

REVIEW OF LITERATURE: THE SEARCH FOR ACTIVITY DEPENDENT BONE MORPHOLOGY

Anatomists and osteologists have long observed that there are marked differences in the relative robusticity of human bone between individuals and groups. Not only are some individual's bones thicker or more gracile, some have more or less developed markings at the points where tendons and ligaments attach. Understanding the cause or causes of this observed variety has been the goal of many, this researcher included.

Wolff's Law and the History of Analyzing Bone Morphology to Infer Activity

One of the earliest and still most popular theories is that activity and use causes bones to become stronger, thicker and to develop more distinct markings at attachment sites. This is an intuitive theory, and is a logical outgrowth of the obvious and fairly rapid hypertrophy response which muscles display when subjected to use stress. In 1892 Julius Wolff published a mathematical formula designed to exactly predict the apposition of new bone in response to mechanical stress. His formula was based on models of bone as "solid, homogeneous and isotropic structures subjected to static applied loads" (Ruff et al. 2006: 485). This is clearly a set of assumptions that bears no resemblance to the complex nature of bone biology and the dynamic stresses that it is subjected to. Although the processes of bone remodeling were later shown to be too complex to follow Wolff's formula, the general idea that bone responds to stress with remodeling and growth is still known informally as "Wolff's Law".

Ruff and co-workers (2006) recommend that the more general term “bone functional adaptation” be used in place of “Wolff’s Law”. Using the term bone functional adaptation will avoid confusion with the original, overly simplistic theory. Research focusing on the more general assumptions of bone functional adaptation is particularly important because there are still many valid criticisms and tests of functional adaptation which need to be addressed.

Interacting Variables and Bone Functional Adaptation

Several animal and human studies have brought up interesting questions regarding the complex interactions between ontology, genetics, environment and bone functional adaptation. Because of the dynamic, complex and incompletely understood biological processes that influence bone morphology, many researchers have expressed misgivings about our ability to infer activity or stress patterns osteologically (Ruff et al. 2006, Zumwalt 2005, 2006, CITE OTHERS). Ruff and coworkers state that “because the general concept of bone functional adaptation is so pervasive in biological anthropology and indeed biology it is important to carefully evaluate these issues/objections and their implications for current research approaches” (2006:484).

Biological Factors Influencing Bone Morphology

Sex. Sex hormones like testosterone and estrogen play an important role in tissue development and maintenance. Testosterone in particular promotes bone growth and thickening. In women, it is well known that reduced levels of estrogen after menopause reduces the body's ability to replace calcium and this can result in osteoporosis, and a heightened risk for broken bones.

Men and women have different levels of testosterone and estrogen. One consequence of this is sexual dimorphism. After puberty, males tend to be taller, have thicker bones and greater muscle mass than females. It has been observed however that different populations exhibit different degrees of sexual dimorphism. Sometimes the males are very tall and robust in comparison with the females. In other groups, both sexes are tall and muscular (females exhibiting morphology nearer the male end of the spectrum) or both sexes may be rather petite (males nearer the female end of the spectrum). This variation is likely due to a combination of genetic and environmental factors.

It is probable that sex hormones influence the degree to which adult bone remodels in response to stress. Since testosterone promotes bone growth, the higher degree of hypertrophy typical of males may be an artifact of their higher testosterone levels as opposed to an indication of higher physical activity or greater health among males. Understanding this relationship is thus vital to interpretation of sexual division of labor from skeletal evidence. Each sex also experiences different hormonal levels at different life stages (youth, puberty, adulthood, old age).

Age. Overall bone morphology (stature, thickness) is more likely to respond to loads experienced during growth and development than at later stages in life (Ruff et al. 2006).

A large number of studies have noted the pattern of older individuals have more distinct muscle attachment markings than do younger, indicating that bony development at attachment sites may be a cumulative, lifelong process (CITE). Others point out that the increased robusticity observed among older adults may be an outgrowth of hormonal fluctuations rather than a direct response to use stress (Zumwalt 2006).

