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Investigating Pterion from Two Perspectives: Phylogenetics and Biomechanics

Nambi Gamet
Western Washington University, gametn@wwu.edu

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Investigating Pterion from Two Perspectives: Phylogenetics and Biomechanics

By Nambi Gamet

Accepted in Partial Completion
of the Requirements for the Degree
Master of Arts

Kathleen L. Kitto, Dean of the Graduate School

ADVISORY COMMITTEE

Chair, Dr. Joan Stevenson

Dr. Sarah Campbell

Dr. Roger Anderson

Masters's Thesis

Signature: Nambi Gamet

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Investigating Pterion from Two Perspectives: Phylogenetics and Biomechanics

A Thesis
Presented to
The Faculty of
Western Washington University

In Partial Fulfillment
Of the Requirements for the Degree
Master of Arts

By
Nambi J. Gamet
March 2017

Abstract

Pterion is a skull landmark located directly behind the orbits where four cranial bones (sphenoid, parietal, temporal and frontal) articulate in 4 basic configurations: spheno-parietal, fronto-temporal, stellate and epipteric. Two hypotheses may explain the configurations and other aspects of pterion: 1) phylogenetic history reflected in conservative development in species with shared ancestry and 2) biomechanical forces due to chewing stressors on skull shape. Impacts of phylogenetics and biomechanics may be highlighted through the diversity of skull used.

Skulls from UW's Burke Museum were assessed for pterion pattern, suture length and masseter and temporalis muscles in: *Canis latrans* (30), *Vulpes vulpes* (30), *Ursus americanus*, (30), *Puma concolor* (18), *Lynx rufus* (30), *Papio hamadryas* (8), *Saimiri sciureus* (8), *Odocoileus hemionus* (14), *Cervus elaphus* (4), *Lepus americanus* (21). Chi-square tests were used to test for an association of pterion pattern x Order, Family and Genus (Phylogenetics). Chi-squares are used to test for an association between pterion pattern and suture complexity (Biomechanics). Linear regressions are used to identify biomechanical predictors on cranial suture length.

The results of the analysis provide evidence to support pterion is conservative at each phylogenetic level and that biomechanical variables do predict some of the variation in cranial suture length. This analysis is one of a handful to move beyond the traditional comparative approach and highlight the importance of phylogenetic relatedness and biomechanics influences on pterion.

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Chapter 1: Introduction

The skull consists of bones surrounding the brain (cranium), the facial bones and the lower jaw or mandible (White, 2012). The developmental trajectory of the skull is typical of other mammals. The factors affecting the human skull bones, and growth and development are still being worked out. The cranium seems to be an invariant structure housing and protecting critical organs, but it is more flexible than that and not uniform in its thickness or in the shapes of muscle attachments. This bony housing protects the brain, sense organs, and is uniquely shaped in every species but there is also much variation relative to sex, age, and the behavioral activities unique to a single individual.

The published literature on the human skull in physical anthropology has focused largely on cranial variation (Boas, 1912; Howells, 1973, Howells, 1989; Gravlee et al., 2003) and the changes associated with the shift from quadruped to obligate bipedal posture (Elftman and Manter, 1935; Fleagle et al., 1981; Lovejoy et al., 2002; Schmitt, 2003; Harcourt-Smith and Aiello, 2004). Brain size has varied among fossil hominins depending on the changes in the underlying soft tissue. The nature of the changes can only be inferred indirectly from impressions on the inside of fossil crania or endocasts (Holloway, 1981; Broadfield et al., 2001; Vannucci et al., 2011). What we know about human evolution has been enriched by the discoveries of *Australopithecus sediba* (Berger et al., 2010) and *Homo naledi* (Berger et al., 2015) with relatively complete cranial and post cranial elements. Other factors causing variability in cranial morphology include, the influence of diet and the muscles of mastication (Herring et al., 2001; Nogueira et al., 2005; Paschetta et al., 2010)

The intricacy of the interrelationships of the various component bones makes it difficult to determine what factors influence 1) the various trajectories for individual bone development as well as 2) evolution of skull bones, muscle attachments, sensory organs and the organization and size of the brain in response to ecological pressures.

The focus of this analysis is to explain factors that influence the articulation patterns at pterion. Pterion is located directly behind the eye orbits in the temporal fossa. Four bones meet at pterion (Murphy, 1956; Ilknur et al., 2009; White 2012). Surgeons prefer to penetrate the cranium at pterion because it is the thinnest part of the skull, close to the optic nerve canal, and the middle cerebral and meningeal arteries which are often sites of aneurysms or hematomas (Yasagril, 1989). Some medical professionals, have mistaken bone contacts at pterion as fractures (Satpute & Wahane, 2015). Thus, there is some confusion about the etiology and typical expression of pterion.

The history of pterion will be reviewed in Chapter 2. The goal of this chapter is to cover the classifications of pterion and how minimally invasive surgery furthered the investigations into pterion. The anatomy and development of the skull as well as biomechanical influence on bone development will be discussed in Chapter 3. The impact of biomechanics on cranial and suture morphology will be reviewed in Chapter 4, in Chapter 5, the phylogenetic relationships among taxa and how their histories are reflected in statistical characterizations will be considered. Sample design and statistics for this research are presented in the Methods, Chapter 6. Chapter 7 will present the results of the research, while Chapter 8 will discuss the broader implications of the analysis. Chapter 9 will present the conclusions of this analysis.

Chapter 2: History of Pterion Research

At pterion, typically four cranial bones, the sphenoid, parietal, temporal and frontal articulate in one of four possible patterns (see Figure 1). These patterns were first noted by Broca in 1875 on his work describing the human skeleton. The research that followed split into two trajectories regarding the nature of pterion. Initial efforts were exploratory and descriptive. Investigators identified the articulation patterns at pterion in human and non-human primates (Collins, 1925; Collin, 1926; Collins, 1930; Montagu, 1930; Montagu, 1933; Murphy, 1956). The second research thrust was to understand pterion relative to clinical concerns (Wilson, 1971; Yasagril et al., 1976; Yasagril et al., 1987; Oguz et al., 2004; Mwachaka et al., 2008; Ma et al., 2012). The clinical goal is to establish a landmark that would serve as an entry point for surgical interventions. Surgeons prefer to penetrate bone that is less obstructive (thinner) and is consistently located relative to structures such as stroke-prone arteries. There has been little research trying to explain the influences on the development of a particular pattern at pterion.

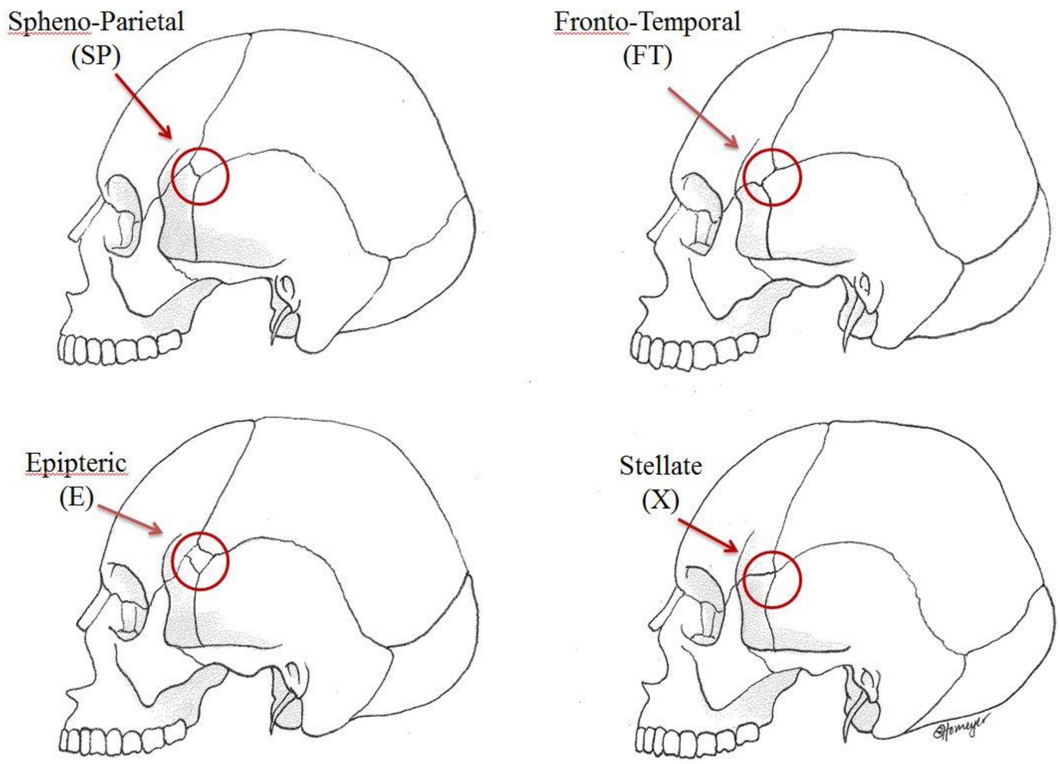

Figure 1. Four classifications of pterion. Drawing by Sarah Homeyer (SH)

2.2 - Classification of Patterns at Pterion

Per Montagu (1933), Broca identified 3 articulation patterns typically found at pterion in humans: the spheno-parietal (SP), fronto-temporal (FT) and stellate (X) pterion patterns. The Epipteric (E) pattern occurs when an epipteric (wormian) bone is present (Parker, 1905). The SP pattern occurs when the sphenoid and the parietal bone articulate and prevent the frontal and the temporal bone from making contact. The FT pattern occurs when the frontal and temporal bones articulate preventing the sphenoid and the temporal bone from making contact. The X pattern occurs when all four bones articulate at a single point. The SP, FT, X and E patterns have been observed in varying proportions in all primates (Montagu, 1933; Murphy, 1956; Wang et al., 2006; Ma et al., 2012).

