

Bioarchaeological Science

What We Have Learned from
Human Skeletal Remains

Elizabeth Weiss



NOVA

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HUMAN SKELETAL REMAINS**

ELIZABETH WEISS

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Dedicated to C.L.

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Chapter 1

INTRODUCTION TO BIOARCHAEOLOGY: HISTORY TO PRESENT

1.1. INTRODUCTION TO BIOARCHAEOLOGY

Bioarchaeology is the study of human skeletal remains from archaeological settings to aid in reconstructing the biological and cultural pasts of populations. This book provides an overview of bioarchaeological theory, methods, and applications with an emphasis on the latest literature published in the top journals. Bioarchaeology is one of the lesser-known fields of physical anthropology, and yet it is one of the most researched topics in physical anthropology. In 2006-2007, a quarter of all the articles published in the *American Journal of Physical Anthropology* (the top peer-reviewed physical anthropology journal) were on studies of human skeletal remains. The next most published theme of population genetics lagged far behind, accounting for only around 15% of all published articles. Furthermore, bioarchaeology has gained in popularity around the world and there are a growing number of bioarchaeological studies coming from European, Asian, and South American anthropologists. Finally, introductory courses in physical anthropology are starting to include bioarchaeology as a topic of importance (see *Our Origins* by Clark S. Larsen) and thus, a new wave of student interest in bioarchaeology may arise. Bioarchaeology is arguably physical anthropology's most important field.

1.2. HISTORY OF BIOARCHAEOLOGY

An extensive history of bioarchaeology has been published in the edited volume by Jane Buikstra and Lane Beck (2006). This section will highlight a few of their findings, especially with regard to reconstructing activity patterns (which are the physical endeavors people engaged in) and understanding pathologies (i.e., diseases). Before delving into these topics of activity pattern and pathology reconstructions, I think that it is important to point out that bioarchaeology began in the 1800s and, as such, is a relatively new field. Early anthropologists who studied skeletal remains, such as Aleš Hrdlička and Ernest A. Hooton,

were generalists who studied everything from Native American origins to case studies (which are studies that involve a single skeleton or a very small sample size and are descriptive) of diseases. Hrdlička was trained in the medical field and as a consequence was very descriptive and relished case studies of individuals. He also spent a great deal of time trying to understand human variation and the origins of Native Americans. Hooton was more embedded in the social sciences and came from a Classics approach; therefore, Hooton engaged in the act of intertwining the research of archaeology and skeletal remains found at sites, such as the Pecos agricultural Amerind (American Indian) site in New Mexico in 1930. Hooton's work on the Pecos Amerind site was problem oriented and probed into questions regarding demography (best defined as the distribution of age and sex of populations) and taphonomy (also known as the laws of burial, describing how remains become buried and what happens to the remains from the time they are buried until their discovery). He was also interested in population health as opposed to the more descriptive case studies of an individual's health. Thus, even though most early anthropological works are described as being purely descriptive in nature, Hooton and Hrdlička went beyond description to attempt to answer questions about the past. (Buikstra and Beck, 2006)

With regard to activity pattern reconstructions, bioarchaeology had modest beginnings. As summarized by Pearson and Buikstra (2006) and Jurmain (1999), J. Lawrence Angel was likely the most productive anthropologist to work on reconstructing activity patterns of past populations. In 1952, Angel produced a description of three skeletal remains that were dated as being 9000 years old from Iran that included likely the first use of bone form and muscle insertion information to reconstruct activities, such as pulling fishing nets (Pearson and Buikstra, 2006). On California remains, Angel talked of the torsion, or twist, of the tibia in cases and related this torsion to running on tough terrain. Angel started a bioarchaeological revolution to use skeletal features (everything from muscle markers to arthritis) to bring the movement to bones (Pearson and Buikstra, 2006). Angel's work was heavily influenced by anatomists who were attempting to understand human biology; for example, German anatomist Julius Wolff tried to understand trabecular (spongy) bone orientation through muscle use and strains placed on bones as early as 1892. Wolff's work will be discussed in the next chapter. Angel was also influenced by Rudolf Virchow, another German anatomist. Virchow's expertise was in pathology (disease) and he demonstrated how the human body's plasticity responded to external forces and strains (Pearson and Buikstra, 2006). This view of the body as a dynamic entity led anthropologists to produce fewer typological (classification) studies and start attempting activity pattern reconstructions.

