4-21-2010

Human Cranial Growth and Shape Change: Are Fetal Rates and Morphologies Extended Throughout the First Year of Life?

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HUMAN CRANIAL GROWTH AND SHAPE CHANGE: ARE FETAL RATES AND

MORPHOLOGIES EXTENDED THOUGHOUT THE FIRST YEAR OF LIFE?

by

DANA J. RUSSELL

Under the Direction of Frank L'Engle Williams

ABSTRACT

Selection for increased encephalization in humans necessitated extensive brain growth after birth. To estimate changes in rates of growth and corresponding shape changes during gestation and infancy, chord and arc distances were obtained from the frontal, parietal, and occipital bones of 44 human fetuses, neonates, and infants (one year old and younger). Rates of growth in chord and arc measurements were calculated and compared using linear regression of log-transformed variables, followed by ANCOVA. Curvature of bone lengths and widths were estimated by chord/arc indices. Fetal rates of cranial growth were significantly slower while the fetal frontal and occipital bones were significantly more curved than those of infants. Fetal rates of cranial growth decrease during the first six postnatal months, in conjunction with rapid changes in shape, except for parietal superior-inferior height where bossing of the bone is similar in fetuses and neonates.

INDEX WORDS: Brain, Cranium, Encephalization, Fetal, Growth and development, Human, Infant, Prenatal, Postnatal, Rate of growth, Shape change

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A Thesis Submitted in Partial Fulfillment of the Requirements for the Degree of

Masters of Arts

in the College of Arts and Sciences

Georgia State University

2010

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May 2010

DEDICATION

To all those who encouraged me to never give up.

ACKNOWLEDGEMENTS

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Chapter I: Introduction

Through approximately two million years of evolution, selection has produced larger cranial capacity in the genus *Homo*. The increasing size of the hominid brain may have been selected for by a number of factors. Determinants may have included environmental and/or climatic changes encountered by early species of *Homo*, the need for improved social behaviors due to population increases necessitating closer proximity of others, or possibly increased competition with other hominid species for scarce resources (Bogin, 1999; Ponce de León, et al., 2008; Rosenberg, 1992; Wortham and Kuzara, 2005).

During ontogeny there must be sufficient increase in the volume of brain tissue before maturation to allow for either of these three theories to accurately explain the evolution of our large brain. The increase in volume of our brain begins, as does all human growth, during the early stages gestation. But there are limitations as to the degree of growth the brain can achieve before a fetus can no longer be born due to its large size. These restrictions originate more from the dimensions of the female pelvis than from the fetus itself. First and foremost the fetus is constrained by the diameter and shape of the pelvic inlet and outlet as it relates to the path the fetus must take to be born.

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If the pelvic dimensions were to increase further to allow for the passage of a larger fetus, the center of gravity would have to have shifted such that our ancestors would no longer have been able to sustain the upright posture necessary for efficient bipedalism (Ponce de León, et al., 2008; Rosenberg, 1992; Wortham and Kuzara, 2005). Therefore, an increase in fetal cranial volume prior to birth may have offset the progression of obligate bipedality. So how does the rate of brain growth before birth

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compare to the rate observed after birth? And, does the degree of curvature for each of the individual cranial bones follow the same growth trajectories seen in overall size?

Brain growth *in utero* beyond 8.5 months complicated the successful passage of a fetus during the birthing process. It is at approximately this point in gestational development, that the fetus reaches the upper limits in size and cranial capacity that can successfully pass through the pelvic outlet of a female during delivery (Berge, 1998; De Silva, et al., 2008; Jordaan, 1976; Ponce de León, et al., 2008; Rosenberg, 1992; Steer, 2006; Whitcome, et al., 2007). Nevertheless, without further extension of cranial volume beyond gestation, the large adult brain size could not be attained. This necessitated the need for continued rates of growth extending after an efficacious delivery (Alba, 2002; De Silva, et al., 2008; Hawkes, 2006a; McNamara, 2002a; Ponce de León, et al., 2008). The continuation of fetal rates of encephalization beyond birth was the evolutionary compromise that emerged. This accommodation suggests that selection for increased brain size had to also effect selection for an extension of the rates seen in the fetal brain. Thus, allowing the efficiency of bipedalism to remain uncompromised by an increasingly larger pelvis.

It can be noted that the human brain grows significantly after birth, whereas in nonhuman primates, brain growth is more rapid during gestation (Alba, 2002; Diewert, 2985; Gould, 1977; Hawkes, 2006a). The cranial capacity of an average human neonate is approximately 25% of adult size, by the end of the first year approximately 50%, and by the fifth year it is estimated that the brain has reached 90% capacity (Coqueugnoit, et al., 2004; Farkas, et al., 1992; McNamara, 2002a; Robson, et al.,

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2006). Because the rate of growth is perceived to be so rapid after birth, at least in the first year, it has been suggested that fetal rates are carried over to attain the large adult size evolution has selected for (Coqueugnoit, et al., 2004; De Silva, et al., 2008; McNamara, 2002a; Thompson, et al., 2003; Vinicius, 2005).

To study the increase of size and degree of curvature in the brain of the fetus and early infant, I have examined bones of the cranial vault of 133 fetuses and infants of spontaneous abortion and natural death as collected by Aleš Hrdlička and housed at the National Museum of Natural History at the Smithsonian Institute. Specifically, the frontal, parietal, and occipital were examined. It has been shown that there is a direct correlation between the brain and skull such that measures of one can be used as a proxy for the other. Therefore, by collecting the measurements of size and curvature for the vault bones, a reasonable expectation can be interpreted for the early growth of the human brain.

Most of the individuals were collected from public hospitals and clinics in Washington, D.C. and the surrounding areas, although a few came from a colleague of Hrdlička's in Germany. The collection dates from approximately 1900 to 1925 and most are in an excellent stage of preservation. Limited information on identification for either the individuals or their families is available, including specifics on social and economic status of the families. With the limited information of the individuals in this collection, one possible area for bias of data collected could be based on nutritional differences and variations in degrees of health stressors. Therefore, future research may focus more on populations with known socioeconomic status and health histories.

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Another bias faced when collecting data based on this collection is that of the osteological paradox. Many physical anthropologists face confounding factors when studying any set of skeletal remains, but even with the limited information available for this collection, possible issues regarding these individuals are satisfied. The most confounding factor noted in Wright and Yoder (2003) is that of sex determination of skeletal remains within a population. Individuals within this collection that were used in this study were assigned a biological sex determination at the time of death and therefore is not ambiguous. A second factor is accurate age determination. For each individual utilized, age was noted from autopsy cards and verified using growth charts established from living fetuses using sonography, as well as from skeletal collections. To address the third factor of individual mortality from illness or disease, all individuals with any diagnosed or visible signs of pathology were excluded from this study.

Data were collected on those individuals with the relevant cranial elements over a period of one week and statistically analyzed for rates of growth and increases in degrees of curvature. Each element was measured for chord in length and width from points described in the Fetal Forensic Osteology by Fazekas and Kósa (1978) with sliding calipers that were calibrated to 0.001mm accuracy 3 months prior to use. Curvature was determined in mm with a paper measuring tape along the same line of bisection as the chord measurements. Age in weeks for each individual was determined using long bone measurements as described in Developmental Juvenile Osteology by Scheuer and Black (2000) and age sets were   determined based on medical viability of the fetus and standard obstetric trimester weeks. All measurements

were input into PAWS Statistics v.18, also known as SPSS, for statistical analysis. Values for age noted in weeks and all measurements taken from the cranial elements were log transformed to align magnitudes for each stage of development to allow for linear regression. ANCOVA was preformed on all measurement values against age to assess rates of growth in the form of slopes for each age set, and allow for comparison between groups.

Individuals in both early and late stages of gestational development showed an increase in brain volume at a rate of growth that was expected, or a rate sometimes faster than expected. Measurements taken for specimens after 40 weeks gestation to the age of three months showed patterns of growth slower than those of the fetuses or at times with almost no increase of size based on age. In the development of curvature for the frontal and occipital, only in the those individuals at the ages 27-40 weeks gestation was expected growth achieved, and during the early to midpoint of gestation between 16 to 26 weeks and the young infant groups, did the amount of change in curvature slow and fall below the rate that would be expected based on an increase in age. This would indicating only minute changes in the degree of curvature for these bones.

These results suggest that the most rapid gains in both size and curvature of individual elements are attained during the final four months of gestation. Additionally, brain volume that is acquired after birth occurs at a slower rate. When viewed overall, brain and cranial development is at its maximum during the third trimester of pregnancy and these total rates do not carry over past birth.

Chapter 2: Theoretical Background

Part I: Examining Life Histories

Life histories are defined by Bogin (2003), Gould (1977), Whitcome, et al. (2007) and others as a set of adaptations and strategies with which an organism allocates energy towards growth, maintenance, reproduction (including the rearing of young), and the avoidance of death within a particular environment. Included within the theoretical frame of life history would be the timing of reproduction, birth, developmental stages of aging, and when to die. All species of mammals incorporate the basic stages of life history including gestation, infancy, juvenility, and adulthood in varying degrees of length (Bogin, 2006). It has been suggested that information on phylogenetic relationships can be determined when the timing and duration of life cycle stages are compared and contrasted between species (Bogin, 2006; Hawkes, 2006a; Leigh, 1992; Robson, et al., 2006; Schultz, 1969).

Gestation: The definition, as well as the length, of gestation is not always clear and can be dependent on the discipline and culture (Scheuer and Black, 2000). Standard agreement is that gestation is the term of life before birth, and medically determined to last approximately 280 days. This stage is further broken into several developmental stages, usually based on viability of the fetus, and includes the the initial perinatal period. Specifically, this is termed the perinatal stage and includes the time between 24 weeks post fertilization to the seventh postnatal day (Fazekas and Kósa, 1978; Scheuer and Black, 2000).

Gestation is the first stage at which humans and their closest phylogenetic cousins begin to differ. When gestation is compared between the two groups, duration of intrauterine growth and development, defined as the length of time from fertilization to parturition, is ten to thirty days longer in the genus *Homo* than that of non-human primate relatives (Bogin, 1999; Robson, et al., 2006; Schultz, 1969). Although the duration of this stage would seem to impart a developmental advantage to humans, it would appear that this is not so, as discussed below.

Infancy: It has been assumed that after birth, great ape and human neonates appear to diverge in the degree of physiological development. Non-human primate infants seem to be more physically and neurologically mature when compared to human infants, which appear to be secondarily altricial (Bogin, 1999; Robson, et al., 2006, Schultz, 1969; Wortham and Kuzara, 2005). Robson, et al. (2006) states that there has been an assumption of great ape infants being born with a unique grasping reflex sufficient to allow them the ability to hang on to the parent for protection and transportation. This has been challenged as far back as 1969 by other researchers stating that human infants have grasping reflexes equal to those seen in apes. These studies suggest that human infants are born with and use equally complex survival strategies and that the perinates of all large apes are born near the same helpless and immature state (Robson, et al., 2006, Schultz, 1969; Wortham and Kuzara, 2005).

As development continues along species-specific patterns, infancy has been determined to have one of the largest discrepancies of duration when compared between human and their closest primate cousins, as originally defined by Schultz

(1969) and shown by Schultz (1969) and Bogin (1999). For non-human primates, the infancy period terminates at the time of weaning and coincides with the eruption of the first permanent molar, which is species specific. The nonhuman primate then moves on to the next life stage of development, juvenility, and consequently lacks a true life cycle stage of childhood (Bogin, 2006; Schultz, 1969).

In contrast, humans end infancy much earlier at a time that does not coincide with the eruption of the first molar (Bogin, 2006; Robson, et al., 2006; Schultz, 1969; Smith, 1991). Bogin (1999, 2006) states that infancy in the human primate ends at approximately three years of age, a time that still leaves the individual almost fully dependent on the older members of the community. This stage of development is characterized by a decline in the rate of growth lasting until childhood.

The relationship in the timing of weaning and M1 eruption has been shown as a disconnect when exploring life histories and the successful transition of the human infant from full, dependent nursing to the complete adult diet (Bogin, 1999, 2006; Hawkes, 2006a; Robson, et al., 2006; Smith, 1991). Ages for weaning were collected from modern hunter-gatherer populations, and it was determined that in these populations the weaning of infants occurs at an average age of 2.5 years, while the eruption of the first molar in the same populations occur at approximately 6.3 years (Bogin, 2006; Hawkes, 2006a).

This discrepancy between weaning and first permanent dentition eruption is termed childhood, one of two life stages seen only in the human primate (Bogin, 2006;

Hawkes, 2006a). Humans evolved the need for childhood as a period of slow physical growth that allows for continued dependence on parental support for development for social learning, nutritional support, and can be viewed as reproductively beneficial for all members of the community (Bogin, 2006; Hawkes, 2006b; Robson, et al., 2006; Thompson, et al., 2003). According to Bogin (1999, 2003), communities most benefit from a lengthy childhood by insuring offspring accumulate sufficient knowledge and skills to survive and reach reproductive age, thus increasing the population fitness.

Childhood/Juvenile: Following infancy in nonhuman primates is the life stage of juvenility, while in humans this period of development is divided into childhood followed by juvenility (Bogin, 2006; Schultz, 1969). This period begins at the end of infancy which is at the eruption of the first permanent molar for non-human primates and the third year of life in humans, and lasts until the beginning of puberty/adolescence (Bogin, 1999, 2006; Thompson, et al., 2003). The period of all primate juvenility has been described as one of extended slower growth to allow for increased size at maturation, environmental knowledge and understanding of social constructs (Hawkes, 2006a; Thompson, et al., 2003). In examining comparisons of the full juvenile period of human and nonhuman primates, this life stage is similar in both duration, with respect to life span, and goals during this time across species (Thompson, et al., 2003).

It should be noted, however, that for humans childhood is defined as a short phase of growth before juvenility, beginning at the end of infancy and ending at roughly the age of seven (Bogin, 1999, 2006). This period is followed then by juvenility from 7 years of age until the onset of puberty. For purposes of research, the stages of

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childhood and juvenility are combined when comparing across species since when condensed in the human species the two are similar in duration, goals, and timing as the single stage of non-human primates (Bogin, 1999, 2006; Schultz, 1969).

Puberty/Adolescence: Following the juvenile period is that of puberty and adolescence, during which sexual maturation is reached (Bogin, 2003, 2006; Thompson, et al., 2003). Puberty is seen in both human and nonhuman primates and is described as the activation of the HPG axis of the endocrine system and is usually a short term event, only lasting days in some species to as long as weeks in others. This influx of sex steroids initiates the life stage of adolescence. In this stage of life history, there is seen a rapid growth spurt and sexual maturation (Bogin, 2003, 2006). During this time, primary and secondary sexual characteristics develop in preparation for reproduction, as well as active learning of parenting techniques and practices from older members of the community (Bogin, 2003, 2006; Robson, et al., 2006). From onset to completion, adolescence lasts on average 8-9 years (Bogin, 2006).

Adulthood: This stage is marked by the cessation of an individual's growth, and begins the contribution of resources and reproductive maturity for the community and ends at the time death (Bogin, 2006). For human females, this life cycle stage is limited and can be separated into two sub-stages: that of childbearing and post-childbearing (Hawkes, 2006a; Robson, et al., 2006). In human populations, the ability to reproduce is reached during adolescence, but does not usually occur until the adult stage is reached (Bogin, 2006).

