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Preliminary Results

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# **Bone Growth, Maintenance and Loss in the Neolithic Community of Çatalhöyük, Turkey: Preliminary Results**

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## **Introduction**

Bioarchaeologists have long been interested in the health and the quality of life of early complex societies, particularly with increased sedentism in the context of the adoption of agriculture (Cohen and Armelagos 1984, Cohen and Crane-Kramer 2007, Larsen 1995, Roberts and Cox 2003, Steckel et al. 2002). While studies of health and disease patterns based on skeletal remains for the ancient Near East are numerous (e.g., Smith et al. 1984, Molleson 1994, Horwitz and Smith 2000, Smith and Horwitz 2005, Eshed et al. 2004, 2006, Schultz et al. 2007, Roberts and Buikstra 2007), few sites have yielded large collections of human skeletons in conjunction with detailed archaeological evidence of settlement, lifestyle, diet, and living conditions. The site of Çatalhöyük in the Konya Basin of south-central Turkey is a rare exception, with remarkable archaeological and paleoenvironmental context, revealing changes in community size and structure, shifts in mobility, and the use of plant and animal resources across time.

Bioarchaeological evidence from Çatalhöyük provides a unique perspective on early population aggregation, resource use, and consequences of early farming and urbanization on health and lifestyle.

Several recent studies have focused on paleopathology, dental morphology, isotope analysis and bone growth and robusticity at Çatalhöyük (Cowgill and Hager 2007, Molleson 2007, Molleson and Andrews 1997, Molleson et al 2005, Pilloud and Larsen 2011). The examination of bone maintenance and loss is another well known indicator of health and stress that has been used in bioarchaeological analyses. Bone is a highly dynamic tissue, its morphology and microstructure change over the life cycle in response to a variety of circumstances. In general, bone mass accumulates during the early decades of life only to have the process reversed leading to a reduction in bone mass, a concomitant deterioration in bone tissue and for some, and an increased susceptibility to fracture in the later decades. This process which extends across the life course is influenced not only by aging, but also by aspects of life history that relate to intensity and patterns of physical activity, social conditions, disease and/or nutrition and is recorded in the human skeleton at the tissue level. At its most basic level, if a child has a lifestyle involving poor nutrition and/or disease, its bone quality is poor, predisposing it to fracture in later life. In the context described for Çatalhöyük we might expect to see evidence for disease states and dietary stress expressed in key indicators of bone metabolism that is, changes or differences in bone quantity, quality and fragility. More specifically, with a decline in living circumstances involving population increase, sedentary lifestyle, and crowding, the expectation is a reduction in health, as indicated by disruption in bone remodeling, low cortical bone mass for age, poor bone quality and fragility fracture.

In this study we present preliminary results on bone remodeling with measurements of rib cortical bone microstructure (histomorphometry) in both adults and juveniles, and loss of metacarpal cortical bone (radiogrammetry) in relation to age. In addition, we assess changes in bone quality and fragility through the examination of vertebral trabecular bone microarchitecture and long bone fracture patterns.

### **Çatalhöyük skeletal sample**

Çatalhöyük in central Turkey is an early settlement dated to 7400-6000 cal BC (Cessford 2005a, Hodder 2006a,b). This site was densely occupied with an estimated 3500 to 8000 people in an area measuring approximately 13.5 ha (Hodder 2007). The Neolithic East mound is approximately 21 m high with eighteen levels of occupation spanning 1400 years of occupation. Each level contains the remains of tightly packed individual mud brick houses (Cessford 2005a) with the house seen as the center of life and production (Hodder 2006a,b). The Neolithic economy of Çatalhöyük was based on a wide range of wild and domesticated plants (Fairbairn et al. 2005, Hastorf 2005) and animals (Russell and Martin 2005). The diet of Çatalhöyük inhabitants was highly variable, comprised of both plant and animal protein with wild plants an important element of daily and seasonal diets (Richards et al. 2003). Atalay and Hastorf (2006) further argue that the Çatalhöyük diet relied on a relatively stable array of food resources across seasons and over the lifespan of the site. In addition, the procurement and production of wild and domesticated food stuffs lead the people of Çatalhöyük to travel to the uplands and mountains surrounding the site (Atalay and Hastorf 2006). Current paleo-environmental reconstructions (Asouti 2005; Rosen 2005) and biomechanical

studies (Ruff et al. 2006) all suggest relatively high mobility. While this provides indirect evidence of relatively good skeletal health, previous paleopathology studies (Angel 1971, Molleson et al. 2005, Boz 2005), cite limited skeletal and dental evidence of periodic metabolic stress in juveniles which also speaks to a lifestyle and activities that promotes good bone health.