Another section of bioarchaeology that has a rich history is that of the study of pathologies. Paleopathology, which is the study of disease in past populations, is one of the most popular research topics in anthropology currently. Paleopathology employs knowledge from medicine, dentistry, and anthropology. It began as a pastime for physicians during the 20th Century (Cook and Powell, 2006). For instance, Sir Marc Armand Ruffer, a British physician who worked on Egyptian mummies, is often thought of as the first paleopathologist. Roy L. Moodie, an anatomist, published some of the first volumes on paleopathology. One of his early publications was titled *Paleopathology: An Introduction to the Study of Ancient Evidences of Diseases* (1923). Most of these early works on paleopathology were descriptive, which is not surprising considering the researchers' medical training and the likelihood that some pathologies were found in single individuals only. It was not until the 1960s that paleopathology took on a more problem-oriented approach (Cook and

Powell, 2006). As an example, anthropologist Saul Jarcho wrote an article that was published in *Science* in 1965 that brought to people's attention the need for within-field and interdisciplinary collaboration, and the necessity for more than just descriptions of the pathologies (Cook and Powell, 2006). Nonetheless, paleopathology remains more descriptive than other aspects of bioarchaeology and struggles to place diseases into a greater contextual framework.

There are many other aspects of bioarchaeology and the history of bioarchaeology that can be covered, such as the study of dentition, the beginnings of genetic evidence, and the beginnings of isotopic analyses. Bioarchaeology is a field with many specialties; specialties, however, are relatively recent developments in this field of study. Thus, to cover the histories of all the specialties is a book in and of itself, and Buikstra and Beck's (2006) book does just that superbly. Let us move on by examining research trends in bioarchaeology prior to probing into the latest findings.

1.3. RESEARCH TRENDS IN BIOARCHAEOLOGY

Analyses of published literature has highlighted trends in Bioarchaeology, both in the USA and abroad. In 2008, anthropologists Samantha Hens and Kanya Godde examined publication trends in the *American Journal of Physical Anthropology* in an attempt to determine whether the call for more analytical research by Lovejoy and coworkers (1982) and Armelagos and coworkers (1982) has been heeded. Hens and Godde found that, although the shift from descriptive studies to analytical studies (which includes having a hypothesis, a theoretical base, and advanced statistics) may not have been as complete as anthropologists have claimed, over the last two and a half decades researchers have attempted analytical research more often than previously. In the last ten years, analytical research has increased dramatically, especially in topics on age, sex, stature, and demography. Descriptive studies, however, still prevail in the United Kingdom (Mays, 2008), which may be in part a remnant of the medical background that anthropologists in the United Kingdom were trained in during the 1960s through 1990s. Furthermore, pathology research is still heavily descriptive (Mays, 2008; Hens and Godde, 2008; Stojanowski and Buikstra, 2005). Some of the descriptive research is important in cases where new characteristics arise in skeletal material that may aid others in identifying diseases. Description also may be useful when new methods are being employed and the theoretical framework for the data has not been laid down. Nonetheless, descriptive studies have far less impact on the field, are published more often by novices, and are cited less frequently (Stojanowski and Buikstra, 2005). Thus, the majority of studies reviewed in this text are analytical rather than descriptive.

Another interesting aspect of bioarchaeology research has been the increase in use of traits to identify diseases, environmental stresses, and population health. Case studies that focus on single individuals have declined in the last few years, (Mays, 2008) as have studies on single skeletal health indicators. Anthropologists are recording more indicators of health and disease, genetics, and activity than previously and are often using sample sizes large enough for statistical analyses. Finally, an important trend in research has been the rise in technology as indicated by an increase in genetic research (e.g., ancient DNA) and isotopic studies, which can aid in understanding diet and weaning patterns. This trend is particularly

strong in the United Kingdom and Germany (Mays, 2008). Interestingly, some of these research methods are destructive and, thus, may face difficulty being approved in the USA where ethical issues surrounding prehistoric Amerind remains are especially sensitive.

In conclusion, bioarchaeology is a relatively young field that has grown immensely, but is still feeling its growing pains. To better understand bones and human biology, many anthropologists have turned to medicine and sports literature, which is where information on bone biology and theories of bone remodeling arise that help us better understand the past.

Key Terms

Bioarchaeology
Paleopathology
Demography
Case Studies

Chapter Questions

- 1) Who were the key researchers in the early days of bioarchaeology and what were their contributions?
- 2) What is the difference between bioarchaeology and paleopathology?
- 3) What research trends have appeared in bioarchaeology?

Chapter 2

BONE BIOLOGY AND HUMAN OSTEOLOGY: BASICS TO UNDERSTANDING OSTEOLOGICAL RESEARCH

Anthropologists examining skeletal material from archaeological sites use skeletal evidence to reconstruct past lives with an emphasis on referencing medical and sports literature to understand the characteristics visible on bone. Thus, understanding bone biology is essential in the study of bioarchaeology.

