.6

MSM	Side	N	Percentage present (%)	Percentage absent (%)
DI4	L	21	57.1	42.9
	R	21	61.9	38.1

Abbreviations used: APT = adductor pollicis (transverse head), ODM = oppenens digiti minimi, FDS = flexor digitorum superficialis (2-5), PI = palmar interosseous, DI = dorsal interosseous.

Table E.29. McNemar test of association between left and right gorilla hand MSM.

MSM	N	Sig. (2-tailed)
APT	20	p = 1.00
ODM	21	p = 0.22
FDS	-	-
PI2	21	p = 1.00
PI3	20	p = 0.38
PI4	21	p = 1.00
DI1	21	p = 1.00
DI2	20	p = 1.00
DI3	19	p = 1.00
DI4	21	p = 1.00

N = number of comparisons performed. FDS not included in analysis as no individuals changed score between ‘present’ and ‘absent’ categories. Due to the low number of cases where score changed between categories, binomial distribution was used in place of the chi-squared statistic. Abbreviations used: APT = adductor pollicis (transverse head), ODM = oppenens digiti minimi, FDS = flexor digitorum superficialis (2-5), PI = palmar interosseous, DI = dorsal interosseous.

E.8. Musculoskeletal stress markers (MSM) in the gorilla humerus

Table E.30. Data from gorilla humerus MSM presence/absence analysis.

MSM	Side	N	Percentage present (%)	Percentage absent (%)
Delt	L	21	71.4	28.6
	R	21	71.4	28.6
TMj	L	21	95.2	4.8
	R	21	100	0
LD	L	21	23.8	76.2
	R	21	14.3	85.7
PM	L	21	100	0
	R	21	100	0
CB	L	21	19.0	81.0
	R	21	23.8	76.2
IS	L	21	100	0
	R	21	100	0
SSp	L	21	71.4	28.6
	R	21	66.7	33.3
TMn	L	21	71.4	28.6
	R	21	81.0	19.0

MSM	Side	N	Percentage present (%)	Percentage absent (%)
SSc	L	21	76.2	23.8
	R	21	85.7	14.3
CFO	L	21	95.2	4.8
	R	21	95.2	4.8
CEO	L	21	90.5	9.5
	R	21	81.0	19.0

Abbreviations used: Delt = deltoid, TMj = teres major, LD = latissimus dorsi, PM = pectoralis major, CB = coracobrachialis, IS = infraspinatus, SSp = supraspinatus, TMn = teres minor, SSc = subscapularis, CFO = common flexor origin, CEO = common extensor origin.

Table E.31. McNemar test of association between left and right gorilla humerus MSM.

MSM	N	Sig. (2-tailed)
Delt	21	p = 1.00
TMj	21	p = 1.00
LD	21	p = 0.63
PM	21	-
CB	21	p = 1.00
IS	21	-
SSp	21	p = 1.00
TMn	21	p = 0.69
SSc	21	p = 0.50
CFO	21	p = 1.00
CEO	21	p = 0.63

N = number of comparisons performed. PM and IS not included in analysis as no individuals changed score between ‘present’ and ‘absent’ categories. Due to the low number of cases where score changed between categories, binomial distribution was used in place of the chi-squared statistic. Abbreviations used: Delt = deltoid, TMj = teres major, LD = latissimus dorsi, PM = pectoralis major, CB coracobrachialis, IS = infraspinatus, SSp = supraspinatus, TMn = teres minor, SSc = subscapularis, CFO = common flexor origin, CEO = common extensor origin.

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