Burials at Çatalhöyük have been primarily inside houses beneath plastered floors although some remains have been recovered from external spaces. Funerary practices show a preference for adults to be placed in flexed position in oval pits dug below clay covered platforms that are found in the central living space of a house. Juvenile burials are more variable occurring in a variety of contexts and locations (Boz et al. 2006). Some graves contain the remains of stone, shell or animal bone artifacts and pigments. Most burials are primary but were disturbed by later internments or human activity. Human burials included in this analysis span levels IV to VIII with the majority recovered from levels VI through VII which are thought to correspond with peak occupation size and density around the middle of the seventh millennium BC (Fairbairn et al. 2005, Cessford 2005b). Biological sex of the individuals was determined on the basis of scores and weighting of a variety of morphological indicators. Morphological features of the skull and jaw (including: supraorbital ridge, glabella, mastoid process, nuchal line, external occipital protuberance, ramus, gonial angle, mental eminence) were evaluated on a five point scale after White and Folkens (2005) and Buikstra and Ubelaker (1994). Features of the hip (ventral arc, subpubic concavity, ischiopubic ramus) were scored as either absent or present (Phenice 1969) with the exception of the sciatic notch which was also scored on a five point scale (Buikstra and Ubelaker, 1994). Age related changes to the hip

(including pubic symphyseal surface and auricular surface) were evaluated according to Brooks and Suchey (1990) and Lovejoy et al. (1985) as well as dental attrition after Smith (1984). Adults were placed into three broad age categories: young adult (YA) individuals approximately 20-29 years of age, mature adult (MA) individuals around 30-49 years of age, and old adult (OA) those individuals roughly 50 years of age or older (Table 1). These age cohorts are correlated with changing patterns of bone maintenance typically observed in modern human populations, and provide a baseline from which to assess age and sex-related patterns of bone loss in the Çatalhöyük remains. The youngest age cohort likely captures the period of peak bone mass (the maximal bone mass/density that is accrued by the end of skeletal maturation), the middle age cohort captures pre-menopausal females, and the old age cohort captures both elderly females and males experiencing the onset of accelerated cortical bone loss associated with combined ageing and loss of sex steroids (Riggs et al. 2008). For both sex determination and age-at-death estimates all available indicators for each individual were verified by both authors and compared against the Çatalhöyük human remains database comprised of estimates made by multiple trained researchers on site.

### **Age and sex related patterns of cortical bone loss**

Age and sex-related patterns of bone loss in adults have been examined in metacarpal (also see Glencross and Agarwal 2011) and rib cortical bone. All statistical analyses were conducted at the  $p=0.05$  significance level using the statistical software package SPSS 15.0

## **Metacarpal radiogrammetry**

X-rays of 49 adult metacarpals were collected that include 27 females and 22 males, and grouped into the 3 broad age groups (see Table 1). To empirically assess bone loss, measurements of total bone width (TW) (reflective of gross size) and medullary width (MW) (which reflects the extent of bone loss by endosteal resorption) were taken with electronic calipers using the methodology of Dequeker (1976), Mema and Mema (1987) and Mays (1996). These parameters were then used to calculate cortical thickness (CT) or the net amount of cortical bone carried, and cortical index (CI) a standardized comparator according to Dequeker (1976), Mays (1996, 2000, 2001) and Ives and Brickley (2004):

$$CT = TW - MW$$

$$CI = (TW - MW)/TW \times 100$$

The Student *t*-test was used to test whether bone size and bone loss differed between paired right and left metacarpals in a small control sample also, whether bone size and bone loss differed between males and females, age cohorts, individuals from North and South areas of the site, as well as individuals from Building 1 and other identified houses.

To test for differences between left and right metacarpals, a sub-sample of eleven paired second metacarpals was selected from the total sample. Means of all the measured variables show slight differences between the eleven pairs with the right metacarpals consistently larger than the left. The exceptions to the latter are cortical thickness and cortical index for which the left metacarpals are larger than the right.

However, none of the differences are statistically significant indicating that the selection of left or right metacarpals will not influence subsequent results (Table 2). In order to test the effect of sex on metacarpal measurements, particularly in relation to size, length and total width were tested for differences between males and females. Means of length and total width are not significantly different between males and females. The mean of medullary width is larger in females while means of cortical thickness and cortical index are larger in males although none are significantly different.

Figure 1 and figure 2 show results for cortical index plotted against medullary width thus allowing visual assessment of bone loss trends with age in males and females separately. Both males and females demonstrate an inverse relationship with decreasing cortical index and increasing medullary width with overlap between the three age cohorts. Means for the young adult female variables and old adult male variables were not subject to further testing due to their small sample sizes. Table 2 shows the mean values for medullary width, cortical thickness and cortical index when stratified by the remaining age cohorts and sex. There are no significant differences between the means for any of the measured variables in young adult and mature adult males and similarly in mature adult males and females. There are significant differences between the means for medullary width and cortical index for mature adult and old adult females.

Table 2 also shows the mean values for medullary width, cortical thickness and cortical index when individuals are grouped on the basis of burial location including, South and North areas of the site, and Building 1 and other identified houses. There are



no significant differences between the means for any of the measured variables for the South and North areas of the site or for Building 1 compared to other identified houses.

A general pattern of age-related bone loss is known for modern and historic populations (Garn 1972, 1992, Mays 2000, 2001, 2006, Riggs et al. 2004, Szulc et al. 2006, Lauretani et al. 2008). Sex specific patterns of bone maintenance and loss are also well documented in modern and historic populations where males and females are affected by differential amounts of bone apposition and endosteal loss over the life course. Females lose more endosteal bone particularly during pregnancy and lactation, and menopause leading to lesser amounts of compact bone (see for example Garn 1972, 1992, Lazenby 1990, 2002, Parfitt 2003, Riggs et al. 2004, Szulc et al. 2006, Lauretani et al. 2008). The patterns of cortical bone loss in the metacarpals are similar, and suggest significant bone loss by endosteal resorption in those over 50 years of age, particularly females leading to reduced amounts of compact bone in the hands.