The E pattern complicates classification schemes because it is unknown why the epipteric bone occurs. Patten (per Montagu 1933) operated under the assumption that epipteric bones were simply wormian bones. Wormian bones are extra sutural bones that occur in various sutures (Parker, 1905). However, Ranke (as in Montagu 1933) believed that epipteric bones occur because of a separate ossification center from the sphenoid. If the portion of the wing of the sphenoid does not fuse, it becomes a single bone known as an epipteric bone. It also makes the classification of the E type difficult because epipteric bones can vary in number and size. The size of these extra sutural bones range from less than a millimeter to greater than five millimeters and the number of bones can range from one to greater than ten (Parker; 1905; Bellary et al., 2013). There are many differing categorizations based on the presence of epipteric bones (Montagu, 1933; Murphy, 1956; Agarwal et al., 1980) but none has become the standard for classifying epipteric bones at pterion. Regardless of the origins of epipteric bones or the categorization used, studying the origins behind epipteric bones may reveal the mechanisms that affect pterion. Contemporary investigations of epipteric bones have concluded they are likely wormian bones that originate as a combination of genetic and epigenetic factors (Cremin, 1982; Sanchez-Lara et al., 2007; Bellary et al., 2013).

Montagu (1933:161) noted that there were at least 100,000 mentions of pterion in primate anatomy literature during the 58 years that followed Broca’s publication, but no one before 1933 had attempted to characterize the patterns diversity systematically. He noted confusion about the morphologies of different patterns and a lack of consistency in the reporting of the patterns at pterion (Montagu, 1933). Montagu notes that patterns are discerned more readily with larger samples (N = 7828). He reviewed the definitions of pterion and then devised his own definition that he thought was more replicable. New ordinal descriptors were based upon the types of contact between bones; sphenoid, parietal, frontal, temporal. These ordinal descriptors were further discerned based upon pterions location on the skull. Such as low, medium or high, and whether the contact between the bones was broad, moderate or narrow. Montagu derived a sequence of primitive to more derived characteristics of pterion and used the sequence to determine phylogenies. He then examined pterion patterns in 183 species of primates using the 16 patterns he found among the order. Montagu concluded that the SP occurred most frequently in *H. sapiens sapiens* (87.8%), *P. pygmaeus* (orangutans) 67.7% and *H. lar* (gibbons) 84.3%, but the FT patterns occurred most frequently in *G. gorilla* 94.7% and *P. troglodytes* (chimpanzees) 95.8%.

Montagu (1933) argued the 16 patterns of pterion resulted from an evolutionary sequence of changes, and thus represented phylogenetic relationships. Montagu used his 16 patterns to justify pterion as a diagnostic characteristic to establish phylogenetic relationships. These 16 patterns were established by observing the subtle morphological differences among the primate order. The size of the malar is used as a diagnostic character in establishing the pterion pattern. Two of Montagu’s patterns are the zygomatic spheno-parietal type (ZSP) and the basal zygomatic spheno-parietal type (BZSP). The ZSP occurs when the alisphenoid (greater wing of the sphenoid) and frontal meet at the mid-malar level “thus narrowly disrupting the contact between the malar and the parietal, the malar remains broadly flared upon the side of the skull” (pg. 291). The difference between the ZSP and the BZPS is that “the alisphenoid articulates with the frontal and the parietal at a higher level, that is, to within one-fourth of the fronto-malare level” (pg. 291). The difference between the two lays a fraction of the distance above the fronto-malar level. Montagu’s classifications are impacted by the existing cranial morphology, which show only a few millimeters in difference. It is important to note that he is only confident that pterion can be used as a diagnostic character at the family level. This is likely due to the frequency of multiple patterns within a lineage.

Montagu's investigations also included a sample of human populations, to which he applied the standard three pterion patterns identified by Broca. Montagu's classification of pterion in human populations came to these conclusions 1) the SP pattern occurs most frequently in "higher races" otherwise those of Caucasian descent and 2) that the FT pattern occurs in the "lower races of mankind." Montagu did admit that it is the frequency of patterns and not the patterns themselves that were used to distinguish "higher and lower races." Unfortunately, Montagu's conclusions were generated during the racist paradigms of the 1930's. His later works, however, did much to combat racism in anthropological research. His meticulous efforts to describe the basic sutural configurations laid the groundwork for future research efforts to explain the diversity of patterns at pterion.

Murphy (1956) extended the efforts of Montagu by examining whether some of the variation was due to sexual dimorphism, age and bilateral asymmetry in a sample of Australian Aborigines (N = 368, 185 males: 131 females). Like Montagu he found no difference by age or sex in the types and relative frequencies of the various pterion patterns. Sides matched about 73.9% of the time no matter what the pterion suture pattern. Murphy (1956) also measured four scale variables: pterion value (length of sutural contact depending on the pattern), cranial index (the ratio of cranial width/cranial length x 100), post-orbital constriction (narrowing of the skull behind the eye orbits) and basi-cranial angle (angle created between the dorsum sellae, nasion and basion). Murphy hypothesized that all four of these features capture unique aspects of the human skull that might affect growth of the four bones comprising pterion.

Murphy plotted the frequency distribution of pterion pattern lengths noting a bimodal distribution, which he concluded to reflect developmental pressures. Murphy then averaged each of the three remaining variables for each suture pattern. The averages differed little although he did not perform t-tests or ANOVA. He also counted the proportion of skulls with an ethmoidal spine for each sutural pattern and again the proportions present were similar no matter what pattern. Like Jones (1928), Murphy concluded that the uniform findings—no matter the pattern— imply genetic control but there is also much variability within humans, even within ethnic groups.

The statistical manipulations by Murphy are difficult to interpret and statistically inaccurate. For example, he attempted to correlate a categorical variable of pterion, with the mean value of the cranial index, post-orbital breadth, basi-cranial angle and presence/absence of the ethmoid spine. Correlations measure the linear relationship between two scale variables (Ha & Ha, 2012; Whitlock & Schluter, 2014), expressed as a value between -1 and 1. In Murphy's analysis, only the mean value and standard deviations are provided for each variable.

Murphy briefly discusses how biomechanical and genetic factors may affect pterion but fails to connect his work to these hypotheses. He is the first however, to suggest biomechanical and genetic perspectives be considered when studying pterion. Murphy was the first to provide a quantitative assessment of pterion in relation to variables such as cranial flexion, ethmoid spine and post-orbital breadth. His work showed that pterion occurs symmetrically more than asymmetrically and that age, sex and side have no significant impact on the type of pattern and that the SP type occurs most frequently in Australian aborigine.

Investigations into pterion over the last two centuries primarily focused on identifying frequencies of patterns within various populations. The most cited studies focused on pterion patterns in human and non-human primates (Montagu, 1933; Murphy, 1956; Agarwal et al., 1980; Oguz et al., 2004; Wang et al., 2006; Ilknur et al., 2009). See Table 1 for the frequency of pterion patterns in several studies of human populations.

The limitations of the above-mentioned studies are 1) they are all qualitative, 2) they lack a comprehensive identification method for patterns, and 3) they do little to identify the factors behind the variation found at pterion. The research has remained mainly descriptive, but even though these descriptive patterns were useful, when minimally invasive surgery began, it became clear that more quantitative methods would be needed. This is because population variation was relevant to surgical success (Wilson, 1971; Yasagril et al., 1976; Yasagril et al., 1987).

Table 1. Pterion frequency in various populations (*) indicates a recalculation of data.