Bone functions include the protection of organs and the support of soft tissue, such as skin; providing a surface for muscles and connective tissues, such as tendons and ligaments, to attach onto; and acting as a lever system that is intrinsically involved in all our movements (White and Folken, 1991). The skeletal system also stores fat and calcium, and provides locations for the production of blood cells. Bone tissue is a dynamic material that changes with the growth of an individual and interacts with stresses placed on it by mechanical loading (White and Folken, 1991). We will return to bone remodeling later in the text after a brief description of bone biology.

Bone is a strong, hard substance due to its combination of organic and inorganic components, which consist mainly of collagen and minerals (such as calcium). Bone responds to stresses, which are internal forces on bone, with various levels of stiffness relying on the rate and duration of the stress applied to it (Hamill and Knutzen, 1995). Collagen provides bone with ductile properties that allows the bone to warp or deform rather than break when stressed, whereas mineral constituents of bone account for brittleness and provide strength to the skeletal system. This combination of deformability and brittleness is especially important when anthropologists consider bone form in regard to past activity patterns.

At the macroscopic level, the skeletal system of an adult consists of two basic types: cortical (compact) and trabecular (spongy) bone (Figure 2.1). Cortical bone is solid and dense; it makes up the shafts of long bones and the other surfaces of all other bones (Bass, 1987). In skeletal remains found in the archaeological record, cortical bone is the most abundant since its denseness aids in its preservation (Bass, 1987; Swartz, 1996). On the other hand, trabecular bone is porous and lightweight, which reduces the chance of its preservation (White and Folken, 1991). Trabecular bone can be found at the end of long bones, such as at the femoral head. Blood-forming tissue lies in the areas of trabecular bone in the growing skeleton and is then replaced by yellow marrow in the medullary canals of long bones.

Epiphyses are the end of long bones, which fuse once growth has ceased, and metaphyses are also known as shafts (White and Folken, 1991).

During life, bone is covered with a tissue called the periosteum, which aids in nourishing bones but is not found in the bioarchaeological remains. The inner surface of bone is lined with the endosteum. Both the periosteum and endosteum are bone-forming (osteogenic) tissues where cells that form bone material are plentiful in young individuals, and are still active and present throughout adulthood (White and Folken, 1991). These tissues are especially active during trauma, such as when a bone is broken and new bone is required for healing.

On the microscopic or histological level, bone is better understood by breaking it down to immature and mature types. Immature bone, which occurs throughout life and is found in very young individuals or soon after trauma has occurred, is disorganized and is replaced by mature bone. Mature bone (also known as lamellar bone) is arranged in a canal system called the Haversian system (Hamill and Knutzen, 1995) (Figure 2.2). The Haversian system consists of a central canal that is surrounded by lamellae (thin sheets), lacunae (small cavities), and canaliculi (small canals) (Tortora, 1995). The central canals run through bone longitudinally and are surrounded by rings of calcified matrix that are called lamellae (Tortora, 1995). Between these hard sheets of lamellae are spaces called lacunae that contain mature bone cells, and radiating from these lacunae are minute canals (or canaliculi) that are filled with fluid (White and Folken, 1991). Canaliculi connect lacunae with each other and with the central canals. This Haversian network provides routes for nutrients and oxygen to allow for bone to stay alive and dynamic.

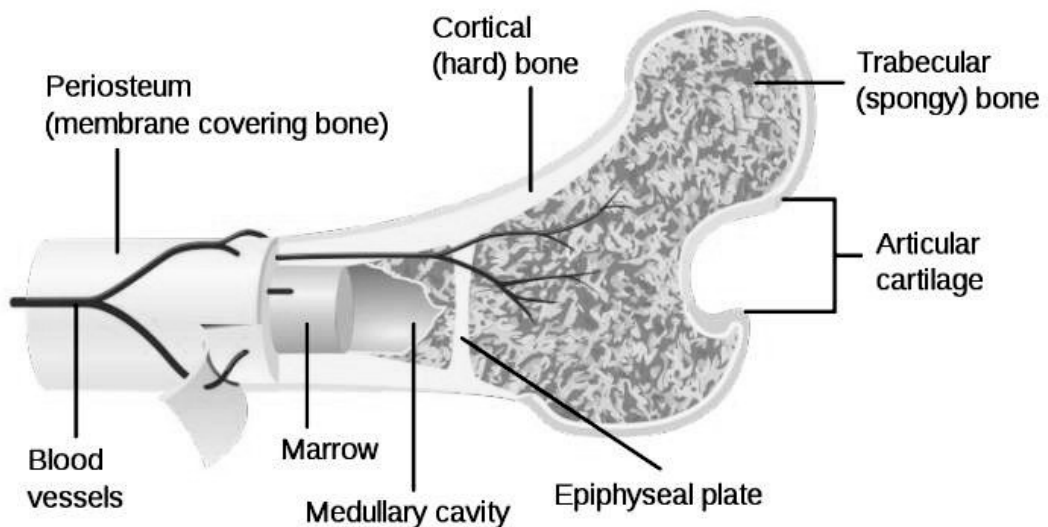


Figure 2.1. Macroscopic view of bone biology. Taken from Pbroks13 on Wikipedia Commons.