Discrete Traits. It is conceivable that some of the morphological variation observed at entheses is strictly or primarily under genetic control rather than being plastic and responsive to environmental factors. This has been observed to occur in other skeletal non-metric traits (suture patterns, tooth morphology, variable present foramina, and so forth) on both populational and idiosyncratic levels.

Stature and Robusticity. Intuitively, one might expect taller individuals to simply have overall larger bones than shorter individuals. This is not always the case, as tall individuals with long but relatively gracile bones exist as well as shorter individuals with thicker bone structure. The question is how to interpret these patterns. Any given diameter which might be interpreted as “thin” or “gracile” on a very tall individual might be seen as “average” or even “robust” on a much shorter individual. One might be tempted to use a simple formula of diameter over length to arrive at a standardized “robusticity” measurement, but if activity influences bone morphology we might expect

taller individuals to have a different pattern of loading stress than shorter persons. How might each of these body types interact with development of musculoskeletal stress markers (MSM)? Should stress markers of equal size be interpreted as more significant on a short, gracile individual than on a tall robust individual? What about a tall gracile person as opposed to a short but robust person? These questions are complicated in that height and robusticity are determined by the interacting variables of genetics, sex, diet and health. The resulting body shape may in turn influence the type and magnitude of strain experienced during daily activities. MSM are both the result of strain experienced at specific sites and directly influenced by diet, sex, health and genetics.

Side Dominance. Most individuals are either right or left side dominant. We typically think of this as being right or left handed, but in addition to determining which hand an individual chooses to write with, the dominate side is generally better developed. The interpretation of asymmetry in robusticity or MSM development is complicated by the fact that the dominant site is also used preferentially in many tasks.

Physiology . Some attachment sites or regions of bone may be more responsive to mechanical stress than others. It is well known that some bones remodel at a faster rate than others (CITE). Those features that remodel more readily may be more apt to show evidence of activity pattern.

Environmental Factors Influencing Bone Morphology

Nutrition & Health. Each individual is born with a given genetic potential, but the degree to which that potential is reached will depend on environmental influences such as nutrition and disease.

Bone serves many biological functions and should not be assumed to be mechanically ideal. To put it another way, the body must balance its priorities. Bone is the body's reservoir of calcium, which is needed for proper nerve function and muscle contractions. Since it is essential for basic life functions, a consistent supply must be available at all times, regardless of recent dietary intake. Calcium is absorbed or released from the skeletal system in order to maintain levels of dissolved calcium in the blood stream.

For females, the additional nutritional demands of menstruation and pregnancy put them at greater risk of bone loss and may make it more difficult for them to devote resources to bone maintenance and build up. Similarly, any pathogen which puts additional stresses upon the body will reduce the resources that the body can devote to bone development.

Extreme Cold. Ruff and coworkers (2006) have postulated that extreme cold may reduce the body's ability to repair and build bone. The mechanism proposed for this is reduced blood flow to extremities, in order to maintain core temperature. Essentially the body is allocating resources to the urgent issue of keeping warm, and neglecting less pressing tasks such as osteogenesis to repair micro damage at attachment sites. The result,

according to Ruff and coworkers is a reduction of hypertrophy at attachment sites and an increase in stress lesions (depressed or eroded areas at attachment sites).

Training in Youth. Ruff and coworkers (2006) note that while many studies find that exercise resulted in a net gain of bone (as is predicted by the theory of bone functional adaptation), intensive exercise in immature individuals has been noted to actually retard the growth process.

Threshold Effect. Many researchers (Ruff et al 2006, Zumwalt 2005, CITE OTHERS) have postulated that use stress may have to reach a certain threshold before it initiates a response in the bone. Benjamin and coworkers (2006) point out that since the bone microstructures are designed to dissipate and accommodate the stresses of daily activity, only unusually high loads or extremely vigorous activity are likely to necessitate a hypertrophic response. Given this there has been some semantic argument over whether to consider bony response at this level “pathological” or “normal”. So long as we are talking about manifestations of chronic stressors due to habitual activity as opposed to acute injuries due to accident, there is no practical relevance of the outcome of the pathological/normal terminology debate to interpretation of bone morphology.