Population (n)	**SP Pattern (%)**	**FT Pattern (%)**	**X Pattern (%)**	**E Pattern (%)**	**Source**
Nigerian (62)	86.1	8.3	5.6	0	Adejuwon et al., 2013
Indian (450)	71.2	4.35	2.17	23	Agarwal et al., 1980
Anatolian (128)	85.2	1.1	5.5	8.2	Aksu et al., 2014
Nigerian (50)	83	5	6	6	Eboh & Obaroefe, 2014
Anatolian: 13th Century (16)	87.5	6.25	0	6.25	Ilknur et al., 2009
20th Century (28)	89.2	3.6	3.6	3.6	Ilknur et al., 2009
Indian (40)	86.25	11.25	2.5	0	Kumar et al., 2013
*Indian (76)	78.3	5.2	0	16.4	Ma et al., 2012
*Australian (368)	73.25	7.75	18.3	2.5	Murphy, 1956
Kenyan (90)	66	15	12	7	Mwachaka et al., 2009
Turkish (26)	88	10	0	2	Oguz et al., 2004
Nigerian (80)	84.79	10.11	5.06	0	Saxena, 1988
Indian (144)	95.13	3.46	3.46	0	Saxena, 1988

2.3 – Pterion and Minimally Invasive Surgery.

Minimally invasive surgery stimulated a new wave of investigations into pterion because variation in the expression of this trait would require adjustments to a procedure advocated in 1971 by Wilson, the pterion keyhole approach. In this approach, an incision is made anterior to the ear towards the fronto-zygomatic suture. Burr holes are then drilled between the frontal bone and pterion anterior to the zygomatic arch. The wing of the sphenoid is then removed providing access to critical soft tissues.

This protocol reduces brain exposure and shortens recovery time (van Lindert et al., 1998; Wang & Luo et al., 2016), thus it is a preferred entry strategy to treat brain aneurysms and hematomas or to gain access to the optic canals (Wilson, 1971; Yasagril et al., 1976; van Lindert et al., 1998; Wang & Luo et al., 2016). The pterional keyhole approach highlights the importance of an adequate understanding of pterion. The ensuing investigations into population variation provided the groundwork for better identification of pterion's location.

Research on pterion has increased as the pterional keyhole approach gained popularity. Investigations primarily focused on establishing pterion's location relative to other cranial landmarks (Oguz et al., 2004; Mwachaka et al., 2008; Ilknur et al., 2009; Ma et al., 2012; Adejuwon et al., 2013; Aksu et al., 2014; Eboh & Obaroefe, 2014). Consistent relationships between pterion and the surgeon's target tissues would make a successful outcome from surgery more likely.

Pterion itself is a region located in the temporal fossa (Montagu, 1933), but a region that has no set landmark, thus making it important to establish a location when making linear measurements. Multiple methods, however, have been employed when trying to locate the center of pterion. Oguz et al., (2004) draw a circle with the smallest diameter that included all four bones at pterion. Ilknur et al., (2009) use this method when identifying the center of pterion in the E pattern. In Ma et al., 2012, the center of pterion was established by diving the length of the SP and FT suture by 2. There has been no discussion as to establishing the center of pterion in the X pattern. Meindl & Lovejoy (1985) use the anterior junction where the spheno-parietal suture meets the frontal bone as a landmark for pterion. Once the center of pterion has been established, linear measurements have been taken to establish pterions relationship to various cranial landmarks.

Landmarks used to orient pterion on the skull include: the zygomatic arc, midpoint of the zygomatic arc, and fronto-zygomatic suture (Oguz et al., 2004; Mwachaka et al., 2008; Ilknur et al, 2009; Ma et al., 2012). Almost every study measuring pterion relative to cranial landmarks have used the zygomatic arch and the fronto-zygomatic suture as reference points (Oguz et al., 2004; Mwachaka et al., 2008; Ilknur et al., 2009; Ma et al., 2012; Adejuwon et al., 2013; Aksu et al., 2014; Eboh & Obaroefe, 2014). The location of pterion has been identified in Turkish, Kenyan, Nigerian, Anatolian and Indian populations by various researchers and can be found in Table 2.

Table 2. Localization of Pterion. Mean distances from the center of pterion to the fronto-zygomatic suture (FZS) and zygomatic arc (ZA). (*) indicates centimeters.

Population (n)	**Pterion to FZS**	**Pterion to ZA**	**Source**
*Turkish (26)	Left: 3.44±0.40cm Right: 3.30±0.39cm	Left: 3.85±0.25cm Right: 4.05±0.39cm	Oguz et al., 2004
Kenyan (50)	Left: 30.34±4.34mm Right: 30.35±3.40mm	Left: 38.24±3.47mm Right:38.88±3.49mm	Mwachaka et al., 2008
Nigerian (62)	Left: 30.82±0.80mm Right: 31.52±.067mm	Left: 38.77±0.63mm Right: 39.10±0.58mm	Adejuwon et al., 2013
Anatolian (128)	Left: 31.44±4.73mm Right: 31.80±4.51mm	Left: 39.88±4.01mm Right: 40.02±4.06mm	Aksu et al., 2014
Nigerian (50)	Left: 31.08±2.24mm Right: 32.06±2.62mm	Left: 39.52±3.32mm Right: 40.22±2.98mm	Eboh & Obaroefe, 2014
Indian (76)	Left: 25±4.0mm Right:26±4.0mm	Left: 34±4.0mm Right: 34±4.0mm	Ma et al., 2012

Except for Ma et al., (2012) pterion lies approximately 30mm posterior to the fronto-zygomatic suture and approximately 40mm above the zygomatic arch. There is evidence to support that there is no significance between sides for both variables (Mwachaka et al., 2008; Adejuwon et al., 2013). However, Oguz et al., (2004) report a statistically significant difference in sides from pterion to the zygomatic arc. Ma et al., (2012), also report significant differences between the different populations for the two variables. These measurement differences may be due to the method used to measure the distance between variables. In Ma et al., (2012), the horizontal and vertical measures from pterion to the zygomatic arc and pterion to the fronto-zygomatic suture are taken. Other studies measure the direct distance between the center of pterion to the fronto-zygomatic suture. The lack of consistency among the methodologies used to establish pterions location on the skull make it difficult to interpret the variation found among the different populations. However, these investigations provide an approximate location to pterion on the skull. Knowing pterions location can aid surgeons when performing the pterional keyhole approach.

These studies also provide additional knowledge in regards to the patterns at pterion. All support previous finding that the SP pattern occurs the most in human populations and that the FT, E and X patterns occur at different frequencies within populations (Oguz et al., 2004: Mwachaka et al., 2008; Ma et al., 2012; Adejuwon et al., 2013; Aksu et al., 2014; Eboh & Obaroefe, 2014). No study found sexually dimorphic variation among pterion patterns. Yet this recent research does not address functional or evolutionary explanations for the frequencies at which pterion patterns occur within a population. Murphy suggests that the articulations at pterion may be biomechanical but this hypothesis has yet to be tested. Another hypothesis is that the variations arise due to environmental (epigenetic) and genetic factors (Berry & Berry, 1967; Hauser & DeStefano, 1989; Oguz et al., 2004: Mwachaka et al., 2008; Ma et al., 2012; Adejuwon et al., 2013; Aksu et al., 2014; Eboh & Obaroefe, 2014). Contemporary studies of pterion in non-human primates have had a more explicitly evolutionary focus; studies of macaques (Wang et al., 2006) and howler monkeys (Halenar, 2015) highlight the evolutionary significance of pterion suggesting that phylogenetic relatedness may illuminate our understanding of pterion as well.

2.4 – Testing New Hypotheses.

The consistency of patterns in humans and non-human primates has led investigators to hypothesize a genetic component to pterion (Murphy, 1955; Berry and Berry, 1967; Hauser and Destefano, 1989; Mwachaka et al., 2008; Ilknur et al., 2009). Wang et al., (2006) investigated the heritability of the pterion patterns in Rhesus macaques. The strength of this study is that the genealogies of the macaques are well documented. The study included a sample size of n=422 skulls, that represents 66 macaque families. The hypothesis put forward is that the variation in sutural patterns is random in each family, indicating no evidence of heredity. The most frequent pattern in the 66 macaque families was the FT type (86%), followed by the SP type (14%). There was one case of the zygomatico-temporal type (a fronto-temporal variant) type and four X patterns; the epipteric type was not present in the study. Wang et al., (2006) indicate no significant differences between sex. The study indicates that most occurrences of the SP patterns occurred in familial groups, of the 66 groups, 26 (33.1%) exhibited the SP variant. If a mother had the SP pattern her offspring had a greater than 33% chance of also have the variant. Within families', sex also had no impact on the pterion pattern (P=.11).

Based on the results of the study by Wang et al., (2006) it's understood that the less frequent patterns of pterion are heritable. In this case, it is postulated that the SP variant is recessive and that the FT variant is dominant. Since sex has no impact on the formation, the suggestion is made that the trait may be autosomal recessive. It is unclear whether the patterns are a result of mutations, and if they are, how that mutation may have affected the development of the cranium. Based on the findings of Wang et al., (2006) there is evidence to support the hypothesis that genes regulate the patterns at pterion.