Compact Bone & Spongy (Cancellous Bone)

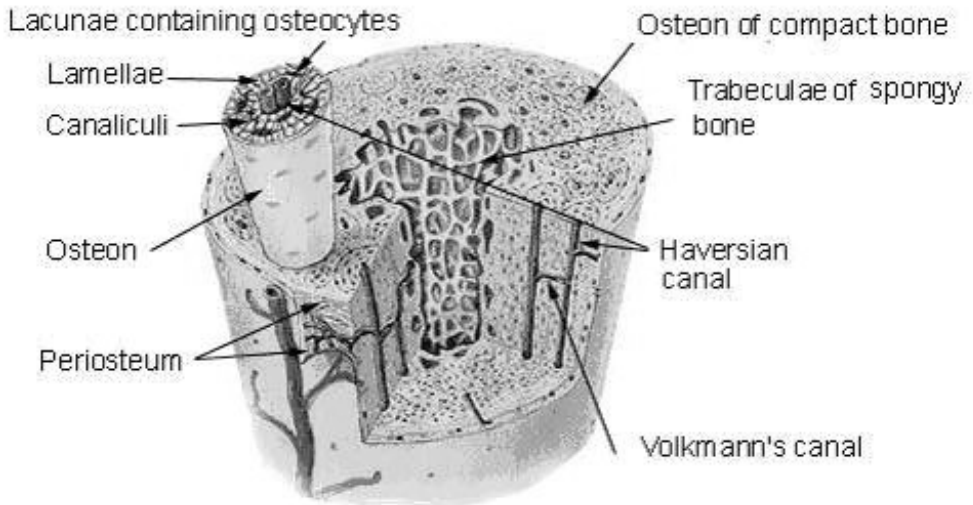


Figure 2.2. Microscopic view of the Haversian system. Taken from U.S. National Cancer Institute's Surveillance, Epidemiology and End Results (SEER) Program. (<http://training.seer.cancer.gov/index.html>).

With this brief introduction to bone biology, we can now move on to understand how anthropologists use bone to look at past activities, trauma, and diseases.

Key Terms

Cortical Bone
Collagen
Endosteum
Osteon
Periosteum
Haversian System
Trabecular Bone

Chapter Questions

- 1) What are the functions of bone?
- 2) What are some of the properties of bone that make it flexible and what are some that make it hard?
- 3) What are the differences between trabecular and cortical bone?
- 4) How do mature bone and immature bone differ?

Chapter 3

RECONSTRUCTING ACTIVITY PATTERNS: MAKING DEAD PEOPLE MOVE

3.1. INTRODUCTION TO RECONSTRUCTING ACTIVITY PATTERNS

One of the main research trends bioarchaeologists engage in is the reconstruction of past activity patterns. Anthropologists have been trying to determine the things people did who lived in prehistory. For example, they want to know whether males and females engaged in different activities (i.e., was there always a sexual division of labor or is this something new). They are also interested in determining how people's lives changed with the advent and adoption of agriculture, with the invention of various tools, and with the contact of other people (i.e., when Europeans made contact with Native Americans). In order to reconstruct activities, such as hunting, long-distance traveling, and food preparation, anthropologists have utilized a variety of methods. These methods can most easily be broken down into those that invoke the theoretical basis of Wolff's Law and bone remodeling, such as cross-sections, muscle markers, and asymmetry, and methods that look at bone deterioration (or wear and tear), such as osteoarthritis and vertebral stress fractures. Any trait that is examined has complications and confounds, which will be addressed in the following sections. However, there is promising data throughout the literature that suggests activity reconstruction can be accurate when conducted with care in respect to controlling for biological confounds.

3.2. WOLFF'S LAW AND BONE REMODELING

Newton's Second Law of Motion states that when a force is applied to an object, the object will accelerate. If, however, restraints are placed on the object that prevent it from moving, then the movement will occur within the object in the form of deformation to accommodate the force. All biological tissues deform to an extent when forces are applied, even if motion occurs. Thus, when a limb muscle places force on a bone, the limb will move (and perhaps even move the entire organism), but some deformation will also occur due to restraints. Mineralized tissues remodel in order to reinforce themselves to prevent breaking from these deformations and this is where bone remodeling comes in.