When the active reproductive stage of female humans and great apes are compared in duration, they last roughly the same length of time, 25-30 years (Robson, et al., 2006; Schultz, 1969). It is the period following that most distinguishes humans from the great apes. The human female has extended the life span after reproductive ability has ceased to include an additional 25-30 years (Schultz, 1969). In the great apes, individuals generally do not live past the ability to produce offspring. Although there have been rare instances where a female chimpanzee has lived into a post-childbearing stage of life in captivity, it is only for a relatively short time when compared to their reproductive period (Hawkes, 2006b). Thus, the post-childbearing period of the human female adult is seen as unique to our species and is viewed by some as an adaptation distinguishing humans from the great apes (Hawkes, 2006b; Robson, et al., 2006; Schultz, 1969).

Part II: Human vs Nonhuman Life Histories

In examining life histories of modern humans, researchers have consistently used the patterns of nonhuman primates as comparative models in hopes of determining the evolutionary process of human life histories and why they developed the length and complexities seen today (Bogin, 2006; Hawkes, 2006a; Leigh, 1992; Robson, et al., 2006). In making the associations between phylogenetic cousins, researchers have concluded that overall size and age at maturity has a positive correlation with the length of life stages experienced by all primates (Gould, 1977; Hawkes, 2006b; Robson, et al., 2006). Investigation has also demonstrated that the

increase in ancestral human adult brain size is closely related to the length of certain life history events and thus, the total life span (Hawkes, 2006b; McNamara, 2002b; Ponce de León, et al., 2008; Rice, 2002; Smith, 1991).

Differences noted between separate species have been used to postulate theories to explain human evolution (Bogin 2003; Ponce de León, et al., 2008; Smith, 1991). To understand the variations among primate families, and thus offer insights to individual evolutionary paths, one must first understand the life stages in primates: gestation, infancy, childhood, juvenility, adolescence, and adult-to-death (Bogin, 1999; Smith, 1991). These divisions of growth are tied to specific developmental events, such as dental eruption and fusion of skeletal elements (Bogin, 2006; Gould, 1977; Robson, et al., 2006; Thompson, et al., 2003). In humans, some life stages are thought to be hyper-extended when compared to other primates. Those determined to be most amplified and unique to humans are an extended childhood and post reproductivity for females and are seen as uniquely human (Bogin, 2006; Hawkes, 2006a; Robson, et al., 2006).

Part III: Life History Theory, Big Brains and the Genus *Homo*

There have been many who have tried to explain how and why humans developed such large brains compared to our body size. Both queries seem to revolve around one central explanation, the unique trajectory of human life history. All primates have life histories specifying the stages of growth and development unique to their species. Some stages are shared between all primate species; gestation, infancy,

juvenility, and adulthood (Gould, 1977; Schultz, 1960). What often marks each life cycle stage as unique is the duration of the stage within the totality of the life span. In examining the life histories of humans, conclusions can be drawn which highlight their evolution into the large-brained *Homo sapiens sapiens*.

As human ancestors began their evolutionary progression towards larger bodies, more complex interpersonal relationships, and more flexible behavior to negotiate and manipulate new environments and situations, the selection for a larger brain occurred (Aiello and Wheeler, 1995; Bogin, 1999; Wortham and Kuzara, 2005). The increase in rate of hominid encephalization began gradually (Leigh, 1992; Rice, 2002). The amount of energy needed to support these demands rose as the brain increased in volume and complexity (Aiello and Wheeler, 1995; McNamara, 2002a; McNamara, 2002b; Robson, et al., 2006; Wortham and Kuzara, 2005). Demands for dietary augmentation could be best met through one of two means: an increase in gut size to process more low nutrient-rich food already being consumed or new choices of higher quality foods processed in a smaller gut. A physiological selection was made for the latter (Aiello and Wheeler, 1995; McNamara, 2002a; McNamara, 2002b; Wortham and Kuzara, 2005).

Other physical demands were also placed upon the evolving hominids by encephalization. Physical limits on evolving hominids required adjustments of timing to achieve an ever increasing brain volume although physiologically, the amount of time required to produce a larger brain was limited to the length of time an individual grew, i.e., from conception to skeletal maturation. Perturbations in the growth patterns were selected for to increase the size of the neonate at delivery, while the evolution of

bipedalism placed unfavorable constraints on the size that the neonatal head could reach for parturition and avoid reducing the of stability of the pelvis (Berge, 1998; Gould, 1977; Jordaan, 1976; Rosenberg, 1992; Schultz, 1969; Whitcome, et al., 2007).

The changes in size of the female pelvis approached the point to where stability in locomotion collided with the need for success in producing viable neonates (Berge, 1998; De Silva, et al., 2008; Gould, 1977; Jordaan, 1976; Rosenberg, 1992; Schultz, 1969; Whitcome, et al., 2007). Hominid evolution allowed for delivery of fetuses developmentally premature, but physically larger, and allow for fetal rates of growth and development to continue past parturition for reproductive success (Alba, 2002; Hawkes, 2006a; McNamara, 2002a; Ponce de León, et al., 2008). Compared to other great apes, gestational length was slightly extended. This allowed more time for intrauterine brain growth, while shifting and adjusting some of the fetal development to occur after birth and the timing of other developmental stages of human life history were adjusted as well (Robson, et al., 2006; Schultz, 1969).

One life cycle stage that was extended to compensate for the prematurity of the newborn hominid was infancy (Alba, 2002; Hawkes, 2006a; Wortham and Kuzara, 2005). This allowed for continued brain and body growth beyond what pelvic restrictions allowed for successful birth. Not only was this life cycle stage extended, but childhood further increased the period of growth and lengthened the time available for individuals to acquire a sufficient knowledge base to become a productive member of the community and in turn successfully produce offspring (Hawkes, 2006a).

The increase in successful production of offspring with extended life cycle phases, thus expanded the life span of individuals within the species. As increases in development became consistent throughout the populations, a balance occurred in the hominid species, bringing the length of life cycle stages into equilibrium with the total life span (Turner, 2007). Continuing evolutionary advancement has thus led to the unique hominid life history derived from these complex changes in the developmental timing of brain and body growth (Bogin, 2003, 2006; Schultz, 1969; Vinicius, 2005).

Part IV: Humans and Neoteny

There are several developmental processes used in evolutionary theory to describe morphological changes over time. These processes are divided into two categories: paedomorphosis and peramorphosis. Paedomorphosis defined as the "retention of ancestral juvenile character or shapes by later ontogenetic stages of descendants", and peramophosis as "extension beyond the ancestral adult characters or shapes, i.e. repetition of ancestral adult stages in embryonic or juvenile stages of descendants" (Gould, 1977). Within each of these categories, there are three individual processes to describe underlying aspects of changes of size, shape, and age at maturation (Gould, 1977).

Gould (1977) demonstrated the concept of neoteny as the prolonging of juvenile size and shape into adulthood with the clock model. When humans and their extant predecessors are compared on the clock model, the result was somewhat different than

what might be expected. In pure neoteny, descendant adults are juvenilized versions of their ancestral adults, maturing at the same time with similar adult body sizes. Since humans are larger than ancestral forms from the Pliocene, the neoteny characterizing *Homo sapiens* shows an increase in the size of the descendant adult compared to the ancestral adult.

Schultz (1969), though, was first to remark upon the observation that human patterns of maturation are mere extensions of those seen in prosimians, anthropoids, and apes. More recent ancestors of humans, most notably *Homo erectus*, may have exhibited ape-like, intermediate, or fundamentally human patterns of maturation. With the evolution of large brain size in archaic *H. sapiens*, the extension of fetal rates of brain growth must have also occurred as implied by similar gestational lengths inferred for Neandertals and exhibited by modern humans.

Gould (1977) suggested that neoteny could account for a number of unique human traits, including the extended life histories of humans, the paedomorphic, or juvenilized, appearance of craniofacial traits as observed in adults, and extended periods of fetal brain tissue beyond parturition. The clinical literature suggests that rates of brain growth during last trimester are mimicked in the first three postnatal months. However, whether fetal rates of brain growth during gestation are maintained during the first year of life has never been adequately addressed.

Of interest to this research is neoteny in its pure form, as describe by Gould (1977). Neoteny is described as when descendant size and maturity are equal in time

to ancestral patterns, but the shape trajectory is retarded and thus descendant adults are similar to the ancestral juvenile or infantile form (Gould, 1977). This process allows the descendant to resemble a juvenile or infant of the ancestor in appearance while maintaining growth and maturation at current rates, and has been applied to the modern human face and cranium (Gould, 1977; Shea, 1989; Williams, et al., 2002; Williams, et al., 2003). It has been implied that modern humans are neotenic with respect to Neanderthals. In the recent past, this has been disputed by several researchers (Shea, 1989; Williams, et al., 2002, 2003). According to other scholars (Anton and Leigh, 2003; Gould, 1977), the continuing fetal rate of brain growth into the early postnatal period and the retention of "relatively juvenile gross skull form with a large, bulbous cranium" could by some be considered an argument for neotney, but Shea (1989) states that there is no "correspondence between extension of growth periods and retardation of shape change". In agreement with Shea (1989) is Williams, et al. (2002, 2003) with regard to modern humans not being neotenic to ancestral *Homo*, although Shea (1989) is exploring the descendant relationship by size, while Williams, et al. (2002) is examining shape. Referring to both sets of research, any similarity of landmarks examined between modern humans and past ancestors of the *Homo* phylogenetic tree is at most a "superficial resemblance" and that modern human craniofacial shapes is "uniquely different" when compared to past species if Neandertals are considered (Shea, 1989; Williams, et al., 2002; Williams, et al., 2003).

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Part V: Brain Growth Rates Pre- to Post-natal: Are They Really Carried Over?

There is much disagreement in the length of time that fetal rates of growth are extended into the neonatal and infant period although the fact that the rates do carry over is not disputed (Vinicius, 2005). The length of time that fetal rates continue post-natally range from a suggested 12 to 18 months as reported by Coqueugniot, et al. (2004), McNamara (2002a), Thompson, et al. (2003) and Vinicius (2005), and to 3 years as suggested by Gould (1977). Even with the duration of fetal rates in disagreement among scientists, most concede that deceleration begins by the age of 3-5 years (Farkas, et al., 1992; Robson, et al., 2006; Sardi, et al., 2005) with full growth being attained by 3 years (Robson, et al., 2006) to 10 years (Coqueugniot, et al., 2004; McNamara, 2002a).

To explore possibilities as to why fetal rates of brain growth may be carried over into infancy, one must understand the physical constrictions placed on the fetus by changing maternal physiology throughout the evolution of *Homo* as well as the reverse (De Silva, et al., 2008; Jordaan, 1976; Ponce de León, et al., 2008; Schultz, 1969; Steer, 2006; Whitcome, et al., 2007). Evolution towards bipedalism of early *Homo* ancestors gradually shifted pelvis, sacrum, and femur morphology to accommodate the new means of locomotion (Bogin, 1999; Jordaan, 1976). The shape of the pelvis and sacrum shifted from long and narrow anterio-posteriorly as seen in ancestral hominids to a short and wide morphology as seen in modern populations. A decrease in the length of the sacrum and pelvis was needed to center gravity as a means to increase balance as individuals stood erect. This change in morphology would hinder the birth

process by shortening the birth canal (De Silva, et al., 2008; Jordaan, 1976; Ponce de León, et al., 2008; Schultz, 1969; Steer, 2006; Whitcome, et al., 2007). The decrease in the height of the sacral elements added stability for upright locomotion, but necessitates the widening of the bones as well. To some degree the widening of the sacral elements would offset the shortening of the birth canal (Bogin, 1999; De Silva, et al., 2008; Jordaan, 1976; Ponce de León, et al., 2008; Schultz, 1969; Steer, 2006; Whitcome, et al., 2007). Maternal constraints of pelvic morphology would place certain restrictions on the size of the developing fetus. This reduction in the size of the pelvic outlet constraining the general overall size of the fetus, while the cranial size was restricted specifically (Bogin, 1999; De Silva, et al., 2008; Jordaan, 1976; Ponce de León, et al., 2008; Schultz, 1969; Steer, 2006; Whitcome, et al., 2007). To compensate for the restriction placed on overall and cranial size, fetal body and brain size would have to come as close to the limit allowed by maternal constraints (Bogin, 1999; De Silva, et al., 2008; Gould, 1977; Schultz, 1969; Whitcome, et al., 2007; Wortham and Kuzara, 2005). Even with fetal size reaching this limit for successful parturition, the length of time needed for brain growth to reach an ever increasing adult size necessitated rapid growth after birth for long periods of time when compared to ancestral forms (Bogin, 1999; Gould, 1977; Jordaan, 1976). Therefore, fetal rates can be determined to extend postnatally due to the degree of size increase needed after parturition (Alba, 2002; Gibson, 2000; Ponce de León, et al., 2008).

The prolonged period of time needed for brain growth has been suggested to be one reason for the lengthy human infancy period (Bogin, 1999; Gould, 1977;

McNamara, 2002a; Thompson, et al., 2003). This in turn also helps to explain the insertion of childhood as one of the extended periods of growth in the evolution of human life history (Bogin, 2006; Gould, 1977; Thompson, et al., 2003; Wortham and Kuzara, 2005). Along with the insertion of childhood, the addition of the juvenile period and lengthening of the remaining life stages prolongs life expectancy. Older individuals would thus add a level of experienced adult members that could care for infants and children and possibly allow for a higher percentage of successful offspring survival (Bogin, 2006; Gould, 1977; Hawkes, 2006a). This supplementary care would then allow for more successful deliveries of less developed neonates while keeping the fetal development under the limits of maternal pelvic constriction (Bogin, 1999; Hawkes, 2006b; Wortham and Kuzara, 2005).

The cranial region and relatively small jaws of juvenile apes and monkeys resemble those of humans at every life cycle stage. This was remarked upon by Gould (1977), Schultz (1969), and others and is often referred to as human neoteny. Nonhuman primates exhibit relatively rapid rates of brain growth during gestation compared to other mammals. Shortly after birth, rates of cranial changes in shape slow considerably such that infant and adult nonhuman primates exhibit similar cranial dimensions. In contrast, human infants exhibit rapid cranial expansion, but relatively slow rates of facial growth during the same postnatal stage. Thus, humans have prolonged the fetal developmental period to include the first 1-2 postnatal years beyond those of the great apes to accommodate this additional advancement in capacity of the brain (Bogin, 1999, 2006; Gould, 1977; Hawkes, 2002b; Schultz, 1969).

Part VI: Human Cranial Growth

All parts of the human body develop from two gametes that combine, multiply and differentiate into specific organs and systems. In the pattern of development, each division within the whole grows and develops. This includes the skeletal system as well, and the bones of the cranial vault conform to this developmental scheme (Baer and Harris, 1969; Epstein and Epstein, 1978; Gould 1977; Jeffery and Spoor, 2002; Morris-Kay and Wikkie, 2005; Turner 2007). The individual elements of the crania originate differently than other bones, deriving specifically from within the membranous covering of the fetal brain (Baer and Harris, 1969; Epstein and Epstein, 1978; Gould 1977; Jeffery and Spoor, 2002; Morris-Kay and Wikkie, 2005; Scheuer and Black, 2000; Schultz, 1969). Of particular interest to this study are the frontal, the parietal, and the occipital bones as these skeletal elements encase the developing brain and are most closely associated with this organ and its size.

Frontal: The frontal bone, located superiorly and anteriorly on the skull, is the first of the cranial bones to begin ossification. The process begins to develop from two centers and is visible microscopically by alizarin-stain as early as 6-7 weeks gestation and radiographically by the 13th week (Fazekas and Kósa, 1978; Morris-Kay, et al., 2005; Scheuer and Black, 2000). As development begins, the frontal ossifies in a radial pattern from each center, as do other cranial elements, but as ossification continues the shape elongates into a recognizable ovoid with the long axis forming anterio-posteriorly (Fazekas and Kósa, 1978; Jeffery and Spoor, 2002; Inman and Saunders, 1937;

Neumann, et al., 1997; Scheuer and Black, 2000).   By birth, the frontal bones are symmetrical and separated by the largest of the fetal fontanelles, the anterior fontanelle, and the metopic suture. Both the fontanelle and the metopic suture close completely by the end of the second year, fusing the right and left halves into a single element that is fully recognizable when compared to the adult bone (Fazekas and Kósa, 1978; Scheuer and Black, 2000).