### **Cross-sectional geometry of the rib**

Analyses of cortical bone loss in the rib were made from examining patterns of cross sectional geometry (% cortical bone), in a total of 57 adults (f=32, m= 25) and 61 juveniles. Macroscopic changes in cross sectional area were observed from the midshaft of a mid-thoracic rib (preferably left, 6-8<sup>th</sup> rib if available) from both juvenile and adult individuals using 1cm thick sections removed using a Buehler Isomet 1000™ precision saw. Sections were processed for ongoing histomorphometric analyses with embedding in Buehler's Epothin® resin and the production of thin sections approximately 70-100

microns using A Buehler PetroThin™ thin sectioning system. Macroscopic analysis was conducted using a Leica MZ6® dissection upright microscope, using plain light at a magnification factor of x0.8 and an eyepiece magnification of x10. Static images were first captured using a QImaging MicroPublisher 5.0 RTV® digital camera and analysed using the Bioquant® software system, and then measured for total bone area and cortical area. The cortical index (CI), representing percent cortical bone of total area, was calculated by creating a formula in which cortical area is subtracted from the total area and then multiplied by 100

$$\text{CI ( \% cortical bone)} = (\text{total area} - \text{cortical area}) \times 100$$

### Adults

Both males and females show no statistically significant difference in % cortical bone between the three age groups (Fig. 3). However, different trends of age-related change between the sexes are observed. Females tend to lose bone in middle age and then stabilize bone maintenance with no significant loss of bone in the oldest age group, while males tend to lose bone later in life, most apparent in the oldest age category. No significant differences are observed between the sexes in % cortical bone with ages pooled. When sex differences are contrasted at each age group, statistically significant differences are seen in the middle age group, with males showing a significantly higher cortical index (see Table 3). Interestingly, both males and females have similar cortical indices in the oldest age group (see Table 3). Burial location,

specifically in regards to North and South areas of the site was also explored. No significant differences for age or sex are indicated for burial location.

These results differ from the patterns of adult age-related loss in cortical bone in the metacarpal. Cortical bone remodeling in the rib likely reflects overall metabolic activity and is less likely influenced by mechanical activity than the metacarpal. Observed bone loss in young age females is not usual in archaeological populations, and could reflect transient bone loss accompanying pregnancy and/or breastfeeding that would be recovered after weaning (Agarwal 2008). In comparison to modern populations, it is unusual that old age males and females would show similar % cortical bone.

### Juveniles

Growth of the subadult rib shows clear and expected patterns of increasing cortical width and overall size with age, with statistically significant differences in growth between each age group (see Figures 4 & 5). When the cortical index is examined for age-related change, a more variable pattern emerges (see Fig 6). The cortical index starts off high in neonates, drops in infants, rises again in children and finally drops off slightly again in adolescence. Two statistically significant differences across age cohorts in subadults are noted for cortical index. Significant changes occurred between infants and children and between children and adolescents (see Table 3). These trends are likely the result of modeling, where % cortical bone is seen as shifting up and down because periosteal expansion and endosteal resorption act to increase overall size during growth, but not always at exactly the same pace. For example, endosteal

deposition in children is outpacing total bone area growth (periosteal deposition) and so the % value of bone increases at that age.

### **Growth and aging in trabecular architecture**

Development and aging of trabecular bone microstructure in the vertebrae are also being examined. Parameters related to trabecular microstructure and connectivity have been examined using a high resolution pQCT (XtremeCT, Scanco Medical AG, Bassersdorf, Switzerland), in the midbody of 4<sup>th</sup> lumbar vertebrae. From this several parameters are obtained that relate to the trabecular structure (ie. trabecular volume BV/TV) and connectivity of the bone (ie. connectivity density Conn.D). Currently, sample size is too small to permit detailed analyses but preliminary results suggest a similar age-related pattern of change as seen in modern populations, with a loss of both trabecular structure and connectivity between middle (30-49yrs) and old age groups (49+ yrs) (see Fig. 7). However, there appears to be no significant difference in trabecular bone loss between the sexes, although further study with a larger sample size is necessary.

### **Bone loss and fragility**

Fragility fractures are the result of underlying disease that adversely affects bone maintenance, quantity and/or quality weakening the skeleton and making it more vulnerable to injury. Nutritional deficiencies and lifestyle factors that cause disturbances in bone metabolism are extremely important to our understanding of fracture patterns. Bioarchaeological studies have frequently recognized the impact of diet and lifestyle

contributing to specific metabolic disorders in past peoples (see for example Agarwal and Glencross 2010, Brickley et al. 2007, Brickley and Ives 2006, Mays 2006, Ortner et al. 1999, 2001, Stuart-Macadam 1988, 1989). Because bone mass is highly correlated with bone strength and has been shown to predict fracture risk in clinical research (Melton, 2005) we have combined observations of bone loss with the direct examination of bone fracture.