Two types of cells are responsible for bone remodeling and healing: osteoclasts and osteoblasts (White and Folken, 1991). Osteoclasts develop from white blood cells and resorb (or take away) bone. Osteoblasts, which make pre-bone tissue known as osteoids, are responsible for new bone material. Osteoid tissue is un-calcified and not hard, leading us to the final step in bone repair and remodeling: calcification. In order for calcification to occur, certain minerals and vitamins are essential. For example, calcium, which is a mineral found mainly in dairy products, is needed for bone development and maintenance. About ninety percent of calcium is stored in bone, where it can be reabsorbed by blood and tissue. Fluoride is another mineral important for bones, especially for growth and protection against demineralization of bone. Fluoride is added to toothpaste and in our water to prevent cavities, which is the demineralization of enamel. Unlike bones, teeth do not remodel, making this protection essential to our health. Finally, vitamin D, which is found in eggs, liver, and fish, and is synthesized by the body with exposure to ultraviolet radiation, regulates calcium absorption. Without these vitamins and minerals, bone health can be severely hampered even if exercise is practiced (Tortora, 1995).

Bones experience external and muscular forces throughout an individual's life that the bone must respond to in order to prevent breakage. Muscle use is important in remodeling bones and maintaining strength because muscle usage places the stress on bones necessary to activate osteoblasts (Hamill and Knutzen, 1995). Bone, in other words, thins with loss of activity and thickens with increase of activity. Osteoblasts, which are responsible for making and depositing bone material, respond to stress by making un-calcified, collagen-rich, pre-bone tissue. The final step in bone deposition is calcification, which leads to the synthesis of true bone; it occurs as the inorganic components of bone are deposited in the pre-bone tissue (White and Folken, 1991).

Bone remodeling has long been thought to occur at particular locations due to specific muscle use. The first person to provide evidence for this was German anatomist Julius Wolff in 1892, whose statement on it became known as Wolff's Law. Wolff's Law states that:

“Every change in the form and function of a bone or the function alone, results in definitive changes in the internal architecture of the bone and equally definitive changes in the external architecture in accordance to mathematical laws.”

According to Wolff's Law, cortical and trabecular bone interact dynamically with specific environmental (which in this case means non-genetic) forces. When such a force is applied to a bone, it causes the bone to deform (or experience strain) which induces local bone formation by osteoblasts (remember these are bone-forming cells) (Amtmann, 1968; Chamay and Tschantz, 1972; Woo et al., 1981). Localized bone remodeling, which is achieved by the addition of new bone by osteoblasts and bone resorption by osteoclast cells, is adaptive since it reduces the threat of bone breakage. The next sections will address how anthropologists use Wolff's Law as a theoretical basis for examining cross-sections of bone to reconstruct the past activity patterns.

3.3. CROSS-SECTIONAL DATA

As mentioned above, bone tissue is a dynamic material that interacts with stresses placed on it by mechanical loading. The result of bone remodeling mentioned above is altered bone morphology, which can be measured by examining cross-sections of bone. Bone repairs itself and alters its configuration in response to mechanical demands (Hamill and Knutzen, 1995). Environments place varying demands on the bones of individuals; thus, determining how environments affect bones can aid in understanding peoples' past lives in different areas. And although genetic factors influence the final form of bone, later bone development is affected by non-genetic factors, such as remodeling after bone breakage and remodeling in response to specific stresses and strains to prevent bone breakage, as mentioned above (Wolff, 1892). Mineralized tissues remodel to reinforce themselves to prevent breaking. Forces, which are referred to as loads applied to solid objects, cause bone deformation known as strain. Forces are often caused by the mechanical environment, such as exercise of muscles. For example, the many muscles attached to the humerus apply force to the bone to create motion. The harder these muscles work, the more force is applied. The physical environment may also influence the amount of work necessary to perform certain tasks, such as walking on treacherous terrain compared to flat terrain.

Activities causing strains on bone lead to internal stresses that can break a bone if remodeling has not occurred (Figure 3.1). Throughout life, loads repeatedly placed on bone may eventually become too great to be resisted by the physiology of bone tissue alone and, thus, remodeling of bone becomes necessary. Changes in cross-sectional geometry allow changes in robusticity, which is the strength that results from remodeling against force-induced strains.

There are five types of strain that can be experienced by a bone: tension, compression, bending, shearing, and torsion. Three types of strain are particularly important in most loadings of human limb bones: compression, bending, and torsion (Table 3.1). Compression is a simple strain that causes shortening of the bone. Bending, on the other hand, is a complex strain because it causes two types of strain: tension on one side, and compression on the other. Torsion is strain that twists an object. Strengths against the different strains are calculated using cross-sectional geometries of the long bones, such as the femur (Alexander, 1968; Swartz, 1996). Compression is the most common strain experienced by bone, and bones best resist it by increasing cortical bone area (Swartz, 1996). Compressional strength, consequently, is calculated by measuring cortical bone cross-sectional area (CA).