Applications for a Successful Method of Inferring Activity from Bones

Given the large number of confounding variables which make interpretation of activity patterns from osteological analysis difficult, one might question the dogged

insistence of some researchers on continuing with this line of inquiry. The answer lies in the phenomenal potential information and research value that would be gained if it is possible to find a way to interpret the data correctly.

Archaeological (reconstructing historic and prehistoric activity patterns).

Forensic (ID athletes/manual laborers?)

Medical (post surgery rehabilitation, astronauts, osteoporosis)

Reasonably Recent Research

Here I will discuss some bone properties that have been used to infer activity.

Bone Mineral Density.

Cross-sectional Properties.

Pathology.

Entheses.

Approaches to Investigating Bone Response to Activity

There are several ways in which researchers have attempted to test the direct relationship between in vivo strains caused by activity and bone morphology. Some

have used animal studies. Animal based studies have the advantages of being able to directly control the activities and stress the subjects experience as well as choose a genetically homogeneous sample and provide identical nutrition. A second approach has been to track the response of human subjects involved in clinical studies. These of course have the advantage of investigating human bone and human patterns of movement, but the disadvantage that stems from a lack of control over several key variables. Finally, a number of studies have examined the patterns of observed morphology in osteological reference collections and in bones recovered from archaeological contexts.

Animal Studies. Many studies have found a correlation between activity and changes in bone morphology. These include a study of rat forelimbs by Robling and coworkers (as cited in Ruff et al 2006)) which found that mechanically induced compression stresses resulted in 70%-100% increases in bending rigidity in the compressed limbs as compared to the uncompressed control limbs of the same animals. No changes were noted in bone mineral density or bone mineral content.

Other animal studies reviewed by Ruff and coworkers (2006) found that bone growth did not always occur at the points of maximum strain calculated through cross sectional geometry, instead adding bone to other regions. The reasons for this are poorly understood, however Benjamin and coworkers (2006) have postulated several mechanisms which may account for it.

Studies of walking or trotting sheep conducted by Leiberman and coworkers did not yield much of an increase in cross sectional strength over sedentary animals, leading Ruff and colleagues to ponder whether more unusual or extreme activity is required for a marked osteogenic effect. This idea of a cutoff point above which activity will contribute to bone apposition, but below which it will not is known as a “threshold effect”.

Many of the aforementioned studies focus on mechanical properties of long bone, such as overall bone thickness, cross sectional geometry and bone mineral density. These do not directly address questions relating to entheses and their response to activity patterns which are the focus of this study. Regardless, entheses and diaphyses are part of the same biomechanical structure (the bone) and the questions raised concerning the effect of genetics, age, and additional biological functions of bone are equally applicable to my investigation of differential entheses morphology.

More recently, Ann Zumwalt (2005, 2006) has investigated the effects of walking while carrying weighted packs on the muscle attachment sites of adult female sheep. She found that while the muscles and tendons in the exercised sheep were larger those in her control group, there were no increases in attachment site surface area or level of surface complexity.

Questions have been raised relating to the length of experimental studies and the possibility that unusually intense activity may be reflected in the bone more so than day-to-day tasks. The variety of responses (and lack thereof) that were observed in the

studies cited by Ruff and coworkers serve to illustrate the point that osteological adaptation to activity related stressors is by no means a 1:1 relationship. Any study attempting to ascertain the relationship between activity and morphology (of enthesis or any other characteristic of human bone) needs to account for or control for the multiple variables discussed in this and other studies.

A basic concern that needs to be addressed according to Marzke and coworkers (2007) is that the attachment site under study is in fact the place where the expected muscle attaches. Marzke and coworkers tested the correlation between the size of the flexor digitorum superficialis (FDS) tendon, which flexes the proximal interphalangeal joint and the lateral fossae, where it has been said to attach. To this end, they dissected the hands of 16 species of living primate (including humans). A total of 43 individuals were included in the study. The dissections revealed that there is considerable variation in the morphology of the lateral fossae and surrounding structures. In no case was the FDS tendon attachment located entirely within the lateral fossae. Attachment sites were noted proximal to, distal to and partly overlapping the fossae. Some species were consistent in attachment site location, while others exhibited different patterns between adults and juveniles. Other species (humans included) had variation in attachment site location that did not correlate with age. The third digit was the main focus of the morphological comparisons, however 5th digits were also examined and found to sometimes display the same morphology as the third for the same individual, and other times deviated from the morphology of the third. Not surprisingly given the morphological non-congruence, no

significant correlations were found between lateral fossae dimensions and tendon size.