Halenar (2015) is the first to investigate Montagu's claim that orbital dimensions influence the patterns at pterion. Montagu posits that orbital dimensions allow for more room at pterion for expansion of the sphenoid bone. Montagu however, does not provide statistical support for this claim. Halenar, (2015) finds no evidence to support that orbital dimension influence pterion patterns in *Alouatta*. Halenar's study suggest that pterion is more reflective of cranial shape variation in *Alouatta* than orbital size. Results presented by Ma et al., (2004) also suggest that cranial size influences pterion.

Wang et al., (2006) and Halenar (2015), provide evidence that pterion traits are under genetic influence and that some aspects of pterion patterns can be attributed to cranial shape variation. These works have all brought forth new questions. Is pterion phylogenetically conservative outside of human and non-human primate species? How do biomechanical forces influence the articulation at pterion? These analyses indicate that pterion has evolutionary and clinical significance.

Chapter 3: Bone Development and Pterion

The human skull comprises three units, the basi-cranium (base), neurocranium (vault) and the viscerocranium face (Som and Naidich, 2013). The process by which the cartilaginous skeletal system ossifies is termed osteogenesis or ossification (Saladin, 2010; Som and Naidich 2013). Cartilage predecessors to bone begin as a fibrous membrane (intramembranous) or as a cartilaginous model (endochondral). At least 100 ossification centers in the skull transform the cartilage to bone starting during the sixth fetal week. Many of the 22 cranial bones develop by both types of ossification. The exceptions are the zygomatics, palatines, maxillae, and lacrimals, which undergo intramembranous ossification. Each bone has ossification centers that begin to appear during the sixth fetal week. Typically, bones have more than one ossification center, e.g., the sphenoid has 19. The following description of skeletal ossification is based on Saladin, (2010); and Som and Naidich, (2013).

There are three cells involved in intramembranous ossification, mesenchymal cells (stem cells), osteoblasts (bone forming) and osteoclasts (bone absorption). The process of intramembranous ossification although complex, can be broken down into four steps. First, mesenchymal cells differentiate into osteoblasts forming an ossification center. See Figure 2.

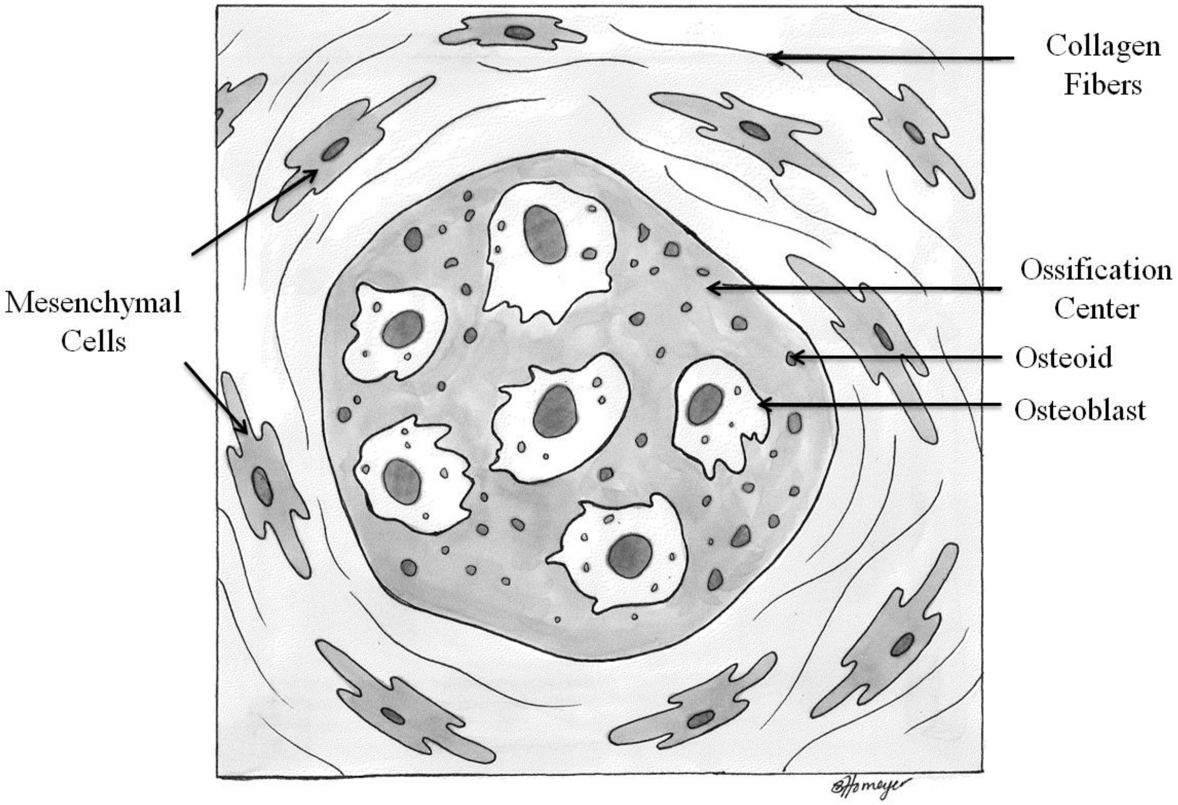

Figure 2. Differentiation of mesenchymal cells to osteoblasts forming a primary ossification center. Drawing by SH.

Second, osteoblasts secrete osteoid (bone matrix) and become entrapped within the developing mineralizing bone. See Figure 3. These trapped osteoblasts become osteocytes tasked with maintaining bone strength and structure. These osteocytes become imbedded in what are called lacunae.

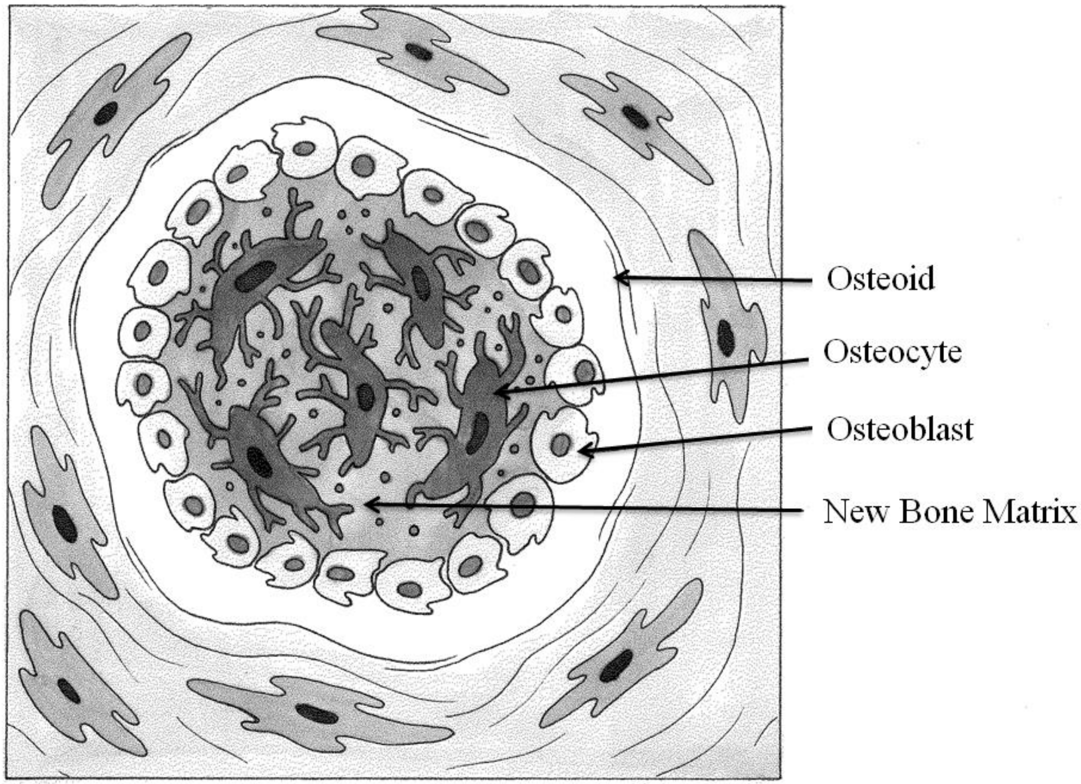

Figure 3. Osteoblasts surrounded in calcified bone matrix becoming osteocytes. Drawing by SH.