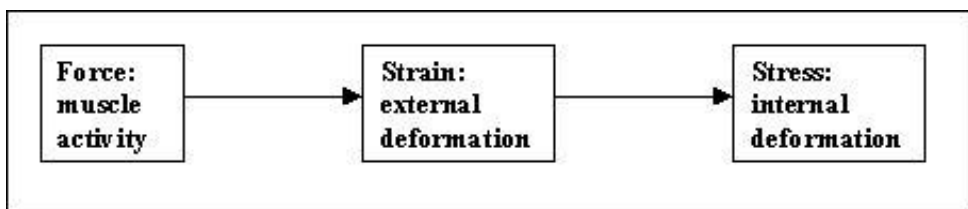


Figure 3.1. Chain of events that occur during mechanically induced bone remodeling. Created by Elizabeth Weiss from San Jose State University.

Table 3.1. Summary of cross-sectional properties and the type of strength they measure

Cross-sectional Property	Strength Measurement
Areal measurements	
Cortical Area (CA)	Compression Strength and Torsion
Total Area (TA)	Compression Strength
Inertial Measurements	
<i>Moments of Inertia</i>	
I_{ap}	Bending Strength in the anteroposterior plane
I_{ml}	Bending Strength in the mediolateral plane
<i>Polar Moment of Inertia</i>	
$J (I_{ap} + I_{ml})$	Torsion Strength

Although compression is the most common strain experienced by long bones, bending is the type of strain most likely to break a long bone (Alexander, 1968). This is in part because the Haversian system is ideal for resisting compressive stresses and, thus, bone is less in jeopardy of breaking from compression than it is of breaking from bending stress. As a result, it is important to determine a bone's strength against bending strains. In order to calculate bending strength, moment of inertia or second moment of area (I) is used, which is equivalent to mass in a rotating system (Swartz, 1996). Moment of inertia is used to determine the magnitude and direction of bending strength; a greater I means a greater resistance to bending in a bone in a given direction. The best morphology, from a mechanical perspective, to resist bending strains is a hollow shaft with a large radius. A hollow shaft is better than a solid shaft because it decreases weight and, thus, eliminates excessive energy needed to move a heavy bone (Alexander, 1968).

Moment of inertia is measured through the center of gravity of a cross-section, which has both area and placement of particular components of area incorporated within it (Swartz, 1996). In order for the direction of bending strength to be determined, I must be defined with respect to particular axes. The axes are usually mediolateral (ml) and anteroposterior (ap) with respect to anatomical positions. The location of bending strength is indicated by ml and ap, with these referring to the axes around which the moments of inertia are calculated (Runestad et al., 1993). An I_{ml} to I_{ap} ratio allows one to calculate where bone remodeling has deposited new bone to prevent breakage from bending stresses (Swartz, 1996). For example, if most of the strain comes from the anterior and posterior sides, then the bone should have more cortical mass on its front and back (Figure 3.2) and a higher I_{ml}/I_{ap} ratio. The biceps brachii and deltoid attach on the front and back of the humerus and cause a strongly anteroposteriorly oriented humerus when used extensively in flexing and extending the arm.

Overall bending and torsion strengths are measured using the polar moment of inertia. Torsion often occurs close to the joints of limb bones because of the rotation of bones at joint sockets (Alexander, 1968). The polar moment of inertia (J) is the moments of inertia about the anteroposterior and the mediolateral axes combined; in other words, $J = I_{ap} + I_{ml}$ (Runestad et al., 1993). Hollow shafts give strength against twisting, which explains why the moment of inertia is used to calculate torsion strength. Unlike bending strength, torsional strength does not require strength in a specific direction, and, as such, the polar moment of inertia is used (Alexander, 1968).