Parietal: There are two parietal bones located on each side of the brain, posteriorly to the frontal bone. The fetal parietals form from two centers of ossification that can be microscopically identified with alizarin-stain by 7-8 weeks gestation (Fazekas and Kósa, 1978; Morris-Kay, et al., 2005; Scheuer and Black, 2000). Ossification of the two centers fuse quickly, forming an hour-glass shape in the early stages and rapidly develop into an ellipsoid recognizable by radiographic measures at around 20 weeks gestation. Although ossification and development begins at an early stage, the parietals are not identifiable by angles and borders until around the 24th week (Fazekas and Kósa ,1978; Morris-Kay, et al., 2005; Neumann, et al., 1997; Scheuer and Black, 2000).

Fetal and infant parietal bones are characterized by relatively large eminences located centrally on each element and which form distinctive curves along the sagittal suture. This arch begins as relatively angular in shape, and smooths out as it reaches maximum curvature by the age of 9 months of postnatal life. At this time growth slows and the vault gently flattens to the adult shape (Fazekas and Kósa, 1978; Scheuer and Black, 2000).

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Occipital: The occipital bone, located at the posterior and base of the skull, is the last element of the cranial vault to begin development and ossification. This element ossifies from four centers, more than any other single element of the crania, and is the only one to form from cartilage rather than directly out of the membranous covering of the brain. The occipital forms in two halves: the top, or pars interparietalis, with an ossification center for the left and right sides, and the lower, or pars supra-occipitalis, also with a center for the left and right sections. Both the pars interparitealis and the pars supra-occipitalis form independently, the latter beginning identifable first at approximately 8 weeks gestation and the former beginning later at approximately 10 weeks gestation (Fazekas and Kósa, 1978; Neumann, et al.,1997; Scheuer and Black, 2000).

The upper and lower halves develop independently. The pars interparietalis develop endocranially, as the portion of the occipital above the highest nuchal line in a fan shape. The pars supra-occipitalis originates below the highest nuchal line and forms as an ellipsoid. Until the fetus reaches 3.5-5 months of gestation, each ossification center is independent of the others. At this point in the development of the fetal cranial components, the four centers begin to join at the midline and fuse outwards towards the margins, along the sutura mendosa. These individual centers of ossification fuse to represent the body of the occipital (Fazekas and Kósa, 1978; Scheuer and Black, 2000).

There are three centers of ossification related to the occipital not included as part of this study as they do not contribute to the overall length or width of the bone: two

centers of ossification for the right and left pars lateralis, and one center for the pars basilaris. These three centers along, with the inferior border of the occipital squama form the foramen magnum. Fusion of these centers begins soon after parturition and is usually complete between 2-4 years, with obliteration seen in approximately half of individuals by the age of 5 years. Full fusion of this suture does not always occur completely, as there are reports of the suture line being visible into adulthood in some cases (Fazekas and Kósa,1978; Scheuer and Black, 2000).

Part VII: The Cranial Vault and Its Relationship to the Brain

From the onset of ossification, individual centers for the elements are already in the general location in which they are found in the fully developed cranial vault. By the end of the fourth month of gestation, all elements are recognizable and similar in relative size and shape to their fully developed counterparts (Jeffery and Spoor, 2002; Scheuer and Black, 2000). During early growth, each of the cranial elements develop an eminence to some degree, located centrally on the element. The eminences mark the most protruding portion of the element (Scheuer and Black, 2000). By the time of parturition, cranial elements have developed to a sufficient size to offer maximum coverage for the rapidly growing and developing brain (Fazekas and Kósa, 1978; Scheuer and Black, 2000).

Conception to Birth: Along with the independent and systematic growth of the cranial elements, there are other factors effecting the rate of growth of the vault. One

factor in the increasing size and shape of the cranial elements is the degree of stimulus occurring as a result of the intrinsic pressure that the growing brain places upon the endocranial surface of these bones (Gould, 1977; Morris-Kay and Wikkie, 2005; Sardi, et al., 2007). Gould (1977) and others suggest that the increase in the volume of brain tissue places sufficient pressure upon the developing cranial bones to generate growth and allow the expanding brain to mechanically increase cranial capacity to adequately mold the skull. Mechanical effects of this type are seen throughout the skeleton and are generally regarded by Turner (2007) and others as one of the major processes of bone development.

The process of bony accumulation begins as the brain grows and develops and pushes against the endocranial surface. This pressure stimulates osteoclasts to break down the interior of the cranial element so as to provide more room for the growing brain. As a direct reaction to the destruction of the inner surface of the bone, osteoblasts on the ectocranial surface activate and begin laying down new bone on the exterior surface of the element. This corresponding action of destruction and construction upon the cranial elements, due to pressure exerted by the brain, causes a direct correlation between the size and shape of the brain to the size and shape of the cranial vault as the skull is essentially formed and molded by the increase of brain tissue (Amiel-Tison, et al., 2002; Baer and Harris, 1969; Jeffery and Spoor, 2002; Leigh 1992; Morris-Kay and Wikkie, 2005; Sardi, et al., 2007; Trenouth, 1991; Turner, 2007). Although each of the individual elements of the cranial vault have been shown to grow independently of the other, the overall osteogenic development of the elements at the

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same time are coordinated with and interact across ontogenic factors of the brain (Sardi, et al., 2005; Sardi, et al.,2007). Thus, any variation in size and shape of the cranial vault is related to variation in size and shape of the brain held within (Sardi, et al., 2007; Trenouth 1991). With the human brain having such a close developmental correlation to the cranial vault, it has been shown that the inverse relationship between the cranial vault and the brain is comparable. This parallel growth allows for the possibility to measure the external dimensions of the cranium and extrapolate the interior volume of the brain (Baer and Harris, 1969; Bogin 1999; Epstein and Epstein, 1978; Jeffery and Spoor, 2002; Leigh, 1992; Morris-Kay and Willie, 2005; Sardi, et al., 2007; Trenouth, 1991). Thus, by examining the size of the individual elements of the vault, it should be possible to interpret the extent of growth attained by the brain, as well.

Birth to 6 Years: During the birth process, the fetal skull undergoes mechanical deformation as it passes through the birth canal. This deformation causes the individual elements of the cranial vault to overlap at the sutures which have yet to ossify (Schultz, 1969). It is this ability of the vault to be manipulated at the sites between the cranial elements allowing the elements to ride over one another that is responsible for the relatively easy passage of the fetus. The deformation of the vault is temporary and within an average of 3-4 days after birth, any shape change from cranial shifting during parturition has been reversed and all elements are in the normal edge-to-edge position (Amiel-Tison, et al., 2002; Schultz, 1969). After the elements have returned to the correct position, measurements (i.e. circumference) taken on the infant's head

throughout the first year will generally be represented on a standard growth chart used by medical personnel as smooth growth curve illustrating a progressive increase of brain tissue (Amiel-Tison, et al., 2002; Farkas and Kósa, 1992; Gibson, et al., 2000; Sivan, et al., 1984).

At the time of birth, it is generally accepted that the infant brain has grown to approximately 25% of its adult size (Coqueugniot, et al., 2004; Jordaan, 1976; Vinicius, 2005). This is not the only accepted figure for the degree of growth the fetal brain reaches before birth. According to Vinicius (2005) one suggested value is 25% of its adult size, although there has been research as stated in Gould (1977) to propose that the figure could be as low as 23% to as high as 31% of the adult brain size.

During the years of rapid growth during infancy and childhood the volume of the brain continues until approximately 10 years of age. There are suggestions that the one-year-old infant brain may reach 50% of its adult size (Coqueugniot, et al., 2004). Other researchers disagree. Gould (1977) suggests that the one year old brain has achieved 70% of the adult size and Farkas and Kósa (1992) suggest a figure of 87%. As a child ages, an agreement on the volume reached by the expanding brain at older ages is also under disagreement. Farkas and Kósa (1992) suggest that the brain reaches 93% of the estimated adult volume by the age of 5 years, and Coqueugniot, et al. (2004) and McNamara (2002) suggest that by 10 years a child's brain has achieved just above that limit to 95%.

Though there is no single consensus as to the percentage of brain growth expected of an infant or child's brain, some researchers propose that the rapid increase begun *in utero* continues until the end of infancy, at approximately 6 years of age. At this time the rate of volume increase appears to slow (Farkas and Kósa, 1992). Coqueugniot (2004) suggests the most rapid growth carries over until at least 12 months, while Gould (1977) suggests that the same degree of development extends throughout the second year of life.

Part VIII: New Questions

Research in medical and anthropological literature has suggested the size of the human cranial vault is directly related to the size of the brain, allowing for the growth of one to be used as a proxy of growth for the other (Baer and Harris, 1969; Bogin, 1999; Epstein and Epstein, 1978; Jeffery and Spoor, 2002; Leigh, 1992; Morris-Kay and Wikkie, 2005). As stated previously, it is generally accepted that rates of growth of the fetal brain are carried over after parturition into infancy (Alba, 2002; Bogin, 1999; Diewert, 1985; Gould, 1977; Ponce de León, et al., 2008; Thompson et al., 2003a), but the length of time that the rate of growth continues has not found agreement. Various researchers report the duration of fetal brain growth continuing until various ages of development: at least 12 postnatal months/1 year of age (Thompson, et al., 2003a; Vinicius, 2005), 2 years of age (Gould, 1977), 3-3.5 years (Bogin, 1999), and 5 years (Farkas and Kósa, 1992; Sardi, et al., 2005). Although these researchers disagree as to

the duration of fetal growth into the postnatal period, they all conclude that the rate is extended at least until the end of the first year of postnatal life. It is the length of time that fetal growth rates extended into the postnatal age that this study will examine. With the previous research for theoretical basis, *I suggest that the rate of fetal brain/cranial growth is carried over into the postnatal period, but not to the extent suggested by earlier studies of 1-5 postnatal years of age (H1) and that there is a significant decrease in the rate of infant brain/cranial growth before the age of 6 postnatal months (H2).*

Chapter 3: Materials and Methodology

Part I: Forensic Fetal Osteology Collection

There are many skeletal collections available for analysis when conducting research on the remains of adults, but the number of collections is limited when research turns to individuals of immature skeletal development, or sub-adult status (Fazekas and Kósa, 1978; Huxley, 2005; Neumann, et al., 1997; Scheuer and Black, 2000). One consideration for the meager number of collections of sub-adult skeletal remains is the lesser number of individuals that adequately preserve during the burial process. There are several explanations for the small number of specimens available for study. One reason for the small number, is the fragility of immature bone. This fragility is a main cause of poor preservation of remains when an individual is interred (Halcrow and Tayles, 2008; Jackes, 1994; Scheuer and Black, 2000). Another cause for the lesser numbers of individuals available for collections is cultural belief systems and alternate burial practices, such as exclusion from community ossuaries with regards to infants and children (Finaly, 2000; Kamp, 2001; Murphy, 1996; Scheuer and Black, 2000). For these reasons and others, there are only a handful of collections of fetal, infant, or child remains for study. One such collection is the Forensic Fetal Osteology Collection.

The Forensic Fetal Osteology Collection, also known as the Mall and Lamb Collection, is housed at the National Museum of Natural History, Smithsonian Institution,

Washington, DC, USA. This collection consists of a total of 320 fetuses and infants (Huxley, 2005). The individuals that comprise this collection were donated to the museum in the late 1800's and early 1900's by private and public physicians, pathologists, medical scholars, and specialists of the time. Donations by physicians came from hospitals in and around the Washington, DC and other surrounding metropolitan areas such as Baltimore, Maryland, though some came from Berlin, Germany (Hunt, personal comm., 2009; Huxley, 2005). Between the years of 1903 and 1917, Aleš Hrdlička curated the collection at the museum, and added to the collection with specimens he had acquired from Columbia Hospital (Hunt, personal comm., 2009).

Most notable of the contributors were Franklin P. Mall and Daniel S. Lamb, the physicians for whom the collection is named. Mall donated the greater number of individuals (n=143) to the collection and was the founder of the *American Journal of Anatomy*. Lamb was curator of the Anatomy Department at the Army Medical Museum from 1865-1917. Both men were colleagues of Hrdlička and, through this relationship, donations and exchanges of specimens were made to the Smithsonian (Hunt, personal comm., 2009). Although the majority of the specimens in the collection are designated with the names of Hrdlička, Mall, and Lamb, many of the specimens were actually collected by other physicians (Hunt, personal comm., 2009).

Individuals within this collection are from spontaneous abortions with estimated gestational ages of three lunar months to still born infants along with some infants who died of unknown causes. Information known for each individual is recorded in the museum card catalog and consists mostly of biological sex of the fetus/infant,

race/nationality of the individual and parents, and estimated gestational age (as determined by methods current at the time) (Hunt, personal comm., 2009; Huxley, 2005). Occasionally, the original card of information from the individual's autopsy is present in the card catalog, and information regarding the maternal parent's health and/or previous children, either successful or unsuccessful, is noted as well. Specific demographics of the collection is not known, but is believed to come from the lower socioeconomic areas in and around Washington, D. C (Hunt, personal comm., 2009; Huxley, 2005).

The individuals of this collection vary in their condition of preservation and completeness of elements. Preservation ranges from mummified fetuses to fully skeletonized, with completeness ranging from a few elements to complete sets of remains. To some degree, the condition of a specimen is dependent on the process of preservation used and the age of the fetus (Fazekas and Kósa, 1978). When the individual is of less than 16 weeks gestation (four lunar months), cranial elements are too small, not much more than the beginnings of ossification centers developing, and too fragile to be subjected to manipulation, or even to be removed from the container while long bone elements are more substantial and are more safe to handle. In the youngest individuals, the cranial elements are translucent.

Most individuals within the collection have the majority of postcranial elements at least represented if not complete, but then here too all is dependent on the degree of development. For individuals less than 24 weeks gestation, some ossification centers of the fingers, hands, toes, and feet have not begun to form sufficiently to be preserved

(Fazekas and Kósa, 1978; Scheuer and Black, 2000). Therefore, younger individual specimens are represented by the long bones of the thoracic cage and extremities, while older individuals include vertebral elements as well as some hand and foot elements.

Cranial elements develop rapidly and achieve a size easily preservable at a later age (Fazekas and Kósa, 1978; Scheuer and Black, 2000). In this collection, most of the measurable cranial elements represent the vault: the frontal, the parietal, the temporal, and the occipital. Facial elements for these individuals are only represented when fully articulated skulls are present. Of the 320 individuals within this collection, only 133 have cranial elements preserved to a condition that allows for precise measuring, including 13 individuals with fully articulated crania.