Interconnected lacunae within the bone matrix form canaliculi (canals), that pass essential nutrients, chemical signals and remove waste to surrounding blood vessels. In the third phase, osteoblasts continue depositing bone forming cancellous tissue or trabeculae. Trabeculae form a honeycomb-like structure that blood vessels penetrate. The remaining mesenchymal cells in the outer fibrous membrane begin to harden and form the periosteum. The periosteum is the most external layer of the bone. In the final step, the honeycomb-like structure is converted into compact bone via osteoblastic and osteoclastic activity. The final form of intramembranous is shown in Figure 4. Most of the bones of the cranium and clavicle form via intramembranous ossification. However, the remaining bones of the skeleton form via endochondral ossification.

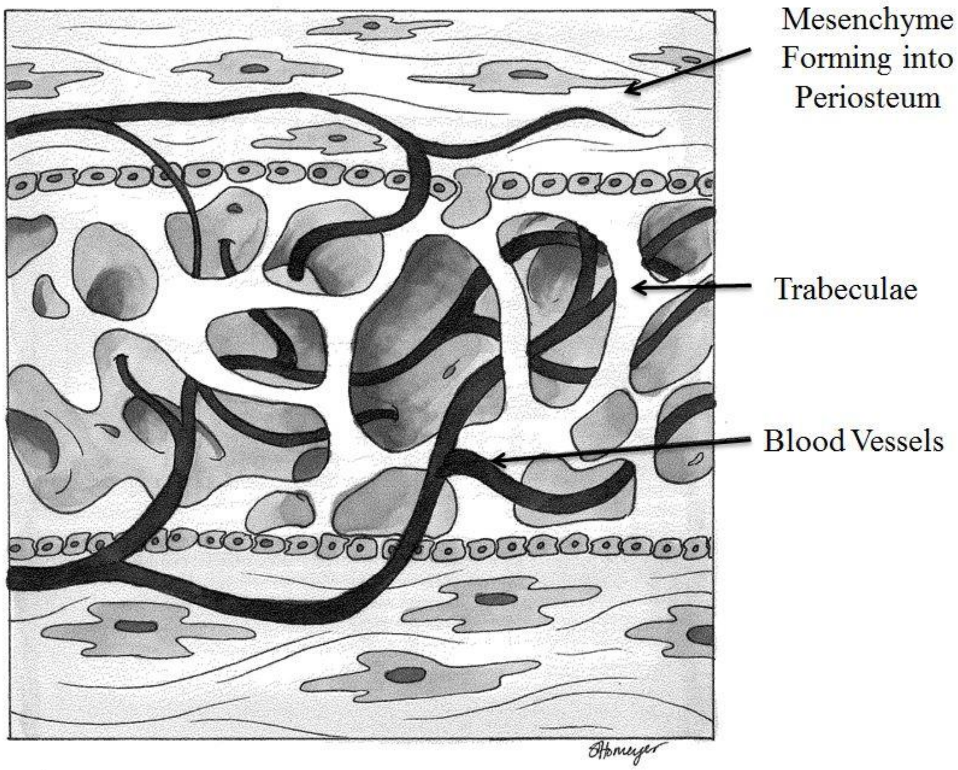

Figure 4. Formation of Honeycomb structure with developing periosteum. Drawing by SH.

The remaining bones of the skeleton including portions of the cranial bones and long bones undergo endochondral ossification. Endochondral ossification is the development of bone within an existing cartilaginous precursor. The existing cartilaginous structure is known as hyaline cartilage, which is made up of large protein fibers of collagen origin. The hyaline cartilage is surrounded by a dense layer of connective tissue known as the perichondrium. See Figure 5.

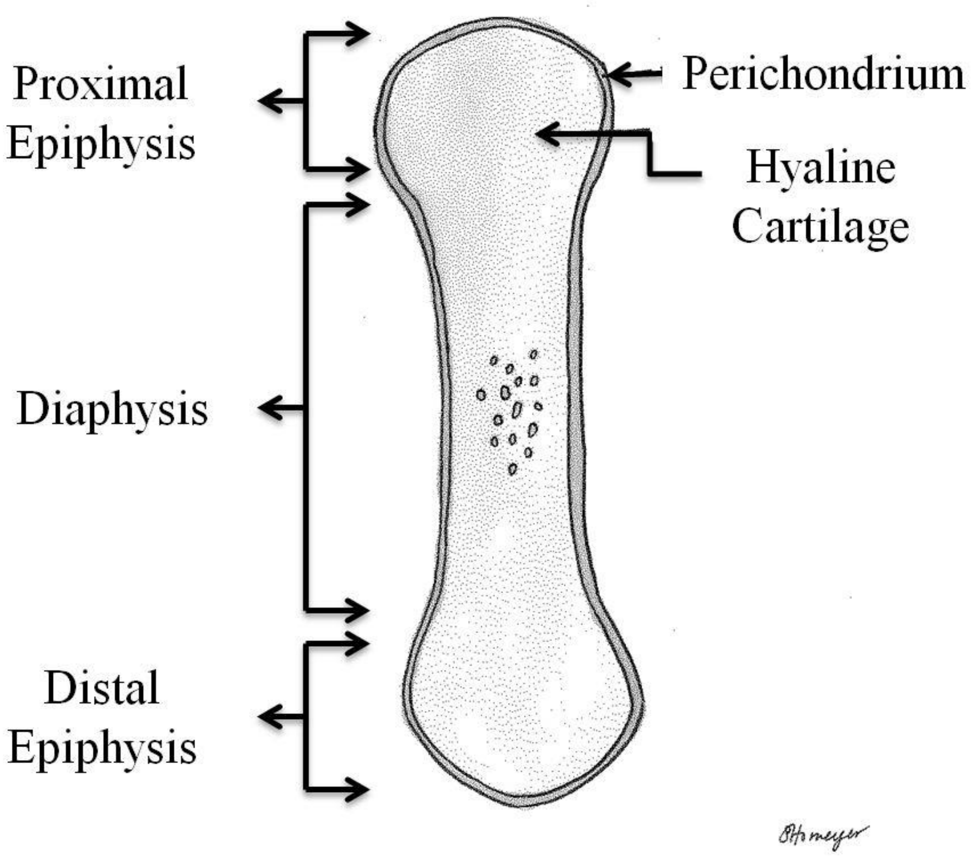

Figure 5. Cartilaginous precursor known as hyaline cartilage. Drawing by SH.

The perichondrium produces chondrocytes, which develop and enlarge the existing cartilage model. Like osteocytes, chondrocytes are housed within lacunae. Chondrocytes create and maintain the cartilaginous model. Once the cartilage model has developed enough in size, the perichondrium begins to produce osteoblasts. These osteoblasts begin to form a bony collar that prevents chondrocytes from producing the cartilaginous model. As the chondrocytes die, they create the calcified collagen matrix and develop into the primary medullary cavity. Next, blood vessels invade the primary ossification center, making it the primary marrow cavity. See Figure 6.

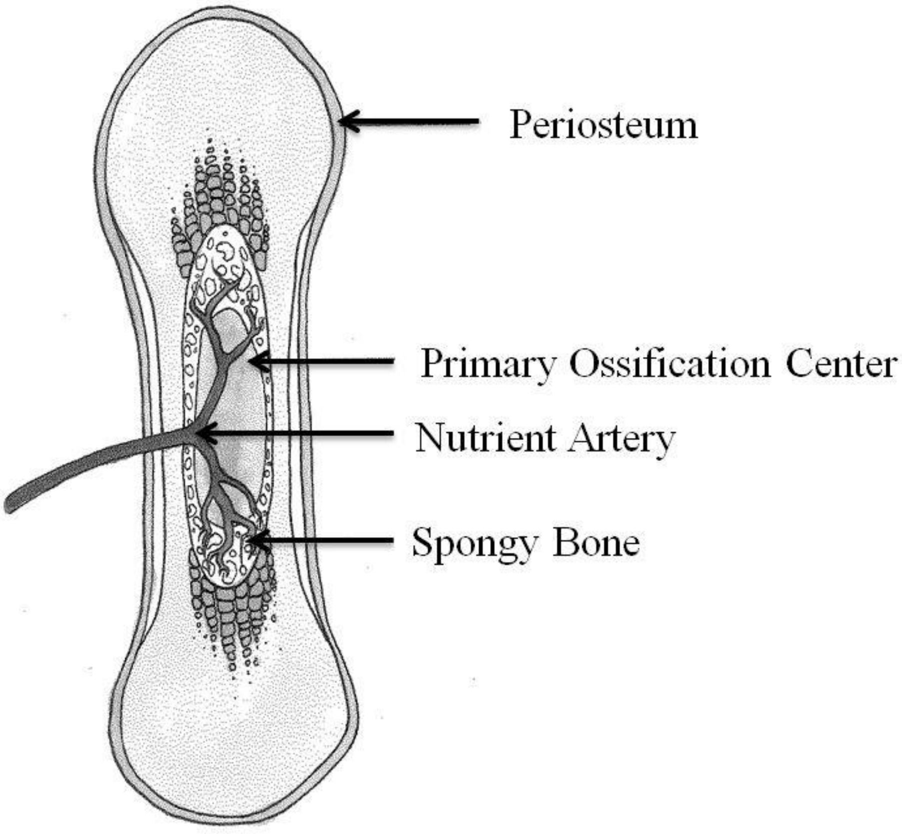

Figure 6. Blood Vessels promoting ossification transforming the primary ossification center into the medullary cavity. Drawing by SH.