While there is currently no direct evidence from the metacarpals or ribs for widespread metabolic stress in the community at large, two individuals show low cortical bone for their age and evidence of fractures. The first, skeleton #3368, a young adult male has significantly lower metacarpal cortical bone in relation to the mean for young adults as well as showing multiple rib fractures. This individual was buried in an external midden or waste area (South area, Level South L, Early period) and has previously been described by Molleson et al. (1998) as suffering from a chronic systemic disorder, mainly affecting the thoracic skeleton. The affected bones are swollen and spongy and many of the ribs show varying states of fracture healing. The second, skeleton # 8113, a young adult of unknown sex also has significantly low metacarpal cortical bone and fractures. This individual was recovered from under a sleeping platform (Bach, Building 3, Level Bach G, Middle period). The spine shows spondylolysis and a healed fracture of the neural arch of the fifth lumbar vertebra, as well as healed fractures of the lower limb bones. In both instances, the metacarpals from these individuals have larger medullary cavities with thinner cortical bone and lower cortical indices suggestive of excessive endosteal resorption in the metacarpal. The fractures provide a second line of evidence suggestive of underlying metabolic disorders in these two individuals.

The prevalence and risk of bone fracture also speak indirectly about bone fragility and provide insights on bone maintenance and bone strength. To this end a study of 119 complete adult long bones were examined for fracture with a total of four fractures observed. Depending on the denominator used prevalence of long bone fracture at Çatalhöyük ranges from 34 to 16 per 1000 long bones, and 2 per 1000 person-years. Rates based on years of exposure are lower than have previously been reported for modern non-human primates, other archaeological populations and clinical studies (Glencross et al. 2007). The odds of long bone fracture for females are slightly greater than for males but, the difference is not significant demonstrating that neither sex was at greater risk of long bone fracture. The likelihood of seeing only one or two fractures in a sample of a given size allows inferences as to whether prevalence is low or high. Assuming a 50% chance of fracture the expected probability for seeing femur, ulna or fibula fractures is extremely low ( $p = 0.0005$ ) at Çatalhöyük. The inferred probability of an individual sustaining one or more long bone fractures over their lifetime also supplies information on whether injury rates are low. The estimated probability of sustaining one long bone fracture in an individual's lifetime at Çatalhöyük is roughly one in four (probability estimate 28%). Modern clinical studies report lifetime risk of sustaining a traumatic fracture to the age of fifty as one in two, double the amount reported for Çatalhöyük.

## **Summary**

Bone quantity and quality of the human skeleton is the cumulative product of health, diet and nutrition, and physical activity and lifestyle over the life course. Further,

while nutrition plays a key role in skeletal growth and maintenance during all developmental stages, diet and nutrition are intricately woven with other biological, social, and cultural influences on the skeleton. Bone tissue is a dynamic medium that is capable of recording many life history events, allowing us to reconstruct some of the key influences on bone loss and fragility in past populations. Although our current understanding of cortical bone loss at Çatalhöyük is preliminary, the results from our study do provide insight on health status at different life stages for the Middle period or peak occupation of the mound. Growth as evidence in rib size and cortical width increases significantly in juveniles and fluctuations in cortical index reflect normal changes in the pace of growth.

Adult cortical bone loss measured in ribs and metacarpals shows some of the expected age-related patterns but also provide evidence of some unique patterns. Cortical bone loss in the metacarpals suggest significant bone loss by endosteal resorption in those over 50 years of age, particularly females leading to reduced amounts of compact bone in the hands. This sex specific pattern of bone maintenance and loss with age is well documented in modern and historic populations. In contrast, the unusual bone loss witnessed in the ribs of young age females perhaps reflects transient bone loss accompanying pregnancy and/or breastfeeding. Also of note, is the similar % cortical bone in old age males and females that is quite different from modern populations, and could reflect the influence of gender roles and lifestyle on life-long bone metabolism that likely differed from modern populations.

Finally bone fractures are often the result of underlying disease that adversely affects bone maintenance, quantity and/or quality. Poor bone metabolism at a young age

is apparent in two individuals with low metacarpal cortical indices and that show bone fractures. Controlled analyses of long bone fractures also demonstrate that risk of infra-cranial skeletal injury at Çatalhöyük appears to be relatively low in the population.



**Table 1.** Çatalhöyük radiogrammetry sample distribution by age-at-death and sex (n = 49).

	<b>Young Adult</b>	<b>Mature Adult</b>	<b>Old Adult</b>
	<b>20-29 years</b>	<b>30-49 years</b>	<b>50+ years</b>
<b>Males</b>	7	12	3
<b>Females</b>	2	15	10