Part II: Methods of Data Collection

Each individual within the collection was examined for the following cranial elements: frontal, parietal, and occipital. For every individual chosen, there was at least one parietal and one frontal, preferably from the left side, and a complete occipital. Four measurements were taken from each element following the methodology laid out by Fazekas and Kósa (1978): measurements for length chord and width chord were taken with Mitutoyo, Model CD-6"C digital sliding calipers (certified calibrated on 03/16/09 by Technical Maintenance Incorporated, in Atlanta, GA) to the nearest hundredth millimeter (mm), and measurements for length arch and width arch were taken to the nearest millimeter, with a standard paper measuring tape to reduce the

possibility of stretching seen in cloth measuring tapes. Measurements of the frontal bone for length were taken from the center of the orbit margin across the frontal eminence to the superior peak; width was taken transversally over the frontal eminence. Length of the parietal bone height was taken from the center of the inferior (squamous) margin to the center of the superior (sagittal) margin, across the parietal eminence; width was taken perpendicular to height over the eminence from the center of the superior margin to the center of the inferior margin. Occipital measurements included height (length), which was taken along the midline from the superior tip to the center of the inferior border, and width taken in the line of the sutura mendosa. All arch measurements were taken along the same line as the chord measurement for both length and width on each element. When fully articulated skulls were available, other measurements were also taken using the same calipers and paper measuring tape as the individual elements. Additional measurements included: cranial length (from glabella to opisthocranion), cranial bi-parietal width (euryon to euryon), cranial height (basion to bregma), and cranial circumference measured around at the greatest bi-parietal width.

Once all measurements of the crania were complete, an age for each individual needed to be determined. The use of cranial bones to establish age was deemed to be inaccurate as there is no standard currently in use based on these skeletal elements. A standard of determination based on cranial elements is difficult due to the fact that the margins of the cranial elements are feathery and not solid nor regular as they grow radially from the centers of ossification, whereas long bones extend from the diaphyses.

Because of this difference in the direction of ossification, cranial vault elements are at greater risk of breaking or deformation over a relatively short periods of time and will result in large errors when used (Fazekas and Kósa, 1978). Therefore, long bones were used for age assessment because of the stability of the bone from the directionality of ossification. Specific elements which have been shown to be the strongest estimators of fetal age are the femur, tibia, and ulnae, where according to Sherwood (et al., 2000), there is a high correlation of the femur, tibia, and ulna with gestational age.

Therefore, long bone measurements for the complete collection were requested from Dr. David Hunt, curator of the collection at the Smithsonian, for the purposes of accurate age assignment. This data set included measurements to the nearest millimeter for all available long bone for each individual within the collection: humeri, radii, ulnae, femora, tibiae, and fibulae. All measurements relevant to the individuals in this study were noted. Values for each element were referenced for age based on length according to Scheuer and Black (2000) and Fazekas and Kósa (1978). Once all measurements had been noted and age ranges assigned based on measurements for each long bone, the mean for all long bones were averaged to determine an approximate age range for each fetus. In most instances, a complete set of long bone measurements was available for each fetus. The age was assigned in weeks, both for gestational age and for postnatal age, for better accuracy in estimating rates of growth.

Approximate ages for some individuals in the collection are noted in the card catalog by the donors and in the data set provided by Dr. Hunt (personal comm., 2009).

In some instances these ages were determined by the physicians based on measurements at autopsy (Huxley, 2005). Other fetal ages were not assigned or noted as gestational age in months or infant age in months. For the purpose of this study, the age-in-months range is too large to estimate accurate rates of growth, and all ages were calculated in weeks. The assignment of developmental age in weeks is imperative for determining rates of biological growth for individuals during gestation and the postnatal period. The rate of growth between 16 weeks gestation until the end of 3 postnatal months will be examined to determine at which point the fetal rate decreases. Notes of interest will be made on development until the age of 10 yrs.

All individuals were then grouped for specific age sets as early prenatal fetuses (≤26 weeks gestation, non-viable), late prenatal fetuses (27-40 weeks gestation, viable), and early postnatal individuals (40+ weeks gestation-10 weeks of life, after birth). These age intervals are based on the average age of viability for a fetus as determined by current medicolegal definition as "between 24 to 28 weeks gestation" (Cory and Collins, 2001).

Part III: Methods for Data Analysis

I will examine the changes for rates of growth with the use of analysis of covariance (ANCOVA) for each of the cranial elements that measurements were collected for (frontal, parietal, and occipital) and plot them against age. Ages of individuals were coded as '0' to represent neonates at the time of parturition, fetal ages as negative numbers, and infant ages as positive numbers. Those individuals coded as

'0' were then added to the postnatal age set for for analysis. One (1) was then added to each age to remove the negative numbers to allow for log transformation. Each age was subjected to log-transformation in order to maximize minimal differences and minimize large differences in the weekly growth rates. By log-transforming the measurements of each element, the data could then be regressed for each element in a linear trajectory for comparisons with age.

The measurements of each element were plotted on the y-axis against age of individuals on the x-axis and the slope determined for fetal and postnatal growth rates conducted separately. A confidence interval of 95% will be computed for each slope to determine if the changes in the growth rates between fetal and postnatal individuals are statistically significantly different. The slopes and confidence intervals of each element will then be compared to determine if the rates of growth are statistically significantly different for each. If a slope value fell outside the 95% confidence intervals for a given life cycle stage, only then were the y-intercepts tested for significance using the same procedure.

ANCOVA was developed using log-transformed data with Least Squares Regression and is thus more appropriate than Reduced Major Axis or other Model II methods. An added benefit to log-transformed data is the ease with which isometry can be identified such that if the confidence interval around an estimated slope overlaps 1, the null hypothesis of isometry cannot be rejected. Slope values significantly greater than 1 can be described as positive and above the line of isometry, while those significantly less than 1 can be described as negative and below the line of isometric

growth. Isometric growth assumes measurements are proportional to age. Confidence intervals were calculated by adding and subtracting the standard error of the estimate multiplied by the corresponding t value obtained from the t-distribution, based on the degrees of freedom for each life cycle stage.

Chapter IV: Results

All measurements taken for prenatal rates of growth, as inferred from the slope values and standard errors, are significantly greater than those deriving from their postnatal counterparts. Among fetuses there is a uniformly strong increases in size as a function of age, while there is more variation in the rates of growth among postnatal infants.

When prenatal remains are compared to their postnatal counterparts, the rates of growth are again significantly greater during the gestational period than after birth. Fetal rates of brain growth are not really maintained during the neonatal period, although they are approximated, particularly in some dimensions. In growth with respect to age, the frontal generally grows isometrically for both pre- and postnatal intervals with two exceptions. The growth rate of frontal width arc is significantly above the expectations of isometry during the prenatal period and the anteroposterior length grows with a rate significantly below the line of isometry after birth.

Curvature of the cranial bones also contributes to total values of size in the cranial vault. In order to analyze curvature as a function of age, arc measurements were calculated for the Smithsonian sample with measurements for length and width on the frontal, parietal, and occipital along the same axis as the that for chord measurements. These values were then indexed with the chord measurements to better understand the increase attained over time. In general, postnatal anterior-

posterior and width dimensions of the frontal and occipital bones and anterior-posterior parietal curvature are all significantly more curved than their fetal counterparts.

Frontal: Specifically for length, Figure 4.1 shows the linear relationship of the chord measurements for the length of the frontal bone of each individual measured. It can be inferred from Figure 4.1 that the slopes of the early prenatal age sets are not statistically different from the late prenatal individuals and both exhibit a faster rate of growth than that of the postnatal age set. The slope of each group is shown, along with standard errors, confidence intervals, with the relevant lower and upper bounds shown in Table 4.1. It should be noted that the slopes for both prenatal groups fall outside of the slope for the postnatal age set. This suggests that the length of the frontal bone grows at a faster rate before birth than after birth.

For width of the frontal, Table 4.2 demonstrates that although this degree of growth is within the expectations of isometry, although the differences between group slopes are significantly less than for length. With this in mind, the degree of growth for the ≤26 age set is greater than either group 27-40 week or postnatal groups, while the 40+ week still exhibits the slower growth of an infant in the trait compared to the fetus.

It has therefore been shown that during the prenatal period, the frontal bone length and width grow with isometry, and in the postnatal period growth is at a substantially slower rate for length and for width increase may also be statistically isometric. Although already large at birth, this cranial element continues to experience substantial growth after parturition. The dimensions of this element increase at a faster rate than other bones of the cranial vault for postnatal infants.

Figure 4.1 Age to Frontal Length Chord

Table 4.1 Frontal Length Chord (FRlc)
Slopes and Y-Intercepts with corresponding Confidence Intervals (low and high) and standard errors for length of frontal bone.

Variable	#	Age	Std Err	Low	B	High	Std Err	Low	Y-Inter	High
FRlc	18	≤26wks	0.250	0.534	1.024	1.514	0.180	3.649	4.002	4.355
FRlc	55	27-40wks	0.071	0.976	1.115	1.254	0.015	3.969	3.998	4.027
FRlc	47	40+wks	0.345	-0.331	0.345	1.021	0.029	3.962	4.019	4.076
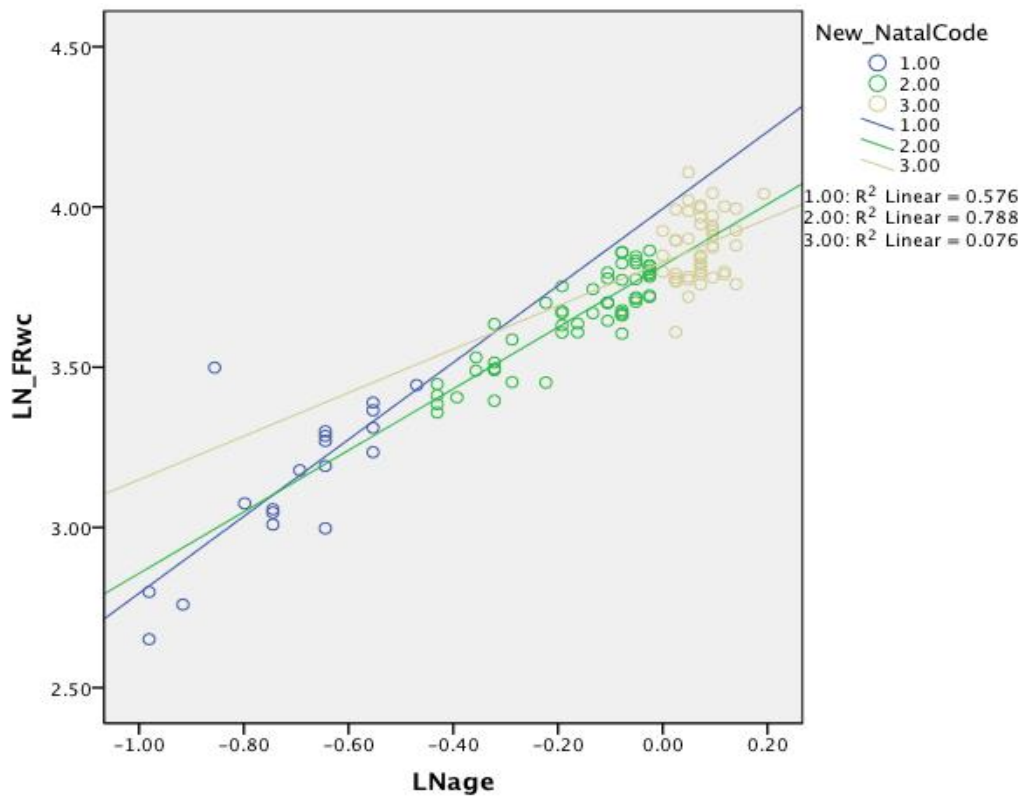
Figure 4.2 Age to Frontal Width Chord

Table 4.2 Frontal Width Chord (FRwc)
Slopes and Y-Intercepts with corresponding Confidence Intervals (low and high) and standard errors for width of frontal bone.

Variable	#	Age	Std Err	Low	B	High	Std Err	Low	Y-Inter	High
FRwc	18	≤26wks	0.250	0.710	1.200	1.690	0.179	3.644	3.995	4.346
FRwc	56	27-40wks	0.067	0.829	0.960	1.091	0.014	3.790	3.817	3.844
FRwc	47	40+wks	0.350	-0.007	0.679	1.365	0.029	3.771	3.828	3.885

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The frontal is one of the two bones of the vault most dependent on age of the developing individual for degree of curvature of the cranial elements. The relationship between the curvature of this element in length and increasing age is negative in slope for early prenatal individuals, falling below zero. This would indicate that curvature of the frontal bone in this direction is slightly flattened during the early development of the element. The rate of increase for postnatal individuals overlaps one and in this age set the null hypothesis can not be rejected for size. The only group that experiences isometric growth for curvature of the frontal is the 40+weeks gestation age set indicating that as the individual grows in the the final thirteen weeks of gestation, curvature of the frontal increases as a function of age. This can be seen in Figure 4.3 with the ANCOVA results noted in Table 4.3. Although, the rates of growth for the arc index measurements differ from the patterns seen for chord measurements, the total values of increase are still statistically significantly different between the fetal and the postnatal phases for curvature in the anterio-posterior direction.

The patterns seen in measurements for the frontal width arc are similar to those in the frontal length arc and are stated in Table 4.4 and demonstrated in Table 4.4. It should be noted that the individuals with the greatest increase in shape is again in the 27-40 week gestation age set. For age sets of ≤26 weeks and 40+ weeks the rate is below what is expected for isometric growth, while individuals in the group of 27-40 weeks gestation are slightly above that of isometric expectations.
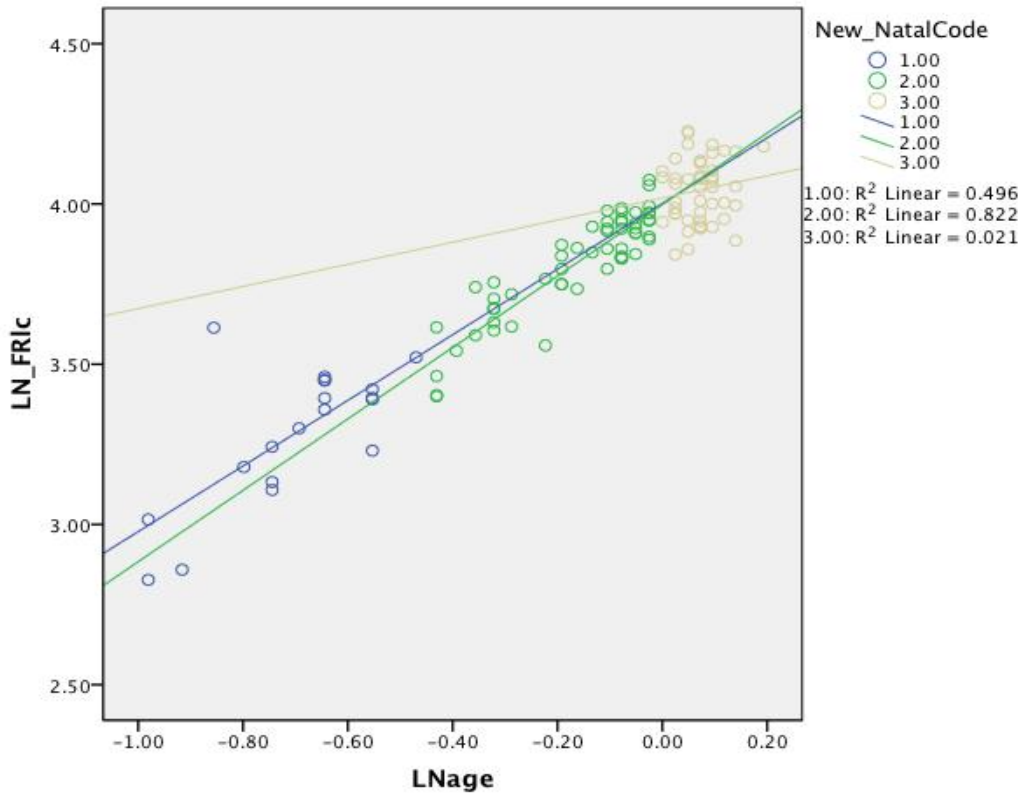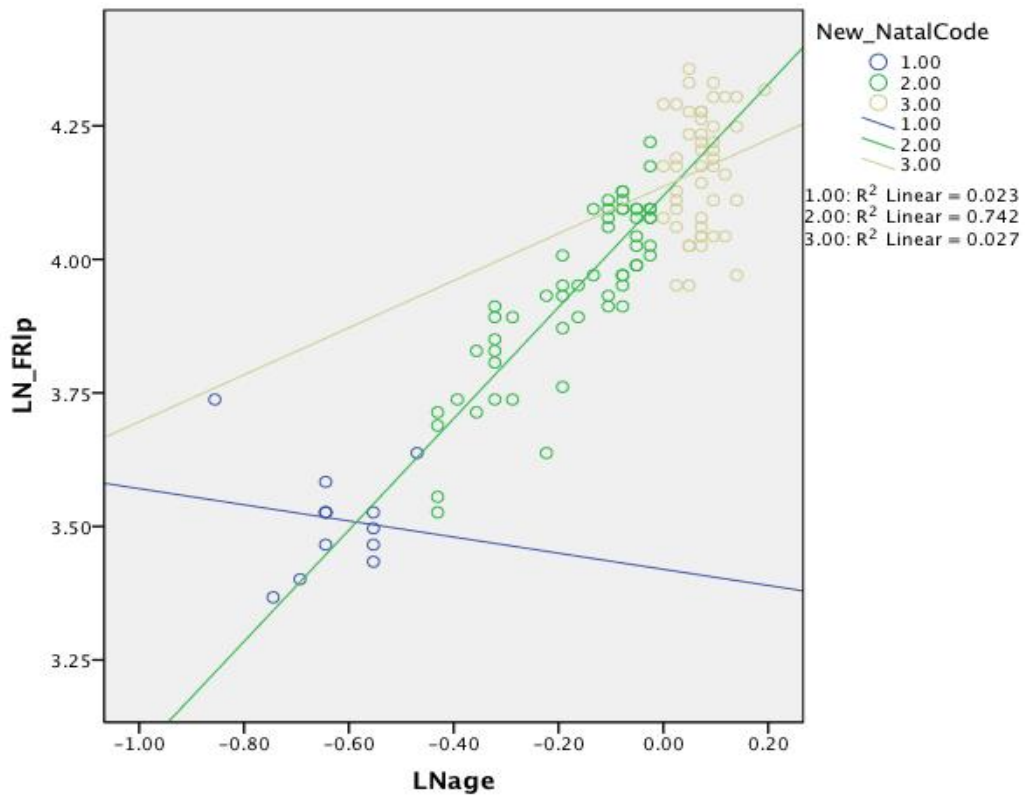
Figure 4.3 Frontal Length Arc to Age