The relevance of the 2007 Markzke and coworkers study the current undertaking is simply that we must confirm that the morphological features under investigation do have the commonly assumed relationship with the tendons and musculature.

Human Clinical Studies. Ruff and co-workers (2006) summarize several studies of bone functional adaptation in humans. Although there is active debate over population variation (genetics) and age dependence of response, several studies have returned interesting results. Among these is a marked increase of bone density among young adult female soccer players over a control group of non-athletes and several studies of bilateral asymmetry of the arms of tennis players. Tennis players who began at an early age showed more asymmetry than those who began to play as adults, however even those who began at age 35 showed results. One critique that has been leveled at many human studies is that they are not long enough. Many studies only follow research subjects for 2 years (the animal studies tend to be much shorter), although the young women soccer players were studied for an eight-year period.

Studies Using Osteological Material. Cynthia Wilczak (1998) examined musculoskeletal stress markers (MSM) of 375 individuals from a wide variety of populations including prehistoric hunter-gatherers, prehistoric corn agriculturalists, Eskimos and American Black and White populations from two early 20th century historical collections.

Wilczak found that the various populations included in her study had significantly different rates of sexual dimorphism. This variety in the degree of sexual dimorphism

between human populations certainly complicates attempts to control for it through simple sorting into male and female categories. Some populations also exhibited a greater degree of asymmetry than others and the degree of asymmetry noted in males and females was also distinct in different populations. Interestingly, Wilczak believes that the sexual dimorphism observed in populations with the lesser degree of asymmetry is more indicative of changes due to activity because most activities involve the use of both hands. This implies that individual asymmetry is usually genetically based rather than a result of using one side more than another. The opposite conclusion was reached by Mays (1999) in his study of a medieval cemetery population. It may be that specialized tradesmen of medieval times were more likely to use one side much more than another while generalized hunter gatherers would be more likely to use both sides equally. More research may be needed to clarify this point.

John Robb (1998) analyzed a population of 56 adults from an historic cemetery in Pontecagnano, Italy. The 56 adults studied by Robb (1998) are a random sample of adult remains among the 800 burials for which osteological studies have been carried out. In total, more than 6,000 burials have been recovered at the site. Robb compares burials from the pre-Roman occupation (prior to 500 BC) to the Roman period internments in his sample.

Robb (1998) is critical of many studies that claim to have identified specific activities such as throwing, stone knapping or rowing from skeletal remains. He warns that such assumptions may be unduly colored by our imagination and limited knowledge of the

range of activities engaged in, particularly for prehistoric groups. Robb points out that even if we are unable to reliably associate hypertrophy at a muscle site with a specific task, we can still get information useful in investigating anthropological research questions using historic and prehistoric populations. It is the patterning of development which is more interesting in Robb's view.

Properties of Muscle Attachments /Entheses

Macro Morphology. Entheses are complex, idiosyncratic structures which are not easily modeled for investigations of mechanical stress.

Histology. Here I need to discuss fibrous versus fibrocartilaginous entheses, adaptation to stress dispersal at the cellular level and how the various biological factors such as sex, nutrition, health and age (as manifest through hormonal levels and available nutrients) might affect bony development at entheses.