The penetration of blood vessels to the marrow cavity promotes the development of osteoblasts and osteoclasts. Osteoblasts line the primary marrow cavity and being to deposit osteoid, developing a network of trabeculae. The existing cartilage from the bony collar and periosteum extend away from the primary ossification center, leaving a layer of cartilage at the ends of the bone. At the ends of the bone, chondrocytes are still depositing cartilage, forming the metaphysis.

The metaphysis is a zone of bone growth between the diaphysis and forming epiphysis. The cartilaginous areas at the end of the bone called the epiphyses. The epiphyses are areas of bone growth that develop separately from the diaphysis. See Figure 5.

In each epiphysis, a secondary ossification center forms, promoting bone development. Undergoing the same process as the primary ossification center, the secondary ossification center becomes a secondary marrow cavity at one end. Throughout development however, the development of the epiphyses lags behind each other. At birth, the epiphyses develop into spongy bone, but the joints between the long bones remain cartilaginous. See Figure 7. By the age of twenty, the gap between the diaphysis and epiphysis become connected and form one marrow cavity. At this stage, the long bones no longer develop in length. Portions of the skull also undergo endochondral ossification. This is because the base of the skull is derived from three cartilaginous precursors (Saladin, 2010; Som and Naidich, 2013).

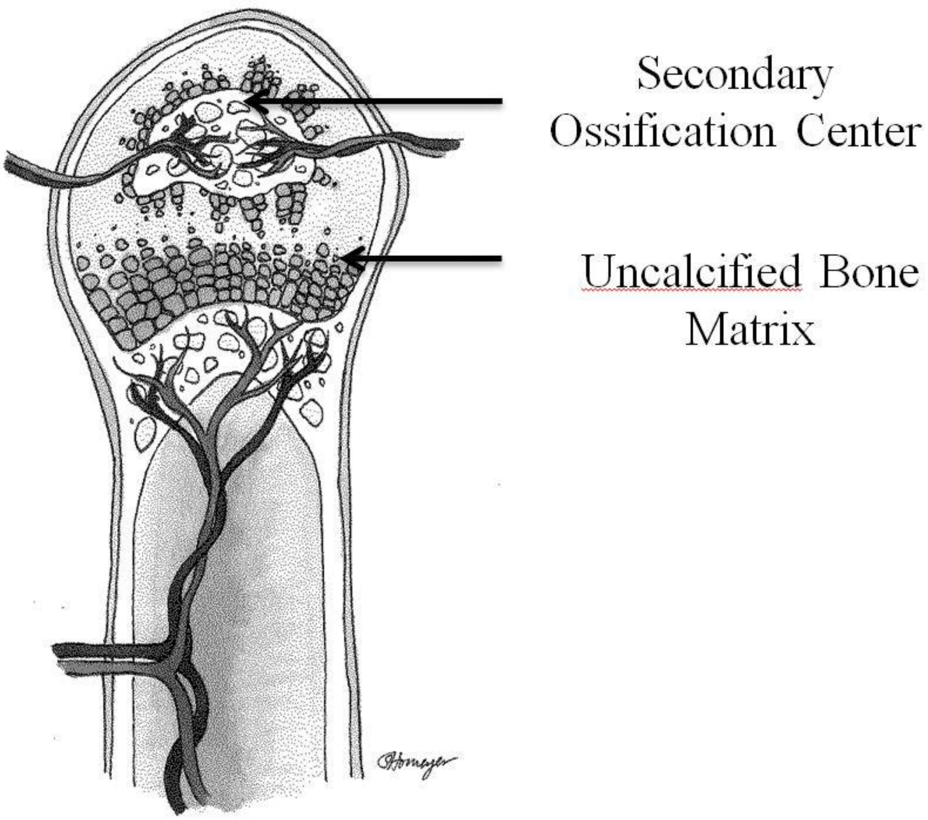

Figure 7. Formation of secondary ossification center. Drawing by SH.

As these bones begin to develop, their edges come together and from various cranial sutures. In the case of pterion, two primary sutures can be identified the spheno-parietal suture and the fronto-temporal sutures, named after the bones that articulate. Classification of a suture for epipteric bones provides some difficulty, as they are predicated on the number of epipteric bones, the size, and where they are located at pterion. The classification of a stellate suture is impossible, as the stellate pattern is the articulation of all four bones at a single point. The sutures are merely continuations of the coronal, squamous, spheno-temporal and spheno-frontal sutures. Fontanelles are cartilaginous soft spots that develop into bone (O’Rahilly and Müller, 2001; White, 2012), there are six primary fontanelles, the bregmatic, lateral fontanelles (located at pterion), the mastoid fontanelle and the posterior fontanelle. As the bones begin to develop and ossify these fontanelles, shrink and become hardened bone.

The ossification centers, growth trajectories, sutures and fontanelles are critical components in cranial development all of which may be subject to biomechanical influences (Moss, 1997a,b,c,d). Opperman (2000), identifies sutures as intramembranous growth sites, meaning that sutures develop bone within a membrane, not needing a cartilaginous precursor. Thus, one may infer pterion is a location in which sutures develop and promote bone growth.

3.2– Constraint in Cranial Morphology

The concept of functional matrices is that the interaction of every component from the genes to the environment plays a critical role in the final form of an organism. Modularity is the idea that components of a system are highly integrated; these modules are then responsible for the genetic, morphological, and evolutionary changes in an organism (Klingenberg, 2008; Esteve-Altava, 2016). Similar to functional matrices, modules are found at the genetic, developmental, functional and evolutionary level (Klingenberg, 2008; Esteve-Altava, 2016). Modules are identified based on the covariation between phenotypic traits. The skull is divided into two major matrices, the craniofacial complex and the vault of the skull. Take for example the vault of the cranium; its functional components include the brain, bones, arteries, and muscles. The sphenoid and zygomatic connect the face to the vault therefore making them components of both the face and vault (Esteve-Altava & Diogo et al., 2015). Modularity studies are capable of identifying the covariation between existing structures, and how covariation between these modules have changed over time

(Klingenberg, 2008; Esteve-Altava & Rasskin-Gutman, 2014; Esteve-Altava & Boughner et al., 2015; Esteve-Altava & Diogo et al., 2015).

The modularity of the skull has been investigated in human and non-human primates, and tetrapods. The relationships between cranial bones, sutures, and muscles (functional matrices) have been investigated via Anatomical Network Analysis (AnNA). The premise of AnNA, is that the physical articulations between the modules are converted into nodes, which are used to create network models. The relationship between these nodes is mapped and the number of connections these nodes have with each other are used to establish their covariation. The methodology of AnNA can be reviewed in Esteve-Altava & Rasskin-Gutman (2014) and Rasskin-Gutman & Esteve-Altava (2014). Investigations on the relationships between the musculoskeleton of the human skull have found that the musculoskeleton is composed of 10 modules. Relevant to the study of pterion, AnNa analysis reveals that the temporalis and masseter are in the lower jaw/inner module (Esteve-Altava & Diogo et al., 2015). From which I infer that the temporalis and masseter belong in a single module, and that they face similar pressures throughout ontogeny.

Esteve-Altava & Rasskin-Gutman (2014), use AnNA to investigate the functional matrix hypothesis that the skull develops as a result of genetic and epigenetic influences. They compared null network models of human cranial articulations, and concluded that functional matrices (cranial modules) do influence the formation of the skull. Their model accurately predicts the articulations of the cranial connectivity module, which includes the sphenoid, frontal, temporal, parietal (pterion) and occipital bones. The model however, operates under the assumption that bone growth is uniform and unconstrained, which underestimates additional factors that influence cranial development.

In primates, AnNa is used to establish modules of the skull. Throughout the primate order, the skull is divided into two primary modules, the facial and the vault. This is similar to the modules found in humans. There is variation among the craniofacial modules, and some variation in the vault modules. In Hominidae (chimpanzees, gorillas, orangutans and humans), there is variation among the zygomatic, sphenoid, and frontal. However, there is little variation among the sutures found in the vault (Esteve-Altava & Boughner et al., 2015). The application of AnNa analysis supports the validity functional matrix hypothesis in that the interactions between soft tissues do influence cranial morphology. It also provides that cranial morphology is relatively conservative from tetrapods to human and non-human primates.