Table 4.3 Frontal Length Arc (FRlp)
Slopes and Y-Intercepts with corresponding Confidence Intervals (low and high) for arc of frontal bone.

Variable	#	Age	Std Err	Low	B	High	Std Err	Low	Y-Inter	High
FRlp	12	≤26wks	0.296	-0.731	-0.151	0.429	0.189	3.050	3.420	3.790
FRlp	56	27-40wks	0.086	0.874	1.043	1.212	0.017	4.086	4.119	4.152
FRlp	47	40+wks	0.390	-0.323	0.441	1.205	0.032	4.073	4.136	4.199
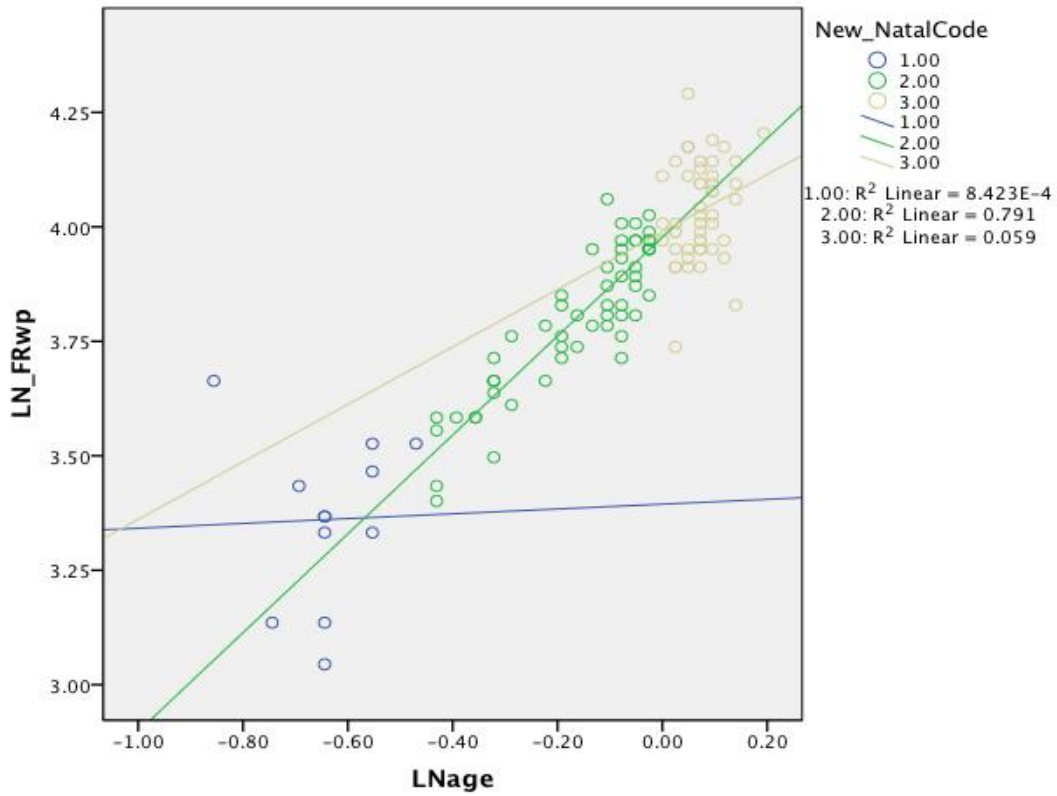
Figure 4.4 Frontal Width Arc to Age

Table 4.4 Frontal Width Arc (FRwp)
Slopes and Y-Intercepts with corresponding Confidence Intervals (low and high) for arc of frontal bone.

Variable	#	Age	Std Err	Low	B	High	Std Err	Low	Y-Inter	High
FRwp	11	≤26wks	0.572	-1.068	0.053	1.174	0.369	2.671	3.394	4.117
FRwp	56	27-40wks	0.075	0.933	1.080	1.227	0.016	3.946	3.977	4.008
FRwp	47	40+wks	0.369	-0.095	0.628	1.351	0.030	3.930	3.989	4.048z

Parietal: Prenatal rates of growth in the length of the parietal are above the expectations of isometry for age. Those of infants during the three months are strongly below the expectations of isometry. This is seen in Figure 4.5 as the slopes of both fetal age sets are strongly above one and the expected line of isometry, while the postnatal group is approaching zero suggesting that increase in size for length is minimal. Table 4.5 shows the relationships of the slopes to the corresponding confidence intervals. Here it can be seen that the differences in rates between groups are statistically significant when fetal measurements are compared to infant values in Figure 4.5.

When the width of the parietal is compared with age, the calculated slope during the gestation period is similar to that determined for the postnatal infants. All values include one within the confidence interval, noting that there continue to be statistically significant differences in rates. However, the rate of parietal growth for both the fetal individuals and neonates are relatively reduced compared to the frontal and occipital bones. These similarities in the slopes can be seen in Figure 4.6 and the slope determinations are noted in Table 4.6.

The parietal is already elongated in fetuses because of particularly aggressive growth during this period. While after parturition, growth for this element is at a much slower rate. Therefore, for all parietal measurements, fetal growth can be described as significantly above the line of isometry, while the postnatal growth is isometric with respect to age.

Figure 4.5 Parietal Length Chord to Age

Table 4.5 Parietal Length Chord (PRlc)
Slopes and Y-Intercepts with corresponding Confidence Intervals (low and high) and standard errors for length of parietal bone.

Variable	#	Age	Std Err	Low	B	High	Std Err	Low	Y-Inter	High
PRlc	14	≤26wks	0.265	1.996	2.515	3.034	0.193	4.738	5.116	5.494
PRlc	44	27-40wks	0.095	1.101	1.287	1.473	0.019	4.165	4.202	4.239
PRlc	48	40+wks	0.073	0.053	0.196	0.339	0.032	4.177	4.240	4.303

Figure 4.6 Parietal Width Chord to Age

Table 4.6 Parietal Width Chord (PRwc)
Slopes and Y-Intercepts with corresponding Confidence Intervals (low and high) and standard errors for width of parietal bone.

Variable	#	Age	Std Err	Low	B	High	Std Err	Low	Y-Inter	High
PRwc	14	≤26wks	0.195	1.264	1.646	2.028	0.142	4.374	4.652	4.930
PRwc	47	27-40wks	0.075	0.908	1.055	1.202	0.015	4.253	4.282	4.311
PRwc	48	40+wks	0.344	0.145	0.819	1.493	0.028	4.243	4.298	4.353

With respect to the parietal, curvature here is highly dependent on age. The relative degree to which the bone is curved continues to increase during the postnatal period, which is due to the need for an increase in volume for the continually growing brain of the infant. Greater curvature here allows more volume to be added without affecting the slower growth and development of the facial bones and their related sutures.

As reflected in the rates of growth calculated for parietal width, the superior-inferior elongation of the parietal grows slower during gestation compared to rates of increase characterizing other cranial vault bones. The reduced rate of growth has implications for the curvature in the parietal when fetal and postnatal bones are compared. The slopes, as noted in Table 4.9 and demonstrated in Figure 4.9 for parietal length arc, are patterns comparable to those seen in other measurements with fetal age sets growing at significantly greater rates than postnatal infants. This is seen in the fetal rates of increase as significantly above the expected line of isometry and the rate of the 40+ week age set again falling below one and approaching zero as the expected rate of increase. This slope is significantly below the determined slope for the 27-40 week age set. In the age set for 40+ weeks, the null hypothesis can not be rejected.

As seen in Table 4.10, slopes for the indices of parietal width arc are similar to those seen in Table 4.9 for the parietal length arc. This would suggest parallel trajectories for the arc indices for length and width across age sets. The fetal parietal is already highly curved in early osteogenesis and continues to exhibit eminences that

allow for an increase in the size of the cranial vault without further expanding the perimeter and thus the size of the articulations with the frontal and occipital bones. Parietal bossing is pronounced in fetal and neonatal material and can remain extreme throughout infancy.
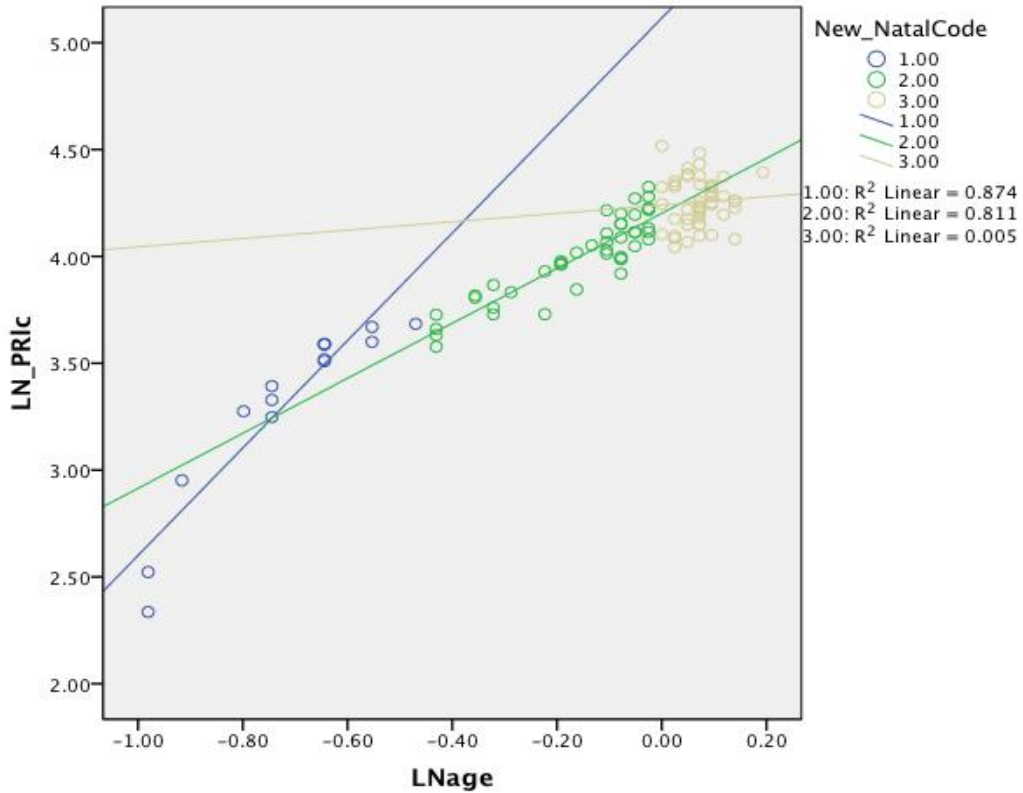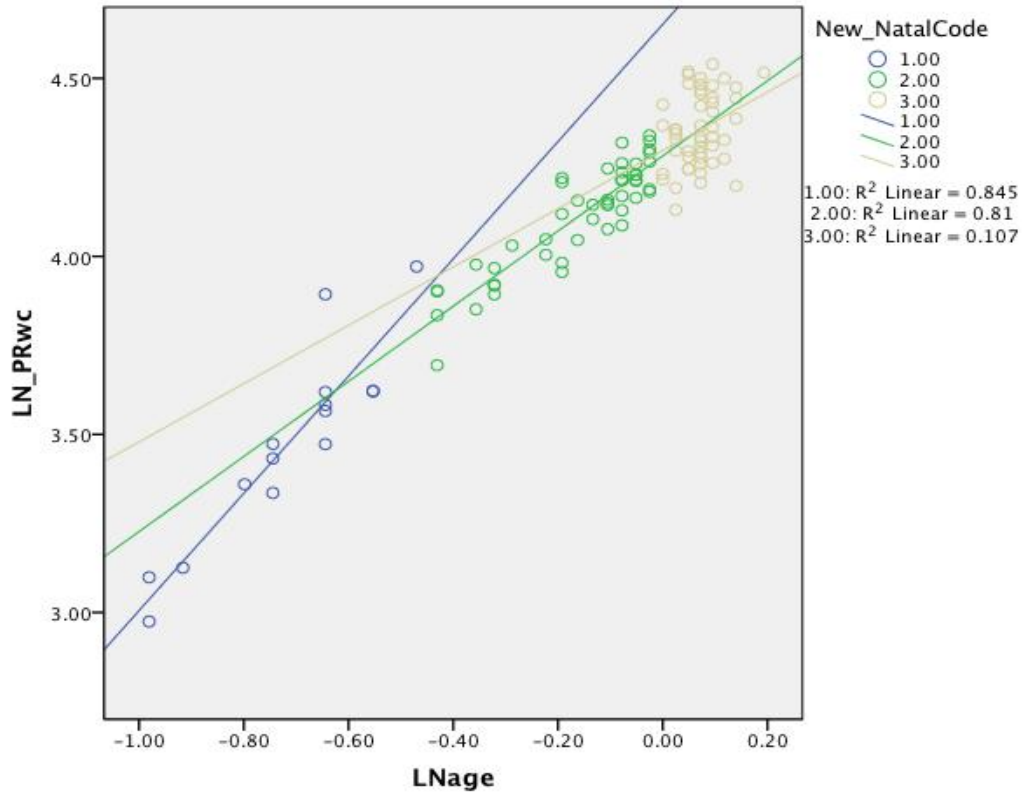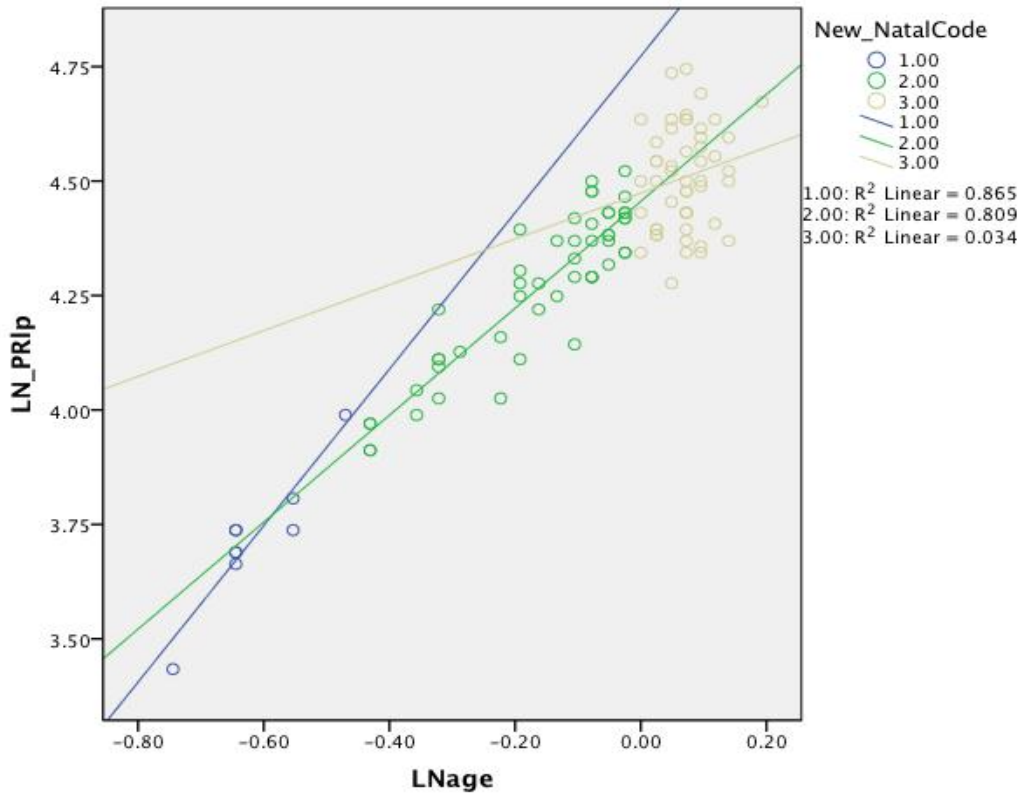
Figure 4.7 Parietal Length Arc to Age