Benjamin and coworkers (2006) classify entheses into two types, fibrous and fibrocartilaginous. These two terms are analogous to the terms direct (fibrocartilaginous) and indirect (fibrous) attachments (direct and indirect are terms used by Woo et al. 1998). Indirect entheses are so called because the attachment is by way of the periosteum. With direct entheses the attachment occurs at a joint where there is no periosteum. Other authors have divided entheses in to essentially the same two groups by basing their division on what region of the bone the attachment is on. Attachments along the diaphyses (periosteal-diaphyseal attachments) must pass through the periosteum and

are therefore indirect or fibrous attachments. Enteses at epiphyses (chondral-apophyseal) attach directly to the joint cartilage and bone and are of the fibrocartilaginous type using Benjamin and coworkers' favored terminology.

In fibrocartilaginous enteses, the tissues gradiate from dense white fibrous connective tissue (DWFC) into uncalcified fibrocartilage, calcified fibrocartilage and bone without clear boundaries between the DWFC and the rest of the tendon or ligament or the boney portion and the rest of the bone. Since there are no Sharpey's fibers at these locations, the attachment is secured by the interdigitation of the different tissue types. Many enteses consist of areas of both fibrocartilaginous and fibrous attachment.

Evaluation of MSM

Qualitative Approaches. John Robb (1998) developed a five-point scoring system which he used to analyze a population of 56 adults from an historic cemetery in Pontecagnano, Italy. In order to establish the gradients within his scoring system, Robb examined 61 interments of working-class adults buried during the 19th century in Syracuse, Sicily. The 19th century remains were seriated visually by degree of development for about 40 different attachment sites (serration completed separately for each attachment site). The remains were then sorted into five groupings based on their degree of development. Descriptions and photography were used to describe the morphology characteristic of each grade, thus establishing the standards to be used in the study. Robb selected 18

attachment sites for his analysis of the Pontecagnano cemetery. He notes that the standards developed are intended for use at this site, and that a grade 3 at Pontecagnano is not necessarily equivalent to a grade 3 at another site.

Hawkey and Merbs (1995) developed the most commonly used version of a qualitative method. This was a huge step in the right direction in that it created a standardized scale which could be used to compare results from multiple populations. Observations of each attachment site are scored for three criteria. The three criteria are: Robusticity (size and degree of normal raised bone), Stress Lesion (depression) and Ossification (abnormal bone growth or spur). Each of these is graded on a scale from 0 to 3. Photographic examples are provided for each of the criteria.

Robust morphology at the attachment site is hypothesized to be due to a normal hypertrophic response to use stress. Stress lesions are thought to be the result of continued stress such that the bone has little chance to rebuild. For this reason, Hawkey and Merbs assign them higher values when calculating total expression scores for each attachment site. Ossification is described by Hawkey and Merbs as resulting from injury and was therefore not included in the calculations of total expression. One potential downfall is that a slight degree of ossification could be confused with normal robusticity. However, Hawkey and Merbs report that previous studies using this method have found that inter-observer and intra-observer error was at an insignificant level “(p< 0.5)” (Hawkey and Merbs 1995:327) “Expression scores were assessed for statistical analysis with the following numerical values: 0=no expression, 1 =robusticity grade 1 (faint), 2

=robusticity grade 2 (moderate), 3=Robusticity grade 3 (strong), 4=stress lesion grade 1 (faint), 5=stress lesion grade (moderate), and 6=stress lesion grade 3 (strong)”(Hawkey and Merbs 1995:329). Judging from this value assignment system, It appears as though stress lesions were interpreted as significant enough that recording even a faint lesion (value = 4) made the degree of robusticity irrelevant. Hawkey and Merbs state that they believe “a continuum often occurs between the robusticity and stress lesion markers” (1995:329). They do not make the case (other than indirectly through the scoring system presented above) that the relationship between robusticity and stress lesions are always the same. Indeed they weaken this assumption when they discuss training in youth and exertion in very cold conditions as a potential determining factors between lesions or robust attachments. Other, as yet unexplored factors may well influence this relationship. Several likely candidates include diet and overall health (essential for any repair and tissue building function). For this reason, it may have been more advantageous to analyze robusticity and stress lesion scores separately, or at least given equal weight and added to achieve a total score.