**Table 2.** Student's *t*-tests of Çatalhöyük radiogrammetric data.

Test	Variable	Mean (mm)		df	Result	<i>p</i>	Implications
		Left	Right				
Left & Right Sides	MW	4.02	4.39	20	0.740	0.468	MW greater in right metacarpals
	CT	4.66	4.60	20	0.168	0.868	CT greater in left metacarpals
	CI	54.02	51.65	20	0.545	0.592	CI greater in left metacarpals
Females & Males		<b>Female</b>	<b>Male</b>				
	L	67.67	66.24	26	0.811	0.425	L greater in females
	TW	8.26	8.33	37	0.263	0.796	TW greater in females
	MW	4.16	3.78	37	1.290	0.205	MW greater in females
	CT	4.10	4.56	37	1.666	0.103	CT greater in males
	CI	49.62	54.92	37	1.788	0.082	CI greater in males
YA & MA Males		<b>YA</b>	<b>MA</b>				
	MW	3.34	3.76	15	0.912	0.377	MW greater in MA males
	CT	4.49	4.83	15	0.915	0.377	CT greater in MA males
	CI	57.48	56.48	15	0.340	0.745	CI greater in YA males
MA Females & Males		<b>Female</b>	<b>Male</b>				
	MW	3.90	3.76	15	0.430	0.686	MW greater in females
	CT	4.33	4.83	19	1.500	0.150	CT greater in males
	CI	52.43	56.48	19	1.160	0.260	CI greater in males
MA & OA Females		<b>MA</b>	<b>OA</b>				
	MW	3.90	4.65	16	*2.157	0.046	MW significantly greater in OA females
	CT	4.33	3.66	16	1.757	0.098	CT significantly greater in MA females
	CI	52.43	44.02	16	*2.257	0.038	CI significantly greater in MA females
South & North		<b>South</b>	<b>North</b>				
	MW	3.78	4.06	21	0.614	0.548	MW greater in north
	CT	4.43	3.98	21	1.105	0.284	CT greater in south
	CI	54.19	49.38	21	1.013	0.324	CI greater in south
House 1 & Others		<b>House 1</b>	<b>Others</b>				
	MW	4.06	3.95	24	0.257	0.797	MW greater in house 1
	CT	3.98	4.43	24	1.100	0.282	CT greater in other houses
	CI	49.38	52.99	24	0.789	0.437	CI greater in other houses

YA (young adult), MA (middle adult), OA (Old adult).

L (length), TW (total width), MW (medullary width), CT (cortical thickness), CI (cortical index).

\*Significant test result measured at 0.05 level.

**Table 3.** Tests of rib cross-sectional geometry.

<b>Age Cohorts</b>	<b>Coded Age Group</b>	<b>N</b>	<b>% Cortical Mean</b>	<b>SE</b>	<b><i>p</i> &lt; 0.05</b>
Neonate (0-6months)	0	15	54.19	3.47	N.S
Infant (6months-3)	1	19	47.15	2.05	1 vs. 2
Child (4-12)	2	19	56.64	2.12	2 vs. 3
Adolescent (13-19)	3	8	53.02	2.85	N.S
F - Young (20-29)	4	4	45.08	2.93	N.S
F - Middle (30-49)	5	19	39.01	2.23	F-5 vs. M-5
F- Old (50+)	6	9	43.78	1.93	N.S
M - Young (20-29)	4	7	48.26	5.50	N.S
M - Middle (30-49)	5	13	48.76	2.32	M-5 vs. F-5
M- Old (50+)	6	5	41.70	3.63	N.S

N.S - not significant.

**Table 4.** Cortical bone loss and fragility fracture.

<b>Skeleton</b>	<b>Age</b>	<b>Sex</b>	<b>CI</b>	<b>Z-score</b>	<b>Fractures</b>
3368	YA	M	42.1	-4.36*	Multiple ribs.
8113	YA	?	45.4	-3.52*	Fibula, tibia(?), lumbar vertebra.

CI (cortical index), YA (young adults 20 - 29 years), MA (mature adults 30 - 49 years), OA (old adult 50+ years), M (male), F (female).

\* Significant result.

**CI %**

**MW in mm**

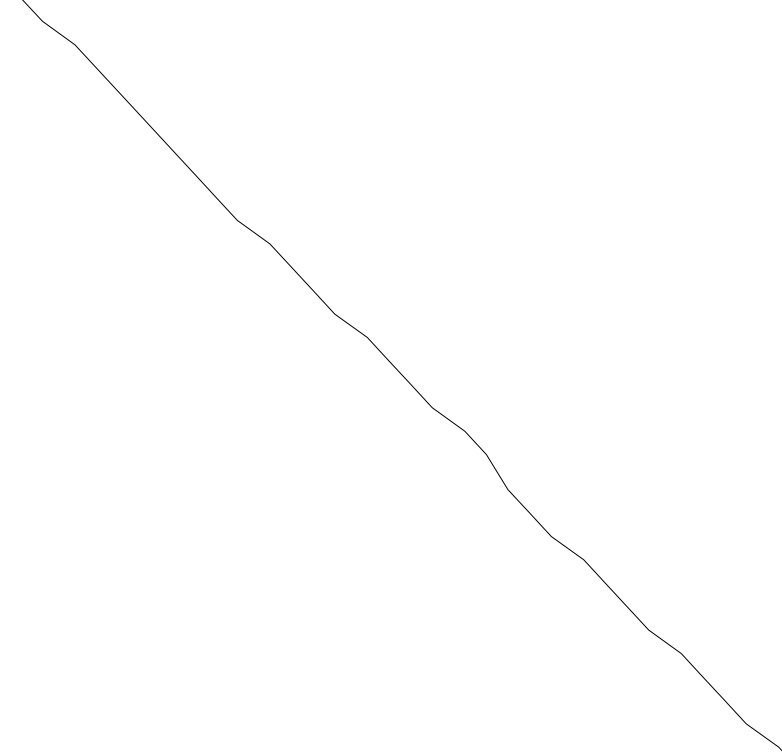
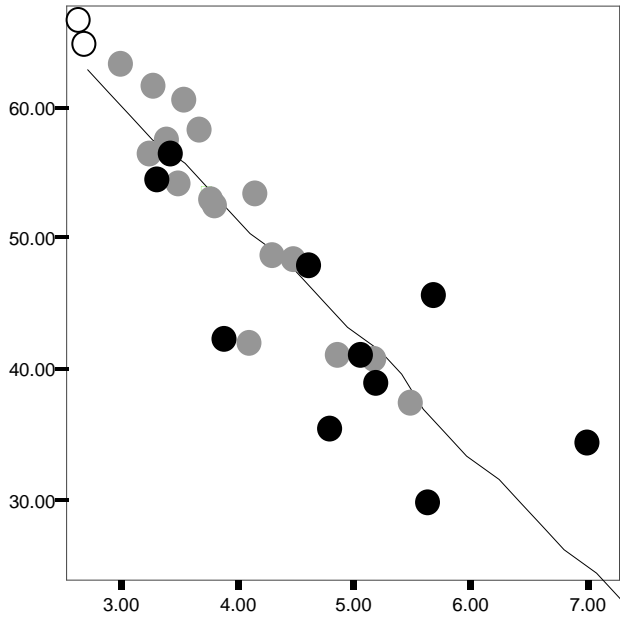