Table 4.7 Parietal Length Arc (PRlp)
Slopes and Y-Intercepts with corresponding Confidence Intervals (low and high) and standard errors for arc of parietal bone.

Variable	#	Age	Std Err	Low	B	High	Std Err	Low	Y-Inter	High
PRlp	8	≤26wks	0.255	1.209	1.709	2.209	0.158	4.463	4.773	5.083
PRlp	49	27-40wks	0.082	1.007	1.168	1.329	0.017	4.423	4.456	4.489
PRlp	49	40+wks	0.383	-0.250	0.501	1.252	0.031	4.413	4.474	4.535
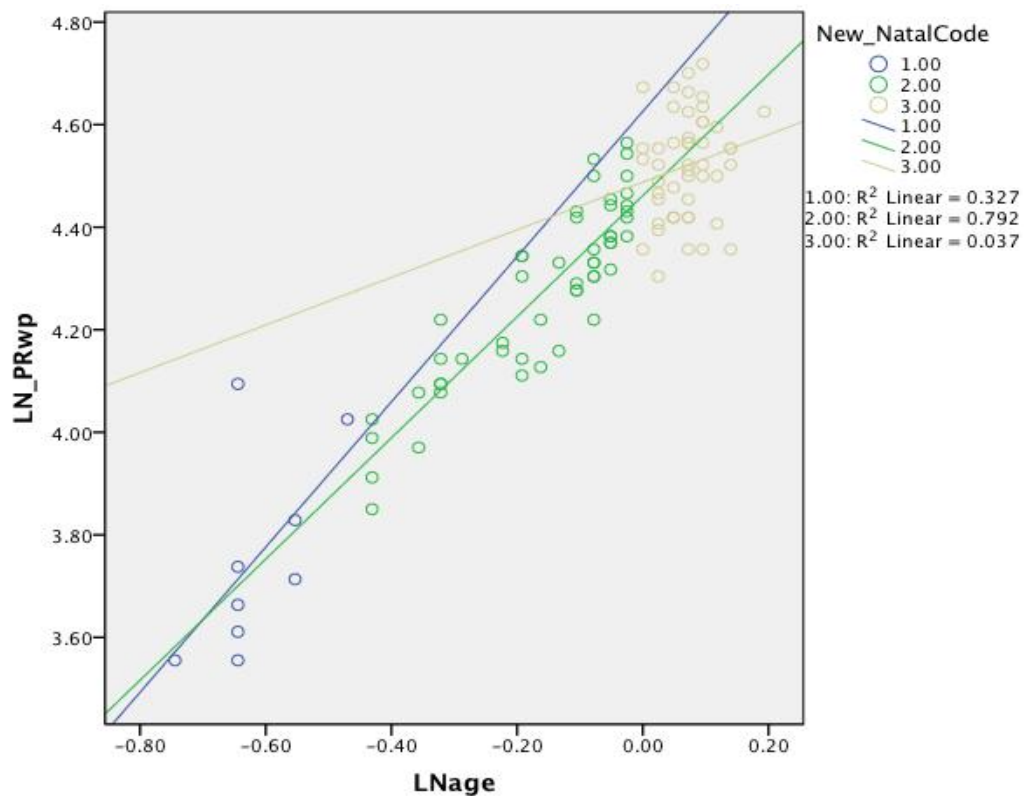
Figure 4.8 Parietal Width Arc to Age

Table 4.8 Parietal Width Arc (PRwp)
Slopes and Y-Intercepts with corresponding Confidence Intervals (low and high) and standard errors for arc of parietal bone.

Variable	#	Age	Std Err	Low	B	High	Std Err	Low	Y-Inter	High
PRwp	8	≤26wks	0.768	-0.089	1.416	2.921	0.476	3.693	4.626	5.559
PRwp	50	27-40wks	0.086	1.013	1.182	1.351	0.018	4.427	4.462	4.497
PRwp	49	40+wks	0.342	-0.206	0.464	1.134	0.028	4.433	4.488	4.543

Occipital: The occipital follows a generally intermediate pattern with respect to the relatively rapid frontal and slow growing parietal bones.   Patterns of growth observed for the parietal are mirrored in the occipital with the prenatal period described as weakly above the expectations of isometry and the postnatal interval characterized as strongly below the line of isometry growth.

The width of the occipital bone grows at a significant rate of increase in the ≤26wks age individuals, and at only slightly reduced rates during the later prenatal period. But when the postnatal interval is examined, rates of growth fall slightly below the line of isometry as seen in Figure 4.9 and mathematically determined in Table 4.9. The same can be said for the growth of all occipital traits after birth.

In Figure 4.10, is appears that slopes for the rates of growth for width in the age sets for ≤26 weeks and 27-40 weeks gestation are strikingly similar to the values for length arcs rates. In the postnatal age set, the degree of increase is somewhat lower than that for length. Table 4.10 shows the values for the slopes of the width arc indices and when compared to values in Table 4.9 for length arc indices, it can be noted that the values for slope in each age set are strikingly similar with values for individuals in the age set for ≤26 weeks are both approaching 2.0 and the slopes for individuals in 27-40 weeks is greater than one. For the postnatal age set the value of the slope of increase, in length and width, both fall significantly below one. Thus, the increase for size of both age sets during the gestational period are significantly above the line of isometry, and the increase of size in postnatal individuals significantly below expectation.   During gestation, both length and width chord measurements for the occipital increase

significantly faster than expectations of isometry would predict. Rates of increase for distances in length and width are examined for postnatal individuals, it is should be noted that the slope for length approaches the line of isometry. While slopes for width fall below the expected line of isometric growth and approach zero.

Figure 4.9 Occipital Length Chord to Age

Table 4.9 Occipital Length Chord (OClc)
Slopes and Y-Intercepts with corresponding Confidence Intervals (low and high) for length of occipital bone.

Variable	#	Age	Std Err	Low	B	High	Std Err	Low	Y-Inter	High
OClc	18	≤26wks	0.470	1.175	2.096	3.017	0.338	3.869	4.531	5.193
OClc	56	27-40wks	0.116	0.978	1.205	1.432	0.024	3.951	3.998	4.045
OClc	48	40+wks	0.412	-0.074	0.734	1.542	0.034	3.921	3.988	4.055
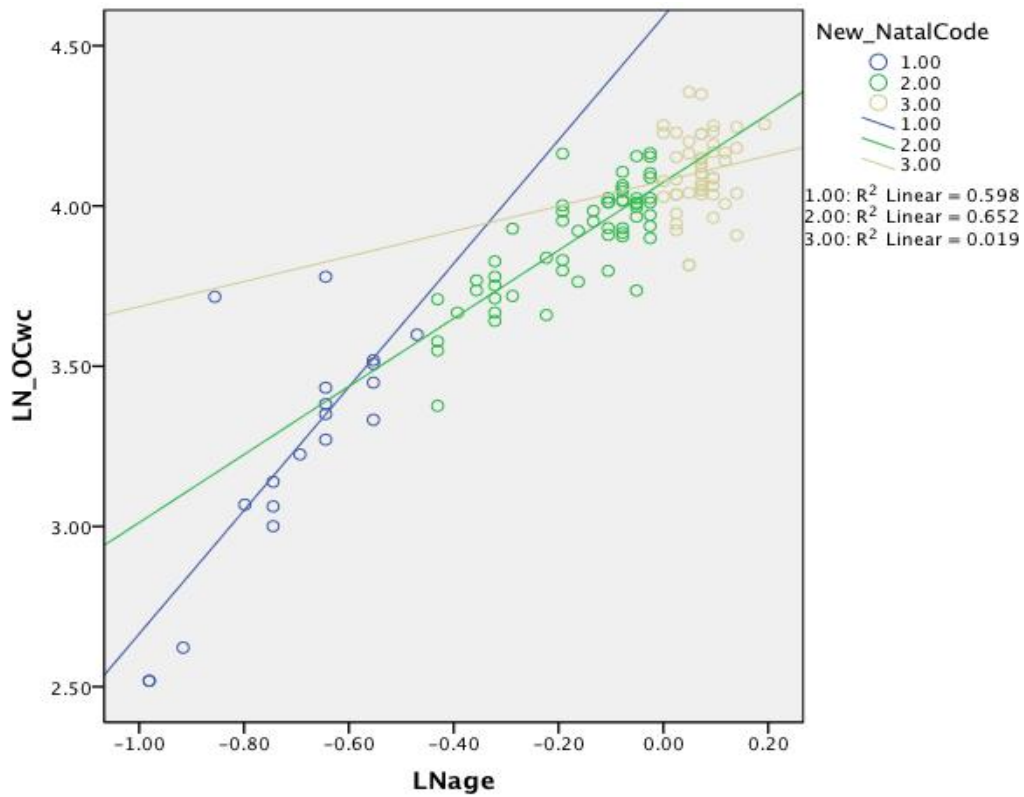
Figure 4.10 Occipital Width Chord to Age

Table 4.10 Occipital Width Chord (OCwc)
Slopes and Y-Intercepts with corresponding Confidence Intervals (low and high) for width of occipital bone.

Variable	#	Age	Std Err	Low	B	High	Std Err	Low	Y-Inter	High
OCwc	18	≤26wks	0.383	1.175	1.926	2.677	0.275	4.052	4.591	5.130
OCwc	57	27-40wks	0.104	0.858	1.062	1.266	0.021	4.033	4.074	4.115
OCwc	48	40+wks	0.406	-0.404	0.392	1.188	0.033	4.013	4.078	4.143

Figure 4.11 shows the arc measurements for occipital length for ≤26 weeks as having a negative slope and fall below the line of isometry when compared with age, while age sets for 27-40 weeks and 40+ weeks have positive relationships to age with slopes greater than isometric growth. The later prenatal age set shows a significant increase for size as the slope is greater than one and above the line of isometry. It should also be noted that the slope for postnatal individuals is significantly lower than that for the 27-40 weeks gestation group and significantly lower that what is expected for isometric growth. This is verified in Table 4.11. Here it is also suggested that although curvature of the occipital increases with age, the change expected over time may not be connected to age or size increase.

The size increase depicted in Figure 4.12, for the width of the occipital, is close to zero in individuals of the ≤26wks age set. This suggests less curvature in the early fetal period than in either the 27-40 weeks or 40+ week age set and that the curvature of the occipital begins later in development than either the frontal or the parietal. As all values for width curvature overlap one (1), the null hypothesis can not be rejected for either age set. The curvature of the occipital width decreases in relation to developmental age after birth, indicating that this element, is has the least curvature of all cranial elements.
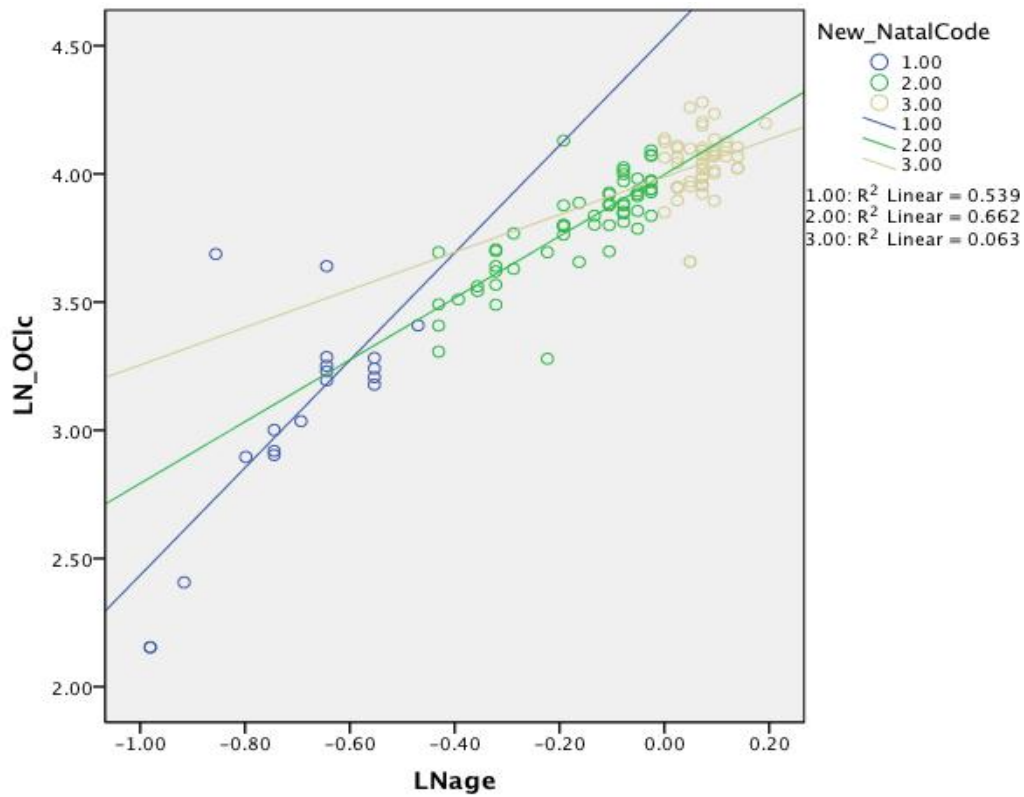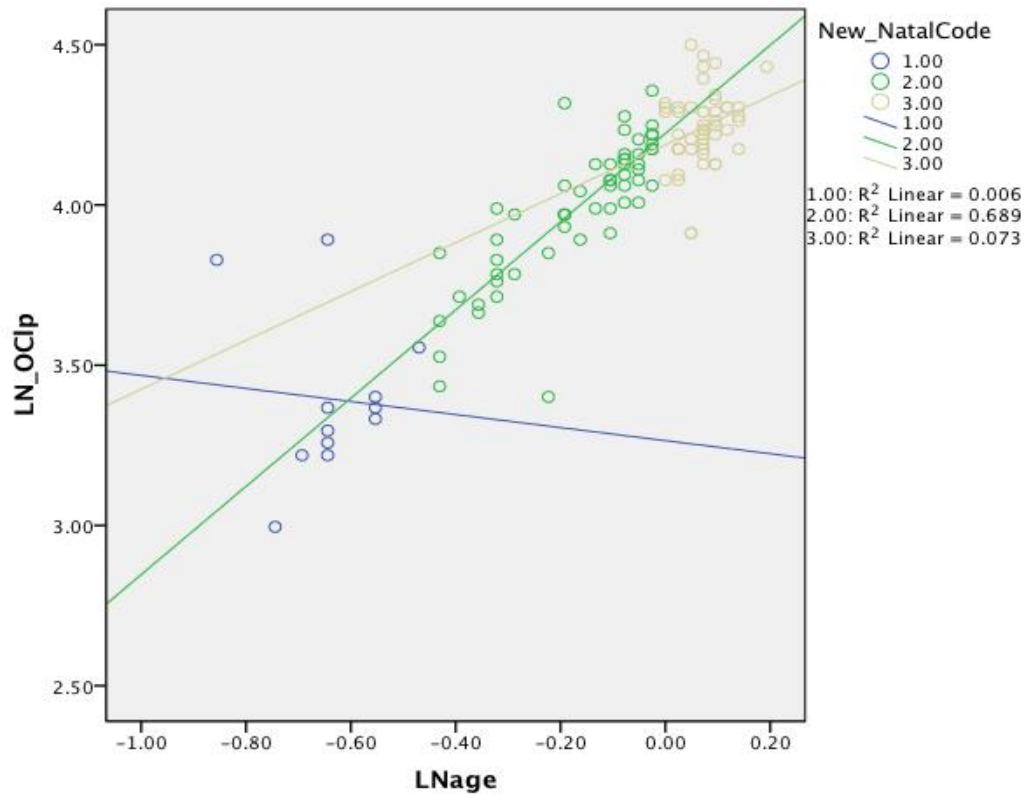
Figure 4.11 Occipital Length Arc to Age