Wilzack (1998) points out that the size and build of the underlying bone may have an implicit influence on the score assigned. Also, while statements can be made as to which MSM are larger or smaller than another, no evaluation can be made as to the degree of difference using relative scoring systems (i.e. the difference between a 1 and 2 score is not necessarily the same as the difference between a 2 and 3 score).

Quantitative Approaches. In order to improve the objectivity and usefulness of the data, Wilczak (1998) uses quantitative data (maximum length and width in millimeters) to compare MSM. Entheses were videotaped in high resolution, and still images were used to digitally measure the entheses in two dimensions. Although this allows much better precision and accurate across-site comparisons to be drawn, Wilczak acknowledges that by taking measurements in two dimensions, she loses information relating to the rugosity of the site (Wilczak 1998).

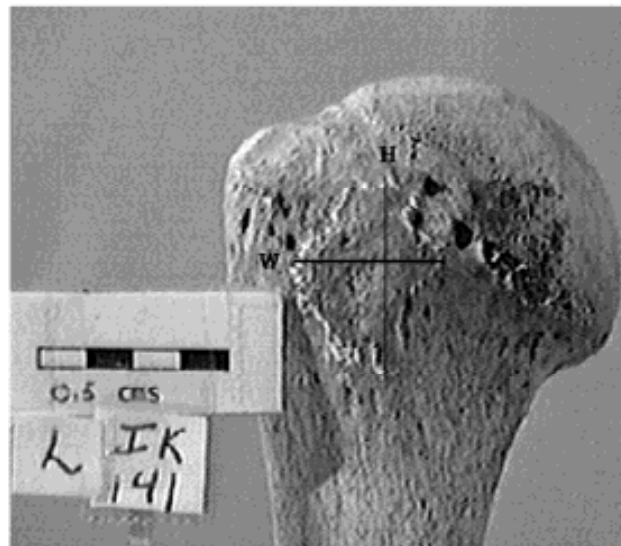


Figure 1. Two Dimensional Quantitative Assessment of Entheses
From Wilczak 1998

Three Dimensional Quantitative Measurement. The ideal remedy to address the lack of quantitative data in the grading systems and the lack of detail concerning rugosity in the length and width measurement systems is to find a way to accurately quantify surface area in three dimensions. This has recently been made feasible with the introduction of relatively light weight, portable and affordable laser scanners with resolution capabilities worthy of complex entheses morphology.

Ann Zumwalt utilized a 3D laser scanner in her recent study of muscle attachment sites in a population of ten exercised and ten unexercised adult female sheep. She compared the muscle attachments of exercised and control groups in a variety of ways, including investigating the fractal properties of cross sections of the attachments and 3D surface area

The study: Ten sheep were subjected to one-hour-long sessions on a tread mill, under gradually increasing weight loads. The weight was placed in backpacks worn by the sheep and was slowly increased over the course of the experiment to a maximum of 20% of the weight of the sheep. This was done five days a week for a period of 90 days (number of days at maximum load not specified). The 90-day period was deemed to be sufficient for the study because a previous study by Turner and Villanueva indicates that the bone turnover time for adult ewes is 74 days (as cited in Zumwalt 2006). The remaining ten sheep were the control group and were not exercised. The sheep were weighed at regular intervals throughout the experiment.

At the end of the 90 days, all 20 sheep were euthanized and dissected. Six limb muscle attachment sites and one attachment site associated with mastication (as a control) were scanned with a 3D scanner and analyzed using GIS software (Zumwalt 2005, 2006). In addition, the muscles and tendons associated with the attachment sites were weighed for each animal.

For the population of exercised sheep, either the muscle or tendon (but not both) gained mass in each one of the limb sites studied (four of the muscles gained between 9% and 15% on average and one tendon was 16% heavier in the exercised group).

Zumwalt examined the surface area data in several ways. She looked for correlations between muscle size and attachment site surface area in the control group (unexercised) and found that there was no significant correlations either before or after controlling for body mass. She examined the exercised animals attachment sites and found that they also did not correlate to muscle or tendon size after controlling for body mass “The results of this experiment do not substantiate the long-held assumption that attachment site morphology reflects in vivo activity and muscle size” (Zumwalt 2006: 448).