Figure 1: Female trends in cortical index and medullary width with age. White (young adult 20-29 yrs), Grey (middle adult 30-49 yrs), Black (old adult 50+yrs).

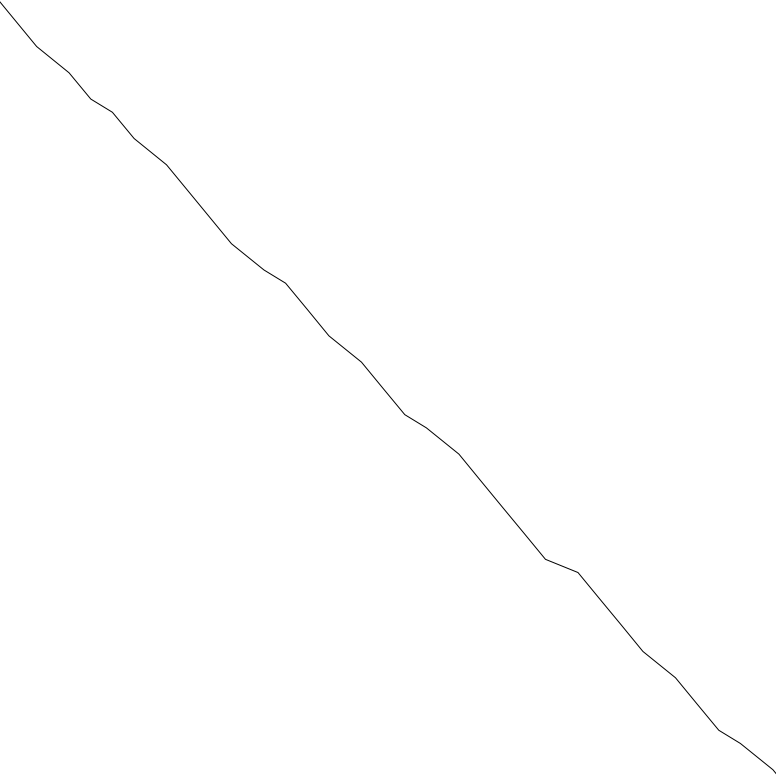
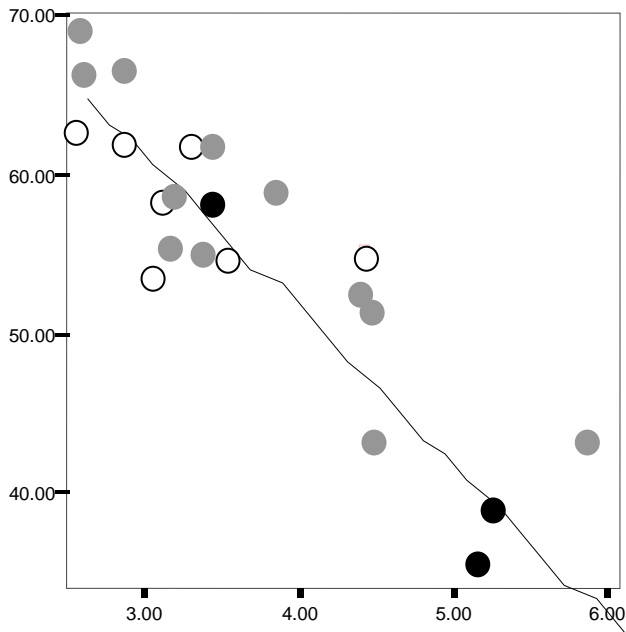


Figure 2: Male trends in cortical index and medullary width with age. White (young adult 20-29 yrs), Grey (middle adult 30-49 yrs), Black (old adult 50+yrs).