Table 4.11 Occipital Length Arc (OClp)
Slopes and Y-Intercepts with corresponding Confidence Intervals (low and high) and standard errors for arc of occipital bone.

Variable	#	Age	Std Err	Low	B	High	Std Err	Low	Y-Inter	High
OClp	11	≤26wks	0.798	-1.768	-0.204	1.360	0.514	2.258	3.265	4.272
OClp	56	27-40wks	0.125	1.132	1.377	1.622	0.026	4.172	4.223	4.274
OClp	48	40+wks	0.397	-0.015	0.763	1.541	0.033	4.123	4.188	4.253
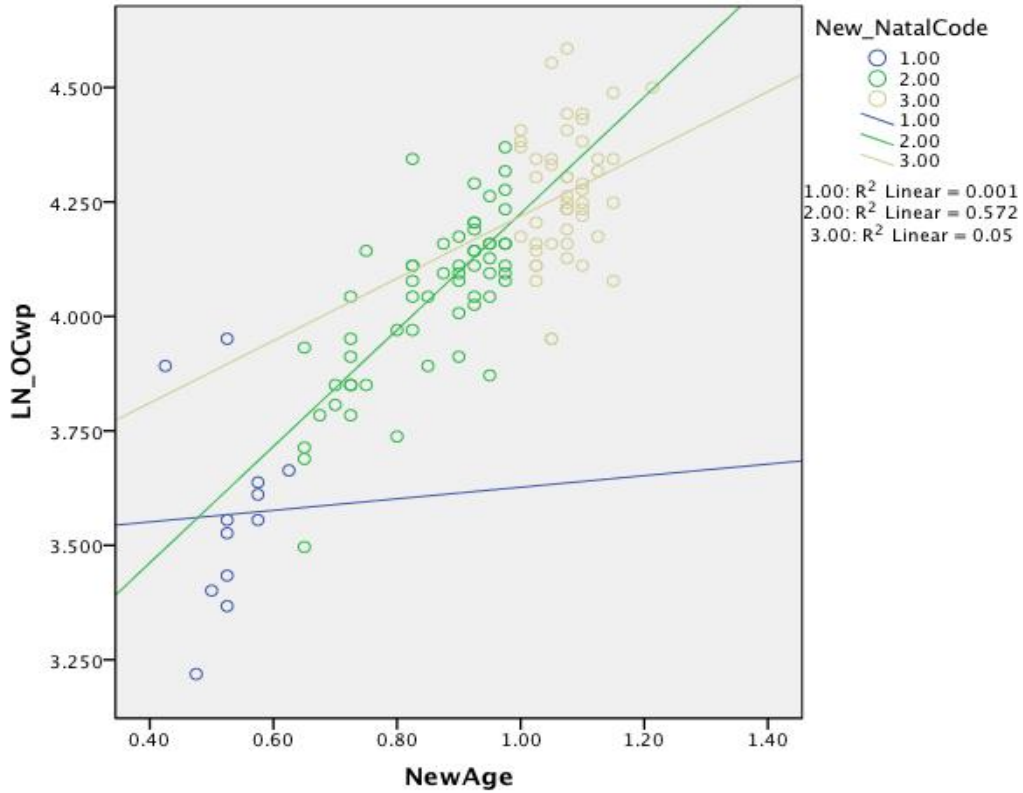
Figure 4.12 Occipital Width Arc to Age

Table 4.12 Occipital Width Arc (OCwp)
Slopes and Y-Intercepts with corresponding Confidence Intervals (low and high) and standard errors for arc of occipital bone.

Variable	#	Age	Std Err	Low	B	High	Std Err	Low	Y-Inter	High
OCwp	11	≤26wks	0.654	-1.278	0.004	1.286	0.421	2.745	3.570	4.395
OCwp	57	27-40wks	0.118	0.814	1.045	1.276	0.025	4.164	4.213	4.262
OCwp	47	40+wks	0.474	-0.208	0.721	1.650	0.039	4.143	4.219	4.295

Pearson's Correlations With and Without Control for Age: Arc and Chord measurements for length and width were also subjected to a Pearson's bivariate correlation. The results can be viewed in Table 4.13 for chord length and width measurements. This table suggests that all measurements are highly correlated when no control is indicated. Correlated values are tightly clustered between 0.929 and 0.973, with a spread in values of only 0.044. When the values are then subjected to a two-tailed test controlled for age against chord measurements, significance for each value falls substantially, as seen in Table 4.14. Correlation between variables are now no longer within such narrow correlation values, but spreads from 0.582 to 0.816, a jump to a difference of 0.234. Correlations with lower values for Table 4.14 are indicative of a lesser relationship of size to age, and shows high values for relationships of measurements of the occipital, and only to a lesser extent for the frontal and parietal.

Results of Pearson's bivariate correlations preformed on arc measurements show similar values compared to those for chord measurements but significant only at slightly lower level correlation coefficients. Values for the relationship of arc to size without the control for age can be viewed in Table 4.15, range from 0.886 to 0.954, with a difference between the highest and lowest values of 0.068, and is slightly wider than that for size, but not significantly so and still similar to that seen with the relationship for size. When the control is applied to the values for shape in Table 4.16, values once again drop while the range widens. With age as the control, values now range from 0.540 to 0.811, roughly the same range of 0.271, as that for size.

Table 4.13 Pearson's Correlation of Cranial Elements (Length and Width) Cord Measurements

		FRlc	FRwc	PRlc	PRwc	OClc	OCwc
FRlc	Pearson Correlation	1	.973**	.959**	.966**	.950**	.941**
	Sig. (2-tailed)		.000	.000	.000	.000	.000
	N	129	129	112	115	127	128
FRwc	Pearson Correlation	.973**	1	.960**	.966**	.938**	.934**
	Sig. (2-tailed)	.000		.000	.000	.000	.000
	N	129	130	113	115	128	129
PRlc	Pearson Correlation	.959**	.960**	1	.948**	.932**	.929**
	Sig. (2-tailed)	.000	.000		.000	.000	.000
	N	112	113	115	112	114	114
PRwc	Pearson Correlation	.966**	.966**	.948**	1	.938**	.939**
	Sig. (2-tailed)	.000	.000	.000		.000	.000
	N	115	115	112	117	115	116
OClc	Pearson Correlation	.950**	.938**	.932**	.938**	1	.955**
	Sig. (2-tailed)	.000	.000	.000	.000		.000
	N	127	128	114	115	131	131
OCwc	Pearson Correlation	.941**	.934**	.929**	.939**	.955**	1
	Sig. (2-tailed)	.000	.000	.000	.000	.000	
	N	128	129	114	116	131	132

**. Correlation is significant at the 0.01 level (2-tailed).

Table 4.14 Partial Correlation of Cranial Elements (Length and Width) Cord Measurements Controlled for Age

Control Variables			FRlc	FRwc	PRlc	PRwc	OClc	OCwc
NewAge	FRlc	Correlation	1.000	.816	.748	.734	.663	.659
		Significance (2-tailed)	.	.000	.000	.000	.000	.000
		df	0	101	101	101	101	101
	FRwc	Correlation	.816	1.000	.779	.749	.582	.610
		Significance (2-tailed)	.000	.	.000	.000	.000	.000
		df	101	0	101	101	101	101
	PRlc	Correlation	.748	.779	1.000	.713	.633	.690
		Significance (2-tailed)	.000	.000	.	.000	.000	.000
		df	101	101	0	101	101	101
	PRwc	Correlation	.734	.749	.713	1.000	.589	.646
		Significance (2-tailed)	.000	.000	.000	.	.000	.000
		df	101	101	101	0	101	101
	OClc	Correlation	.663	.582	.633	.589	1.000	.735
		Significance (2-tailed)	.000	.000	.000	.000	.	.000
		df	101	101	101	101	0	101
	OCwc	Correlation	.659	.610	.690	.646	.735	1.000
		Significance (2-tailed)	.000	.000	.000	.000	.000	.
		df	101	101	101	101	101	0

Table 4.15 Pearson's Correlation of Cranial Elements (Length and Width) Arc Measurements

		FRlp	FRwp	PRlp	PRwp	OClp	OCwp
FRlp	Pearson Correlation	1	.954**	.919**	.924**	.924**	.900**
	Sig. (2-tailed)		.000	.000	.000	.000	.000
	N	124	123	113	114	121	121
FRwp	Pearson Correlation	.954**	1	.932**	.925**	.914**	.886**
	Sig. (2-tailed)	.000		.000	.000	.000	.000
	N	123	123	113	114	121	121
PRlp	Pearson Correlation	.919**	.932**	1	.932**	.912**	.879**
	Sig. (2-tailed)	.000	.000		.000	.000	.000
	N	113	113	115	115	114	113
PRwp	Pearson Correlation	.924**	.925**	.932**	1	.918**	.894**
	Sig. (2-tailed)	.000	.000	.000		.000	.000
	N	114	114	115	116	114	114
OClp	Pearson Correlation	.924**	.914**	.912**	.918**	1	.944**
	Sig. (2-tailed)	.000	.000	.000	.000		.000
	N	121	121	114	114	124	123
OCwp	Pearson Correlation	.900**	.886**	.879**	.894**	.944**	1
	Sig. (2-tailed)	.000	.000	.000	.000	.000	
	N	121	121	113	114	123	124

**. Correlation is significant at the 0.01 level (2-tailed).

Table 4.16 Pearson's Correlation of Cranial Elements (Length and Width) Arc Measurements Controlled for Age

Control Variables			FRlp	FRwp	PRlp	PRwp	OClp	OCwp
NewAge	FRlp	Correlation	1.000	.811	.635	.639	.642	.623
		Significance (2-tailed)	.	.000	.000	.000	.000	.000
		df	0	102	102	102	102	102
	FRwp	Correlation	.811	1.000	.672	.636	.562	.545
		Significance (2-tailed)	.000	.	.000	.000	.000	.000
		df	102	0	102	102	102	102
	PRlp	Correlation	.635	.672	1.000	.644	.576	.540
		Significance (2-tailed)	.000	.000	.	.000	.000	.000
		df	102	102	0	102	102	102
	PRwp	Correlation	.639	.636	.644	1.000	.626	.624
		Significance (2-tailed)	.000	.000	.000	.	.000	.000
		df	102	102	102	0	102	102
	OClp	Correlation	.642	.562	.576	.626	1.000	.786
		Significance (2-tailed)	.000	.000	.000	.000	.	.000
		df	102	102	102	102	0	102
	OCwp	Correlation	.623	.545	.540	.624	.786	1.000
		Significance (2-tailed)	.000	.000	.000	.000	.000	.
		df	102	102	102	102	102	0

Chapter V: Discussion

It has long been suggested that the human infant brain continues to grow at fetal rates throughout the first full year of life, if not beyond (Bogin, 1999; Ponce de León, et al., 2008; Vinicius, 2005). This is thought to be due to the increased degrees of encephalization of the human brain under evolutionary forces. Some forces that may have contributed to the selection for an ever enlarging brain may have included changes in environments and climates, need for additional social skills due to population increases and closer proximity to others, lengthening life histories, or increasing competition with other hominid species (Bogin, 1999; Ponce de León, et al., 2008; Rosenberg, 1992; Wortham and Kuzara, 2005). The hominid brain is the most energy expensive organ to maintain and an increase in size demanded a change in diet. The need for nutritional alterations may have also encouraged an increase in proximity with other members of the same or different species (Aiello and Wheeler, 1995; De Silva, et al., 2008; McNamara, 2002a; McNamara, 2002b; Wortham and Kuzara, 2005).

The shift to upright locomotion of hominids placed physiological restrictions on the dimensions of the female pelvis that could be reached without hindering the ability to be fully bipedal (Berge, 1998; De Silva, et al., 2008; Jordaan, 1976; Ponce de León, et al., 2008; Rosenberg, 1992; Steel, 2006; Whitcome, et al., 2007). Limitations on the size of the pelvic outlet as a result of the change in the overall morphology necessitated a constraint on fetal head dimensions for successful passage a the fetus. Some researchers have stated that a post-parturition increase in brain volume can be seen as

an evolutionary response to the need for a larger adult brain that is restricted for size at birth by bipedalism (Alba, 2002; Berge, 1998; De Silva, et al., 2008; Hawkes, 2006a; Jordaan, 1976; McNamara, 2002a, Ponce de León, 2008Rosenberg, 1992; Steel, 2006; Whitcome, et al., 2007).

Although the infant brain does grow rapidly after birth, studies have not been conducted to determine at what point the speed of growth begins to slow from the rapid pace seen during fetal development. It is with this in mind that the collection and analysis of measurements of fetal and infant crania was undertaken. The purpose of this study was to determine at what point the increase of brain tissue volume and the capacity of the surrounding structures begin to alter the pace of acceleration seen in the fetus. The cranial elements of 133 individuals from 16 weeks gestation to three months post-natal were examined at the Smithsonian Institute in Washington, DC. A total of six measurements were taken to determine size of fetal and infant crania: length chord and arc and width chord and arc of the frontal, parietal and occipital bones.