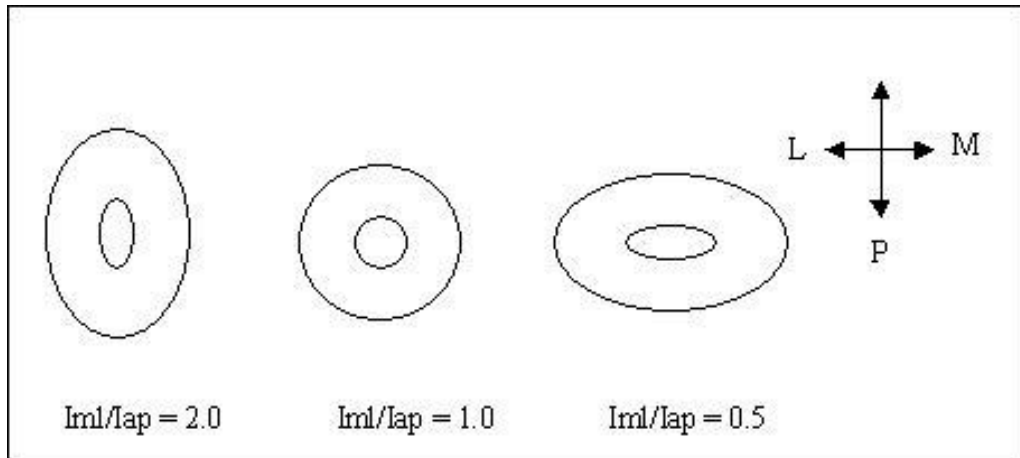


Figure 3.2. Cross-sectional shape as a result of strain direction. The left shows the result of anterior (A) and posterior (P) strains, the middle the result of few strains, and the right shows result of medial (M) and lateral (L) strains. Adopted from Ruff (1987).

The cross-sectional properties described above and outlined in Table 3.1 can be obtained through two main techniques: computer tomography scans (also known as CT-scans or CAT-scans) and radiographs (also known as x-rays). CT-scans are x-rays taken in 360 degrees and then assembled through computer software to provide the completed image. The cross-sectional image (which looks similar to a misshaped doughnut) is then fed through additional software (such as SLICE software) that calculates the cross-sectional properties. X-rays, on the other hand, need to be taken at two orientations (mediolateral and anteroposterior) and then the x-ray is used to measure inner and outer bone diameters. The measurements of inner and outer bone diameters are placed in formulae that utilize Pi to estimate cross-sectional shape and calculate the areal and inertial properties (Biknevicius and Ruff, 1992). X-rays tend to over-estimate cross-sectional strength, but as long as all the measures that are being compared were taken in the same manner, this need not be an issue (O'Neill and Ruff, 2004).

Cross-sectional Studies

Anthropologists have used limb bone cross-sections to examine the effects of division of labor, shifts in subsistence patterns, aging, and physical environments (Bridges et al., 2000; Feik et al., 1996; Ruff, 2000; Ruff and Hayes, 1983; Stock and Pfeiffer, 2001).

In an early study, Kimura and Takahashi (1982) studied femoral cross-sections from Japanese pre-agriculturalists (hunter-gatherer-fishers from 5500 to 2000 years BP – years before present) and Japanese industrial samples (autopsy specimens from anatomy classes). Kimura and Takahashi (1982) found the pre-agriculturalists had more anteroposteriorly - oriented midshaft femoral cross-sections, which indicated high mobility since the muscles used for walking attach to the front and back (at the linea aspera) of the femur. The pre-agricultural male femora were also more anteroposteriorly oriented than were the pre-agricultural female femora. The authors also found that female femoral cross-sections changed little with shift from pre-agriculture to modern industrial cultures. It seems that females were less mobile than males in the pre-agricultural population (that is, the females walked less than the males did). Male femoral cross-sections, on the other hand, became more circular through time as seen in the industrial population. In industrial population, both sexes

were sedentary (that is, they walked very little). Thus, cross-sectional geometry in the femora of both males and females are circular in the industrial population, which is consistent with a sedentary lifestyle.

Bridges (1989a) studied changes associated with the transition from a pre-agricultural to an agricultural subsistence in Tennessee Valley Amerindian populations, and found that male femoral cross-sections underwent few changes across this transition from hunting-and-gathering to agriculturalism, but that female cross-sections increased substantially in cortical bone. Bridges deduced that these changes occurred because females increased the use of their lower limb muscles through agricultural work, whereas males kept similar behavioral intensities from hunting and gathering practices. Bridges also found that female upper limb strength increased with the introduction of agriculture, which she attributed to the grinding of corn. Thus, Bridges concluded that females, but not males, increased their bone strength with the introduction of agriculture due to their intensified labor, which placed more stress on the bones.

Weiss (1998) used CT-scans on 34 adult males and 30 adult females from a Californian hunter-gatherer population to examine the cross-sections of femora and found that the male cross-sections were thicker and more anteroposteriorly oriented than those of the female, indicating that males had traveled more (Figure 3.3, see Weiss, 1998). Thus, a sexual division of labor likely existed in this pre-agricultural population, which included males traveling for hunting, trade, and warfare, and females staying home to prepare foods, gather, and watch the children. This negated the once popular notion that sexual division of labor first occurred with the onset of agriculture.