3.2 – Wolff's Law & The Functional Matrix

Wolff's "Law" (1892) posits that throughout ontogeny, any mechanical loading placed upon living bone will influence the bones existing structure (Moss, 1975; Jaslow, 1990; Anton et al., 1992; Rafferty & Herring, 1999; Frost, 2003; Pearson & Lieberman., 2004; Saladin, 2010; Chou et al., 2015; Cornette et al., 2015). The response of bone to biomechanical influences is not simple because factors such as age, physical activity, and bone density must be accounted for as they influence bone structure (Pearson & Lieberman, 2004). It is however, generally accepted that biomechanical influences on bone do influence bone structure (Jaslow, 1990; Rafferty and Herring, 1999; Herring & Rafferty et al., 2001).

These responses occur through bone remodeling as stress is placed upon an existing structure. These stressors generate cellular activity inducing osteoblastic and osteoclastic activity. Osteoclasts remove existing bone matrix if there is a lack of use. Osteoblasts generate new bone matrix through use or stress and strain. These stresses and strains can be a result of the abutting edges of bone (Jaslow, 1990; Herring and Mucci, 1991; Herring, 2008), mastication (Herring, 1974; Radinsky, 1981a,b; Radinsky, 1982; Janis, 1990; Pucciarelli et al., 1990; Herring, 1993; Perez-Barberia and Gordan, 1999; Sardi et al., 2006; Gittleman, 1985; Mattson, 1998), and headbutting (Nickolay and Vaders, 2006). The interaction between the external stimuli on the existing structure causes the bone to adapt. This concept is highlighted in the Functional Matrix Hypothesis (FMH).

The FMH suggests that external influences and epigenetic factors are the primary cause of all adaptive responses to the cranial bones and organs. This implies that changes to existing structures are not regulated by the intrinsic genetic code, but by the extrinsic stimuli acting directly upon the bones and organs. The skull carries out a specific set of functions such as speaking, respiration, and digestion. These functions are supported by a related functional matrix that includes soft and osseous tissues. The existing soft tissue and bones form what are known as functional matrices (Moss & Salentijn, 1969). There are two primary functional matrices, the periosteal and the capsular matrices. The periosteal matrix is composed of skeletal muscles, blood vessels, teeth and glands. The periosteal matrices respond to forces acting on each unit within a matrix. Forces such as stress and strain generate osteogenesis, thus influencing the size and shape of the existing structures. The capsular matrix is composed of the spaces that surround the functioning portions of the skull such as the eye orbits (eyes) and neurocranium (brain). The major difference between the matrices is that capsular matrices do not generate bone growth. Instead, as these spaces increase in volume due to the mass of the eyes and brain, they force skeletal components of the periosteal matrix to accommodate accordingly, by generating bone growth. This indicates that the size and shape of the skull is influenced by accommodation of the expanding capsular and functional matrices.

Most of the literature is focused on the periosteal matrix (Moss, 1954; Moss & Young, 1960; Moss & Rankow, 1968; Moss & Salentijn, 1969; Moss, 1997a,b,c,d; Moss, 2007). This is because the periosteal matrix is responsible for the growth of bones via absorption and deposition. Bone remodeling is critical to the development of the skull as it allows for its maintenance throughout ontogeny (Saladin, 2010). In 1997, Moss revised the FMH hypothesis focusing on the elucidation of the epigenetic impact down to the cellular reaction to these stimuli. The previous research on the FHM hypotheses could not deduce how the epigenetic stimuli translated into multicellular responses. The functional matrix hypothesis is critical to understanding pterion because it provides evidence that extrinsic influences on the skull can influence the articulation patterns. Extrinsic influences such as diet, mastication and even headbutting, can cause morphological changes over evolutionary time.

Osteogenesis is a pivotal step in the development of bone. Wolff’s Law indicates that bone can respond and adapt to stress and strain. The functional matrix hypothesis tells us that these stresses and strains act upon functional matrices causing changes to the skull. It also highlights the fact that external forces (mastication, diet, behavior) act directly upon the skull ultimately causing the bone matrix to adapt.

Chapter 4: Mastication and Cranial Suture Biomechanics

The goal of this chapter is to provide an understanding of how pterion as a landmark and sutural configuration are influenced by biomechanics. Biomechanical influences via mastication have been implicated as a driving pressure on the morphology of the skull (Radinsky 1981; Radinsky 1982a,b; Rafferty and Herring, 1999; Herring and Rafferty et al., 2001; Christiansen and Wroe, 2007, Herring 2007; Burn et al., 2010, Lieberman, 2011). Through species-specific masticatory movements (Gerstner and Goldberg, 1994), forces are generated which act upon existing functional matrices and cranial sutures. This chapter will discuss the elements that comprise the masticatory apparatus. It will also discuss how mastication generates biomechanical forces on the skull. The biomechanics of cranial sutures will follow as masticatory influences act upon the malleability of cranial sutures.

4.1 Mastication

Mastication is the functional application of the masticatory apparatus and its components employed to break down food (Maynard-Smith and Savage, 1959; Gans et al., 1978; Lieberman, 2011). Mastication is a complex function, involving an array of muscles and bones, responding to a wide range of dietary inputs. The muscles and bones comprising functional matrices are thought to be semi-independent, while undergoing various selection pressures throughout ontogeny (Cheverud, 1982; Moss, 1997a,b,c,d; Noguira et al., 2005; Hallgrimsson et al., 2007; Paschetta et al., 2010). The range of ecological niches and diets seen among mammals provides researchers with opportunities to gain perspective on how these components impact the evolution of the skull in humans and extinct mammalian species (Herring, 1974; Radinsky, 1981a,b; Radinsky, 1982; Gittleman, 1985; Janis, 1990; Pucciarelli et al., 1990; Herring, 1993; Mattson, 1998; Perez-Barberia and Gordan, 1999;

Sardi et al., 2006). By examining these intricate components, one can begin to understand how their interaction influences each other and the evolution of the skull.

The masticatory apparatus is the integration of every component involved in the breakdown of food. It includes but is not limited to; the temporal mandibular joint (TMJ), temporalis, masseter, pterygoideus muscles, teeth, and components of the ascending ramus of the mandible. The primary muscles of this study include the temporalis muscle and the masseter muscle (see Figure 8). During mastication, the temporalis muscle is responsible for the closing of the mandible. The temporalis is a large fan shaped muscle that attaches on the lateral vault. It runs through temporal fossa, (which is located between the lateral walls of the skull) and the zygomatic arches which attach to the coronoid processes (Aiello and Dean, 1990; Hylander, 2006; Saladin, 2010). Size of the temporalis is reflected in the size of the temporal fossa; research suggests that the larger the temporal fossa the larger the temporalis muscle (Maynard-Smith and Savage, 1959; Radinsky 1981a; Samuels, 2009). The larger size of the temporalis suggests enhanced bite force and larger gape size (Christiansen and Wroe, 2007; Slater and Van Valkenburg, 2009). Byron et al., (2004), used mice models that have decreased myostatin, a negative regulator of muscle mass to identify the effects on increased muscle mass on the sagittal suture. Byron et al., (2004) suggest that the fibrous connective tissues in sutures adapted to the demands of muscle stimulation. Jahan et al., (2010) restricted fetal jaw movement in mice in order to identify the relationship between temporalis muscle and jaw movement during development. Jahan’s study indicates that masticatory influence during the prenatal period is critical to proper development. The studies by Jahan and Byron indicate that the interaction between muscles and the skull play an important role in cranial development. It is a clear implication that the forces generated by the temporalis impact the morphology of the skull and its sutures.