The measurements of fetal cranial elements were examined with ANCOVA to extrapolate slopes for rates of growth to determine at what age volume increase slows. This research will suggest that there is a significant decrease in the rate of infant brain/cranial growth well before the age of 6 postnatal months. Through analyzing the slopes, along with the high and low boundaries based on mathematically determined confidence intervals, it was determined that although chord measurements of the fetal and infant crania are tightly correlated to the age of an individual, arc measurements do not adhere to strict increase based on age. The analysis of the data also suggest that

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although the rate of cranial growth of the infant skull is generally at or slightly above that of isometry, fetal rates are significantly above the expectations of isometric growth and rates of growth. Thus, it can be stated that rates are not carried over through the first full year of life.

It is only in the earliest developmental stages of the cranial elements that rates of growth for four of the measurements fall below the line of isometry. During the second stage of growth for fetal skulls, all values for all measurements are at or above expected isometry. While many have suggested that this rate is carried over through at least the first year of life (Coqueugnoit, et al., 2004; Jordaan, 1976; Vinicius, 2005), the speed at which increase occurs declines as soon as three post-natal months. All postnatal rates of growth are estimated above zero, indicating some degree of growth, but still falling far below the rates for prenatal growth and lines of isometric growth.

As a result of this study, it can be interpreted that the evolution of the human species has developed a timing schedule to attain the full adult size that allows for an increase in the degree of encephalization necessary during gestation and in a brief interval after birth. This research shows that during gestation the fetal brain grows much more rapidly during the third trimester than at any time in the human life cycle. Though it should also be noted that when attempting to measure the degree of volume achieved in the adult, that the duration of growth is substantially longer after birth than it is before, continuing until approximately 10 years of age (Coqueugnoit,et al., 2004; McNamara, 2002a). The length of time the human brain grows during gestational is limited to only ten lunar months, but after birth growth is estimated to be as long as ten years before

size reaches 95% of adult values (Coqueugnoit, et al., 2004; McNamara, 2002a). Even with this extended time of increase, development is still occurring as a matter of acquiring knowledge for success as a member of the community after the completion of growth.

Chapter VI: Conclusions

An increase in cranial size occurred about two million years ago in the genus *Homo* and may have been selected for by environmental changes, shifts in the climate, or demographic alterations within groups or between groups. Since the mammalian brain grows primarily during gestation, selection for an extended period of fetal rates of brain growth may be coupled with selection for large brain in mature adults in the genus *Homo*. However, rates of brain growth during the gestational period differ significantly from those characterizing the first postnatal year. Although there is a continuation of basic anthropoid cranial growth patterns, cranial growth rates during the first postnatal year are significantly slower. Nevertheless, the percent total of brain size achieved during fetal development, infancy, and early childhood is remarkable. The human brain at birth is 25% of that achieved by maturation, reaches 80% of the expected total by the second birthday, 90% by six years of age, and is completed by 10 years.

Although fetal rates of brain growth are not maintained throughout the first postnatal year, human neonates should be considered extrauterine embryos with respect to their rates of brain growth during the first three postnatal months. This extension of fetal growth into the first three months may need to be viewed as a post-birth 'trimester' and lends considerable value to the growth and development of the human infant. The immense benefit of growth during this period is due to the absolute

gain in volume of brain tissue at a time when the body remains small and the brain to body size ratio is larger than at any other period of postnatal ontogeny. However, the extension of growth rates is not uniform throughout these early periods of human development.

The pre- and postnatal growth of the frontal bone differs from other cranial regions while the parietal shows relatively slower postnatal growth than other dimensions of the cranial vault. Furthermore, the significantly greater curvature of the neonatal cranial vault, other than the width of the parietal in a superior-inferior dimension, can be explained with respect to rates of growth. Although fetal cranial bones grow at a faster rate, the curvature is greater in postnatal infants because of the absolutely larger cerebral volume characterizing neonates and the concomitantly slower growth of the upper face which must accommodate a comparatively small middle and lower facial skeleton. The first three postnatal months nearly mimic the last three prenatal months in terms of cerebral growth; the cranial vault accommodates this further rapid expansion by increasing in curvature rather than in the absolute lengths and widths of the frontal, parietal and occipital bones. These findings would suggest that while the rates of growth in the first few months following birth are more rapid than those seen later months, degrees of increase are significantly reduced and learning skills and acquiring knowledge is of primary importance.

This research may have implications in the framework of paleoanthropological research for better understanding the timing of fetal encephalization.   Relationships between the evolution of the increase in brain volume to bipedalism, along with its correlation to morphological changes of the pelvis, could be further interpreted in the overall advancement that occurred as a result of upright locomotion.   Other areas of study may include that of growth and development across species of hominids further increasing our understanding of the evolution of life histories in anthropoids. Regarding modern humans, comparisons within and between populations could also be useful as a means to determine the effect of nutrition or disease on the developing fetus and early stages in infancy.   Focuses of research such as these would benefit our understanding of the past as well as the future paths of change possible in the genus *Homo* .

REFERENCES

Aiello, LC, and P Wheeler. 1995. The expensive tissue hypothesis: The brain and the digestive system in human and primate evolution. *Current Anthropology* 36(2):199-221.

Alba, DM. 2002. Shape and stage in heterochronic models. *In*: Minugh-Purvis N, and KJ McNamara, editors. Human Evolution through Developmental Change. Baltimore: John Hopkins University Press. P 28-50.

Amiel-Tison, C, J Gosselin, and C Infante-Rivard. 2002. Head growth and cranial assessment at neurological examination in infancy. *Developmental Medicine and Child Neurology* 44(9):643-648.

Anton, S, and SR Leigh. 2003. Growth and life history in *Homo erectus*. *In*: Thompson, JL, GE Krovitz, and AJ Nelson, editors. Patterns of Growth and Development in the Genus *Homo*. Cambridge Cambridge University Press.

Baer, MJ, and JE Harris. 1969. A commentary on the growth of the human brain and skull. *American Journal of Physical Anthropology* 30(1):39-44.

Berge, C. 1998. Heterochronic processes in human evolution: An ontogenetic analysis of the hominid pelvis. *American Journal of Physical Anthropology* 105(4):441-459.

Bogin, B, editor. 1999. Patterns of Human Growth. 2nd ed. Cambridge: Cambridge University Press.

Bogin, B. 2003. The human pattern of growth and development in paleontological perspective. *In*: Thompson JL, GE Krovitz, and AJ Nelson, editors. Patterns of Growth and Development in the Genus Homo. Cambridge: Cambridge University Press.

Bogin, B. 2006. Modern human life history: The evolution of human childhood and fertility. *In*: Hawkes K, and RR Paine, editors. The Evolution of Human Life History. Santa Fe: School of American Research Press.

Cory, TS and KA Collins. 2001. Pediatric Forensic Pathology. *In* Stocker JT and LP Deher, editors. Pediatric Pathology. Philadelphia: Lippincott Williams & Wilkins.

Coqueugniot, H, J.-J. Hublin, F Veillon, F Houët, and T Jacob. 2004. Early brain growth in *Homo erectus* and implications for cognitive ability. *Nature* 431(7006):299-302.

De Silva, JM, and JJ Lesnik. 2008. Brain size at birth throughout human evolution: A new method for estimating neonatal brain size in hominins. *Journal of Human Evolution* 55(6):1064-1074.

Diewert, VM. 1985. Development of human craniofacial morphology during the late embryonic and early fetal periods. *American Journal of Orthodontics* 88(1):64-75.

Epstein, HT, and EB Epstein. 1978. The relationship between brain weight and head circumference from birth to age 18 years. *American Journal of Physical Anthropology* 48(4):471-473.

Farkas, LG, JC Posnick, and TM Kreczko. 1992. Anthropometric growth study of the head. *Cleft Palate-Craniofacial Journal* 29(4):303-308.

Fazekas, IG, and F Kósa. 1978. Forensic Fetal Osteology. Budapest: Akadémiai Kiadó.

Gibson, AT, S Carney, E Cavazzoni, and JK H Wales. 2000. Neonatal and post-natal growth. *Hormone Research* 53(S1):42-49.

Gould, SJ. 1977. Ontogeny and Phylogeny. Cambridge: Belknap Press of Harvard University.

Halcrow, SE, and N Tayles. 2008. The bioarchaeological investigation of childhood and social change: Problems and prospects. *Journal of Archaeological Method and Theory* 15(2):190-215.

Hawkes, K. 2006a. Life history theory and human evolution: A chronicle of ideas and findings. *In*: Hawkes K, and RR Paine, editors. The Evolution of Human Life History. Santa Fe: School of American Research Press.

Hawkes, K. 2006b. Slow life histories and human evolution. *In*: Hawkes K and RR Paine, editors. The Evolution of Human Life History. Santa Fe: School of American Research Press.

Huxley, AK. 2005. Gestational age discrepancies due to acquisition artifact in the Forensic Fetal Osteology Collection at the National Museum of Natural History, Smithsonian Institution, USA. *The American Journal of Forensic Medicine and Pathology* 26(3):216-220.

Inman, VT, and J B de C M Saunders. 1937. The ossification of the human frontal bone. *Journal of Anatomy* 71(3):383-394.

Jablonski, NG, G Chaplin, and K McNamara. 2002. Natural selection and the evolution of hominid patterns of growth and development. *In*: McNamara, N and KJ McNamara, editors. Human Evolution Through Developmental Change. Baltimore: John Hopkins University Press. P 189-206.

Jackes, M. 1994. Birth rates and bones. *In*: Herring A, and L Chan, editor. Strength in Diversity: A Reader in Physical Anthropology. Toronto: Canadian Scholars' Press.

Jeffery, N, and F Spoor 2002. Brain size and the human cranial base: A prenatal perspective. *American Journal of Physical Anthropology* 118(4):324-340.

Jordaan, HV. 1976. Newborn:Adult brain ratios in hominid evolution. *American Journal of Physical Anthropology* 44(2):271-278.

Kamp, KA. 2001. Where have all the children gone?: The archaeology of childhood. *Journal of Archaeological Method and Theory* 8(1):1-34.

Leigh, SR. 1992. Cranial capacity evolution in *Homo erectus* and early *Homo sapiens*. *American Journal of Physical Anthropology* 87(1):1-13.

McNamara, KJ. 2002a. Sequential hypermorphosis: Stretching ontogeny to the limit. *In*: Minugh-Purvis, N and KJ McNamara, editor. Human Evolution Through Developmental Change. Baltimore: John Hopkins University Press.

McNamara, KJ. 2002b. What is heterochrony? In: Minugh-Purvis, N and KJ McNamara, editors. Human Evolution Through Developmental Change. Baltimore: John Hopkins University Press. P 1-4.

Morris-Kay, GM, and AOM Wikkie. 2005. Growth of the normal skull vault and its alteration in craniosynostosis: Insights from human genetics and experimental studies. *Journal of Anatomy* 207(5):637-653.

Murphy, EM. 1996. A possible case of hydrocephalus in a medieval child from Doonbought Fort, Co. Antrim, Northern Ireland. *International Journal of Osteoarchaeology* 6(5):435-442.

Neumann, K, A Moegelin, N Temminghoff, RJ Radlanski, A Langford, M Unger, R Langer, and J Bier. 1997. 3-D-Computed tomography: A new method for the evaluation of fetal cranial morphology. *Journal of Craniofacial Genetics and Developmental Biology* 17(1):9-22.

Ponce de León, M, L Golovanova, V Doronchev, G Romanova, T Akazawa, O Kondo, H Ishida, and CPE Zollikofer. 2008. Neanderthal brain size at birth provides insights into the evolution of human life history. *Proceedings of the national Academy of Sciences of the United States of America* 105(37):13764-13768.

Rice, SR. 2002. The role of heterochrony in primate brain evolution. *In*: Minugh-Purvis, N and KJ McNamara, editors. Human Evolution Through Developmental Change. Baltimore: John Hopkins University Press.

Robson, SL, CP van Schaik, and K Hawkes. 2006. The derived features of human life history. *In*: Hawkes K, and RR Paine, editors. The Evolution of Human Life History. Santa Fe: School of American Research Press.

Rosenberg, KR. 1992. The evolution of modern human childbirth. *Yearbook of Physical Anthropology* 35:89-124.

Sardi, ML, F Ventrice, and FR Rozzi. 2005. A cross-sectional study of human craniofacial growth. *Annals of Human Biology* 32(3):390-396.

Sardi, ML, F Ventrice, and FR Rozzi. 2007. Allometries throughout the late prenatal and early postnatal human craniofacial ontogeny. *The Anatomical Record* 290(9):1112-1120.

Scheuer, L, and S Black. 2000. Developmental Juvenile Osteology. San Diego: Elsevier Academic Press.

Schultz, AH. 1969. The Life of Primates. New York: Universe Books.

Shea, B. 1989. Heterochrony in human evolution: The case for neoteny reconsidered. *American Journal of Physical Anthropology* 32 S10:69-101.

Sherwood, RJ, RS Meindl, HB Robinson, and RL May. 2000. Fetal age: Methods of estimation and effects of pathology. *American Journal of Physical Anthropology* 113(3):305-315.

Sivan, Y, P Merlob, and SH Reisner. 1984. Head measurements in newborn infants. *Journal of Craniofacial Genetics and Developmental Biology* 4(4):259-263.

Smith, BH. 1991. Dental development and the evolution of life history in Hominidae. *American Journal of Physical Anthropology* 86(2):157-174.

Thompson, JL, Gail E Krovitz, and Andrew J Nelson. 2003a. Hominid growth and development: The modern context. *In*: Thompson JL, GE Krovitz, and AJ Nelson, editors. Patterns of Growth and Development in the Genus *Homo*. Cambridge: Cambridge University Press.

Thompson, JL, GE Krovitz, and AJ Nelson. 2003b. Introduction. *In*: Thompson JL, GE Krovitz, and AJ Nelson, editors. Patterns of Growth and Development in the Genus *Homo*. Cambridge: Cambridge University Press.

Trenouth, MJ. 1991. Relative growth of the human fetal skull in width, length, and height. *Archives of Oral Biology* 36(6):451-456.

Turner, JS. 2007. The Tinkerer's Accomplice Cambridge: Harvard University Press.

Vinicius, L. 2005. Human encephalization and developmental timing. *Journal of Human Evolution* 49(6):762-776.

Whitcome, KK, LJ Shapiro, and DE Lieberman. 2007. Fetal load and the evolution of lumbar lordosis in bipedal hominins. *Nature* 450(7172):1075-1078.

Williams, FL, L Godfrey, and M Sutherland. 2002. Heterochrony and the evolution of Neandertal and modern human craniofacial form. *In*: Minugh-Purvis N and KJ McNamara, editors. Human Evolution Through Developmental Change. Baltimore: John Hopkins University Press.

Williams, FL, LR Godfrey, and M Sutherland. 2003. Diagnosing heterochronic perturbations in the craniofacial evolution of *Homo* (Neandertals and modern humans) and *Pan* (*P. troglodytes* and *P. paniscus*). *In*: Thompson, JL, GE Krovitz, and AJ Nelson, editors. Patterns of Growth and Development in the Genus *Homo*. Cambridge Cambridge University Press.

Wortham, C and J Kuzara. 2005. Life history and the early origins of health differentials. *American Journal of Human Biology* 17(1):95-112.

Wright, LE and CJ Yoder. 2003. Recent progress in bioarchaeology: Approaches to the Osteological Paradox. *Journal of Archaeological Research* 11(1):43-70.