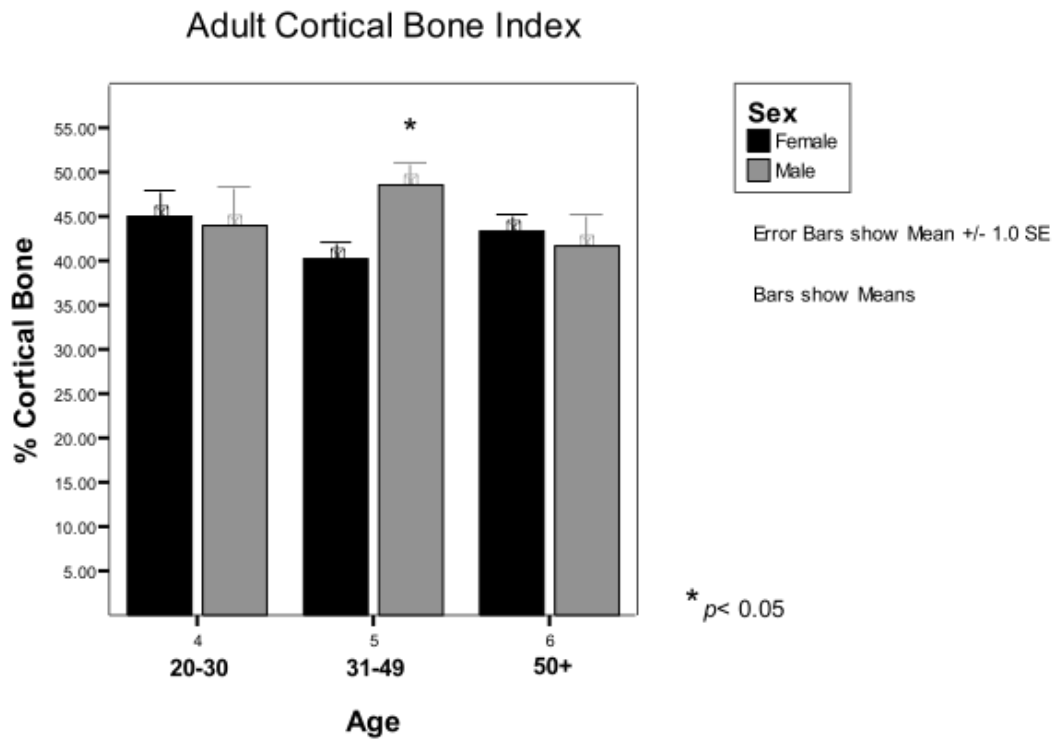
CI %

MW in mm



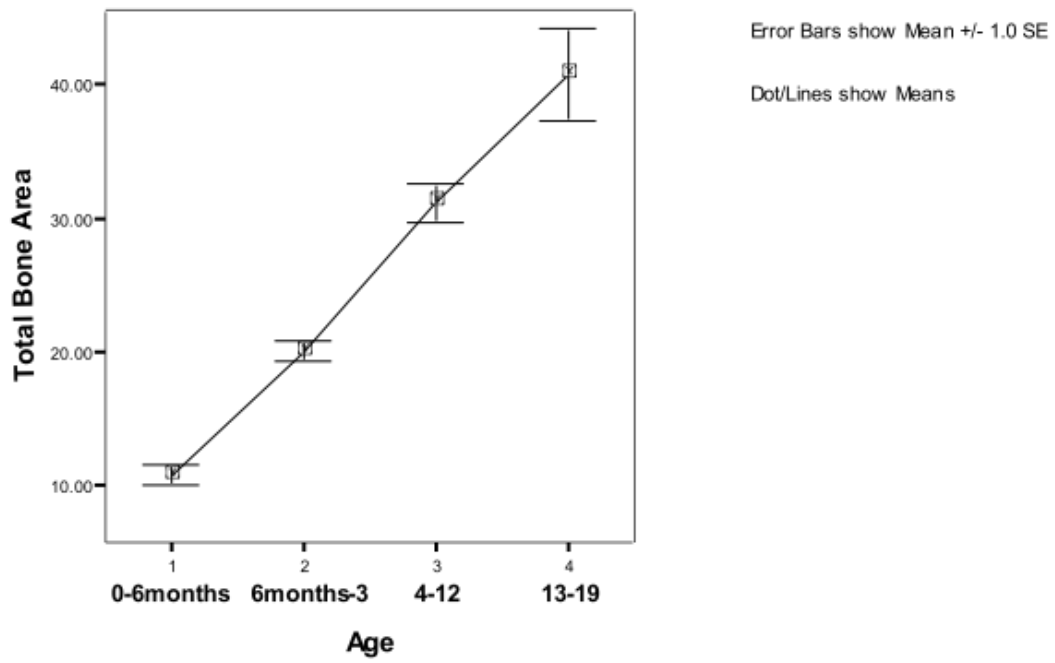
**Figure 3.** Male and female mean values of % cortical bone in three age groups.





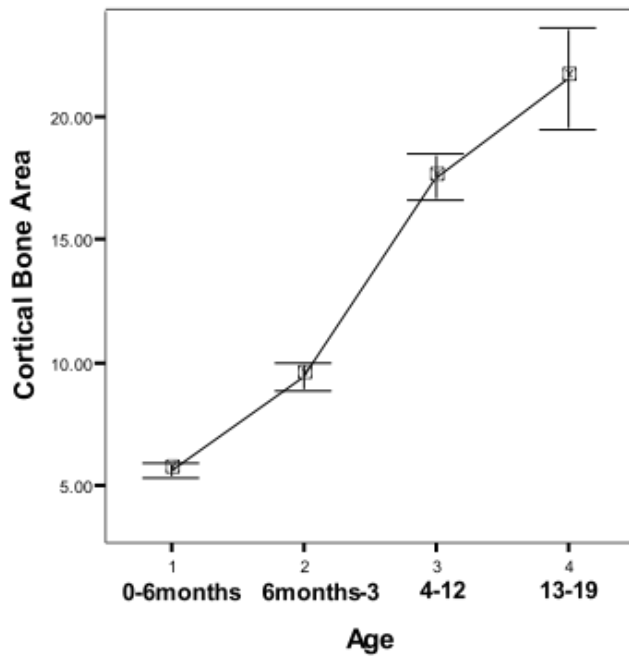
**Figure 4.** Subadult mean values of total cross sectional area in four age groups.