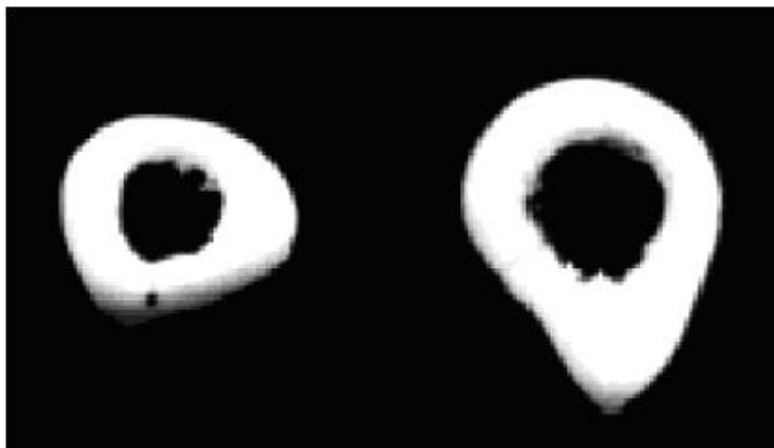


Figure 3.3. Left, a female circular femoral cross-section suggesting infrequent traveling; right, a male anteroposteriorly oriented femoral cross-section suggesting much traveling. Taken from Weiss (1998).

Pomeroy and Zakrzweski (2009) examined sex differences in a medieval Muslim population in Spain ($N = 72$) and compared them to an Anglo-Saxon United Kingdom sample ($N = 42$). The authors found more sex differences in the Spanish population than in the UK population; this difference may relate to religious traditions of Muslims that dictate a woman's realm is in the home whereas a man's realm is out in public. Mobility was further decreased among the Spanish women since they were not allowed out without a chaperone and had a bevy of domestic duties. The same limits were not placed upon the English women,

which results in a reduction of sexual dimorphism (which is the difference between the sexes) among the Anglo-Saxon sample.

In Australia, researchers examined both upper and lower limb cross-sections to determine whether sex differences in hunter-gatherers would compare to ethnographic data on hunter-gatherer activity patterns. Carlson and colleagues (2007) found in a sample of 149 pre- and post-contact Australian Aborigine individuals that males and females did not differ in lower limb cross-sections, but upper limb cross-sections were more robust in males. Ethnographic data supports distance travel by both males and females; perhaps the greater upper limb robusticity in males is the result of hunting with the use of spears. Nonetheless, ethnographic reports suggest that females carried heavy items and ground food and as a result should also display robust upper limbs.

Sládek and co-researchers tried using femoral cross-sectional shape to determine whether Central Europe had settlements during the Late Eneolithic (2900–2000 BC). Sedentary behavior as indicated by femoral cross-sections would support the presence of settlements and corroborate archaeological research that indicated agricultural subsistence. The authors tested the hypothesis by looking for differences in femoral cross-sections between the Late Eneolithic sample and an Early Bronze Age (2000–1700 BC) sample who were known to be sedentary. Few differences were found between the two populations. However, males of the Late Eneolithic had longer anteroposteriorly oriented femoral shafts that indicated higher mobility than the Bronze Age males may have experienced. Contradicting this finding, females of the Late Eneolithic had rounder femoral shafts than Bronze Age females suggesting the Late Eneolithic females were less mobile than Bronze Age females, but the authors suggest this temporal difference within females may relate to body shape rather than activity patterns. Thus, Sládek and co-researchers concluded that since there is not strong evidence of greater mobility in Eneolithic populations and further research needs to be conducted.

Another example of bone remodeling research comes from Ledger and colleagues (2000) who found that 18th Century South African slaves had stronger upper limb cross-sections but weaker lower limb cross-sections compared to Later Stone Age African hunter-gatherers. Ledger et al. attributed these differences to the manual labor required of slaves as opposed to the high mobility experienced by hunter-gatherers. In a similar study, Stock and Pfeiffer (2001) compared Later Stone Age South African hunter-gatherers to 19th Century fishers from the Andaman Islands (between Sumatra and Borneo). Stock and Pfeiffer found that, while the hunter-gatherer population had more robust (stronger) lower limb cross-sections the fishing population had more robust upper limb cross-sections. Stock and Pfeiffer attributed these population differences to the use of particular muscles in relation to specific activity patterns, such as lower limb muscles being used for long-distance travel in the hunting group and upper limb muscles being used for rowing watercrafts, swimming, and fishing.

In the first study to examine direct environmental impacts on bone cross-sections, Ruff (2000) compared six Amerind populations (three non-agricultural and three agricultural populations; $N = 268$) occupying three different environments. Two of the populations (one non-agricultural and one agricultural) inhabited a flat region in the South Dakota Plains; two populations (one non-agricultural and one agricultural) lived in a coastal region of Georgia; and two populations (one non-agricultural and one agricultural) occupied mountainous regions in the Northern Great Basin and New Mexico. Ruff found that Amerinds who walked on mountainous terrain had more robust femora than those who walked on flat terrain. These