Body Size Standardization

Need for Body Size Standardization.

Methods Used in Body Size Standardization. Measurement, Statistics.

The Terry Collection

The Terry Collection currently consists of the skeletal remains of 1,728 individuals, just over 1,6000 of whom have a known age-at-death. The collection includes individuals as young as 14 and as old as 102. Most were classified as either “black” or “white”. The Terry Collection is housed at the Smithsonian Institution, Washington D.C.

History. The historic contexts in which the collection was established and accumulated are relevant to understanding the strengths and weaknesses of the collection for osteological research. Many late 19th and early 20th century osteological collections were amassed by medical schools and for this reason preferentially collected skeletons displaying interesting and unusual pathologies. In contrast, Robert J. Terry set out to collect a large sample that showed the range of normal variation. His motivations and reasoning were influenced by his teacher George S. Huntington, who began the Huntington collection at the College of Physicians and Surgeons in New York (now housed at the National Museum of Natural History). The result is a large collection that is much better suited to developing new comparative osteological standards than the accumulations of medical oddities that were the standard around the turn of the 20th Century. Terry also influenced and was influenced by a small cohort of likeminded peers including T. Wingate Todd, William Montague Cobb, Raymond Dart, Philip V. Tobias, and A. Galloway.

Terry began collecting human skeletal material for reference, training and comparative purposes in 1898 while teaching anatomy at Missouri Medical College. This first attempt was lost in a fire, and the subsequent attempt fell victim to vandals in 1907. The third time proved to be the proverbial charm, and Terry began amassing what is now known as the Terry collection in 1910. Because Terry saw the purpose for his collection as providing a known reference sample for teaching and comparison, he was extremely diligent in collecting all manner of documentation on the individuals who made up the collection. Terry demonstrated an uncommon degree of foresight in gathering not only basic demographic information and coroners reports, but cadaver measurements, photographs, hair and skin samples, death masks and other types of documentation. Coroner's reports are available for each individual, although the other types of supporting documentation are variably present. Terry also pioneered methods for removal of soft tissue and degreasing the skeletal material with a minimum amount of damage and a maximum level of preservation, such as the need to leave some fat in the bones to increase preservation (Hunt and Albanese 2005).

Demography. Robert J. Terry was not the only powerful force shaping the composition of the skeletal collection. Socio-historical, cultural and economic factors also played a role. The skeletons which ultimately populated the Terry collection originated as unclaimed bodies, primarily from local St. Louis, Missouri hospitals and institutions. The peak of Terry's collecting took place within the backdrop of the great depression. Families who could not afford to bury their dead had little choice but to let the state

dispose of the remains as it saw fit. Rather than spend public funds on a traditional burial, many unclaimed bodies were made available to medical schools as teaching cadavers. After the doctors-in-training had dissected the soft tissues, Terry was free to claim the skeletal material for his collection. This had definite advantages for the collection in that each set of remains came with detailed notations from the medical dissection. It had some disadvantages as well, such as the poor state of some of the bodies by the time they reached the medical school and also that the collection is a biased sample of the very lowest socioeconomic strata of St. Louis during that time period. Females were underrepresented both because taboos existed about exposing the bodies of young women to the salacious gaze of the medical students and because men were more likely to be forced into transitory status in the search for employment and to therefore have no friends or family nearby with the capability of claiming the body. Infants and children are likewise absent from the sample. These factors make the collection useless for historical demographic research questions, and may have some influence over the applicability of comparative methods developed using the collection (Hunt and Albanese 2005).

The sex ratio of the Terry collection was greatly improved by the efforts of Mildred Trotter, who took over responsibility for the collection when Terry retired in 1941. Trotter strived to acquire more females, in particular younger white females, to even out the demographic distribution of the Terry Collection. Through preferential collection of young people and females, Trotter did manage to improve the representative nature of the

collection as a whole, however this means that the sex and age of individuals within the collection are heavily biased according to time period. Older men who passed away in the 1940s and 1950s are underrepresented, as are younger women who passed away in the 1920s and 1930s (Hunt and Albanese 2005).

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