### Subadult Total Cross Sectional Area



**Figure 5.** Subadult mean values of total cortical bone area in four age groups.

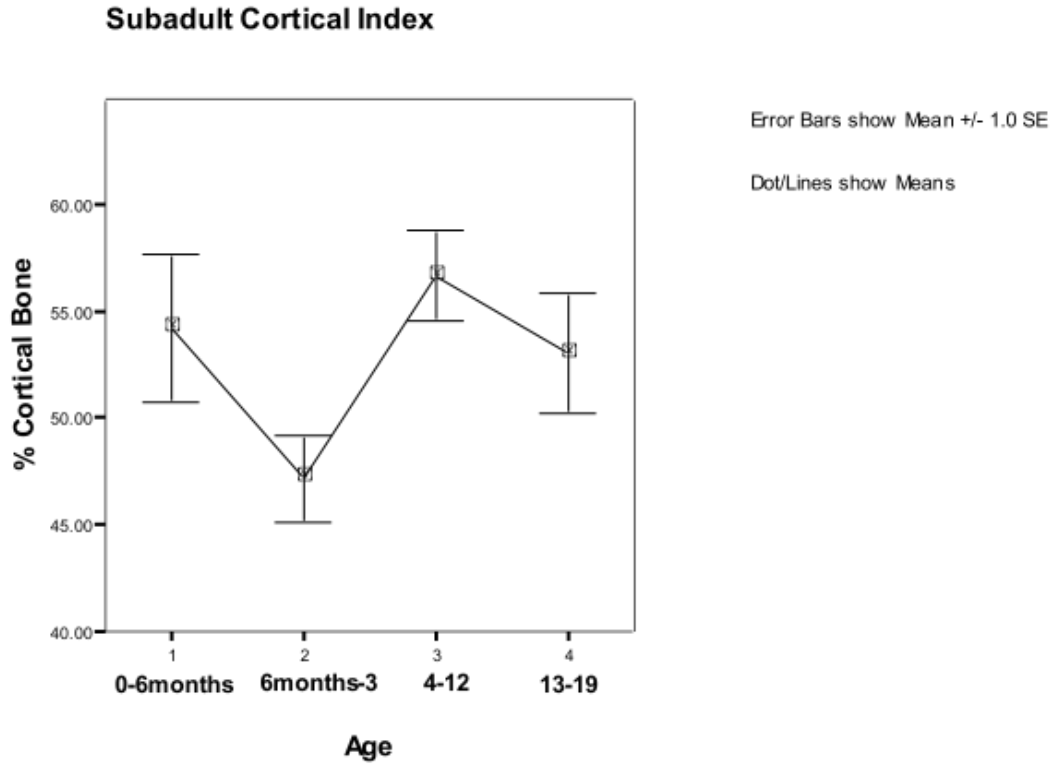
### Subadult Total Cortical Bone Area



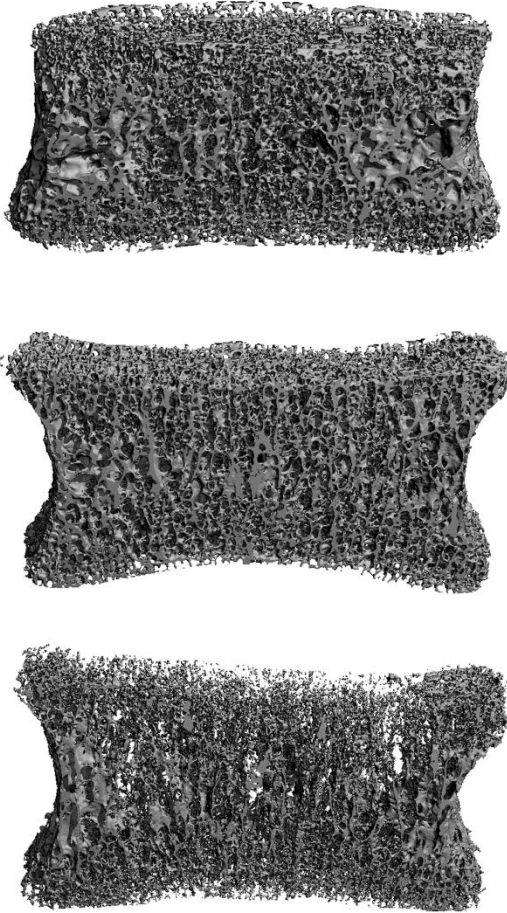
Error Bars show Mean +/- 1.0 SE

Dot/Lines show Means

**Figure 6.** Subadult mean values of cortical index in four age groups.



**Figure 7.** High resolution pQCT images of age-related changes in trabecular architecture in fourth lumbar vertebrae. 3D Images surface rendered images of the segmented trabecular bone of multiple coronal slices at full resolution (3072x3072, 41µm pixel). Top, juvenile individual showing high number of uniform plate-like trabeculae; middle, adult individual showing the typical zonal and anisotropic organization with densely packed trabeculae horizontally and vertically oriented in the superior and inferior region; bottom, mature adult individual showing significant age-related thinning and loss of plate-like trabecular elements. Adapted from Agarwal and Glencross 2010.



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