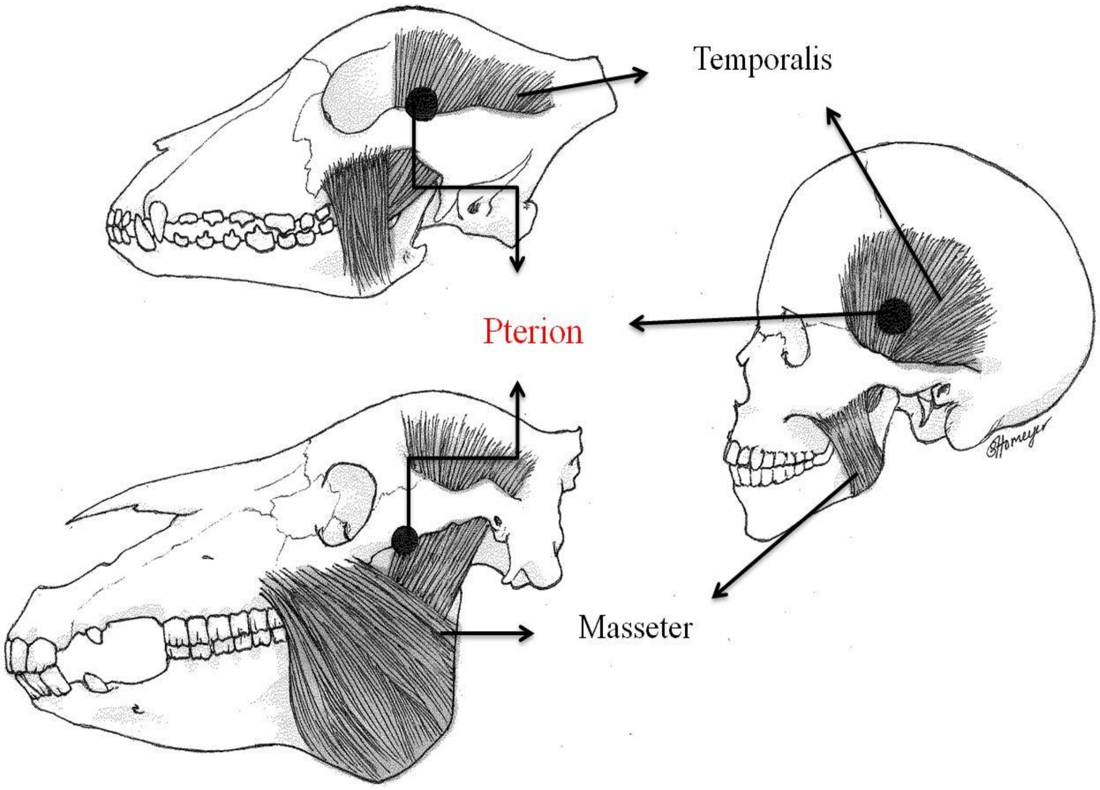

Figure 8. The location and insertion of the Temporalis and Masseter Muscles in homo, Equus and Canis. Adapted to show pterion. Drawing by SH.

The masseter inserts along the zygomatic process and attaches to the lateral portion of the mandibular angle (Hylander, 2006; Saladin, 2010). It is responsible for the opening and closing of the mandible. Hylander investigates the force levels of the masseter during mastication and concludes that increased masseter force, on both working and balancing sides of the mandible is a results of chewing foods that are tougher (Hylander & Johnson, 1992). The zygomatic arc has been known to undergo significant biomechanical strain due to the forces created by the masseter. Herring and Mucci (1991), find that the masseter muscle in *S. scrofa* contributed significant strain on the zygomatic-squamosal suture, creating two specific forms of sutural interdigitation in one suture. The morphology of the zygomatic-squamosal suture reflects multiple strain patterns, which in turn affect the morphology. Herring and Rafferty et al., (2001) find that the strain on the braincase by the masseter was insignificant but they did find that the masseter contributed to strains on the interfrontal suture and the coronal suture. Together, the temporalis, masseter and mandible generate force that impacts cranial sutures. Cranial sutures are natural shock absorbers that dissipate forces throughout the cranium (Opperman, 2000).

4.2 - Cranial Suture Biomechanics.

A suture is an articulation between two fibrous joints surfaces on the skull (Rice, 2008; White, 2012; Som and Nadich, 2013). Sutures are subject to biomechanical forces such as the growth of the brain, strains due to mastication, and sudden impacts such head butting (Moa & Wang, 2003; Alaqeel et al., 2006; Nicolay and Vaders, 2006; Herring, 2008). Sutures are used to estimate age in human and non-human primates (Todd and Lyon, 1925; Meindl and Lovejoy, 1985; Cray et al., 2008, Jayaprakash and Srinivasan, 2013). The primary functions of cranial sutures are to generate bone growth, allow for the passage of the head through the birth canal and to act as absorbers of biomechanical stressors placed on the skull. As the bones of the skull begin to develop, sutures form at the ends of the bones. Understanding the biological function of sutures is critical to our understanding of pterion.

One of the primary functions of cranial sutures is to absorb and dissipate biomechanical forces on the skull. Both facial and vault sutures undergo three primary types of strains: cyclic loading, quasi-static loads and impact loading. Each type may arise due to diet, mastication, growth of the brain, head butting and cranial modification (Anton et al., 1992; Monteiro and Lessa, 2000; Sun et al., 2004; Nickolay and Vaders, 2006). According to Herring (2008), impact loading is defined as the sudden impact of force on the skull as seen in the impact from a fall and impact from boxing. Cyclic loading occurs as a result of pressures from adjacent tissues such as intra-cranial pressure due to the growth of the brain. Impact, cyclic and quasi-static loads are associated with the morphology of cranial sutures.

4.3 – Tensile Stress and Compressive Strain.

Tensile and compressive stresses are the primary forms of stress that sutures undergo through various types of loading. Tensile stress occurs in the form of pulling. The stress created by the masseter muscle on the horizontal portion of the zygomatic arc is an example of tensile stress (Herring and Mucci, 1991). Compressive strains occur as a result of pushing, leading to the compression of a suture. The vertical segment of the zygomatic arc undergoes compressive strain because of masseter muscle contractions (Herring and Mucci, 1991). Stress is the force applied to sutures that causes the suture to deform and change its shape. The deformation can be temporary after which the suture returns to its original state. Strain is the resulting change in shape caused by stress (Yu et al., 2004). Figure 9, provides a visual description of tensile and compressive strain. The stresses and strains induced by biomechanical influences promote bone growth at cranial sutures, altering their sutural complexity which is often used as a proxy for age and biomechanical influence on the suture.

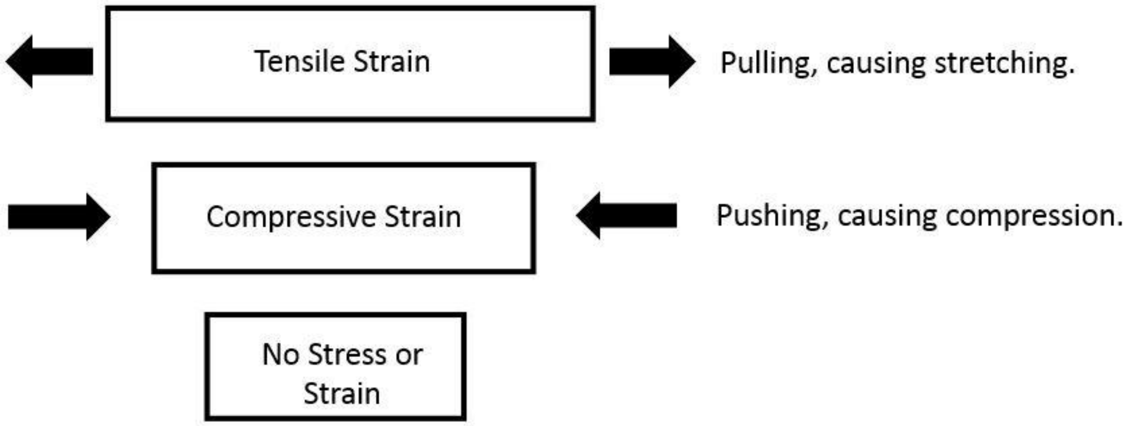

Figure 9. Simple representation of Tensile, Compressive and Natural States.

In Jaslow (1990), bending strength (compressive strain) and impact loads were tested on portions of the skull with sutures and without sutures in goats (*Capra hircus),* indicated that portions of bones with sutures were unable to undergo as much bending force as bone without sutures. However, bones with sutures absorbed five times as much energy before failure as bones without sutures. The increase in energy absorption was found to be significantly correlated with higher sutural complexity. This hypothesis suggests that increased strain on the cranium can lead to highly complex sutures. The morphology of cranial sutures is reflected in their fractal dimensions or sutural complexity (Long, 1985; Lynnerup and Jacobsen, 2003; Yu et al., 2003).

4.4 - Cranial Suture Morphology.

Fractal geometry has made the quantification of sutural complexity possible and allows investigators to identify to what extent biomechanics impact suture morphology (Xu et al., 1993; Yu et al., 2003). The use of fractals may provide an understanding as to what forces impact which suture, and what intrinsic and extrinsic mechanisms may be responsible. Whichever method investigators choose to employ, the underlying goal of their investigations is to understand the various forces and their impact on cranial sutures.

The application of fractal analyses on cranial suture morphology is twofold, brought about through the subjectivity of sutural complexity, sutural scoring methods and the difficulty of identifying morphological variation throughout ontogeny (Lynnerup and Jacobsen 2003). Traditional scoring methods for sutural complexity and obliteration are ordinal such as 0 being open or less complex, and 4 being closed or highly complex (Miendl and Lovejoy, 1985; Falk et al., 1989; Cray et al., 2008; Cray et al., 2012). To enhance understanding of cranial suture morphology and age, Lynnerup and Jacobsen (2003) use fractal dimensions to identify age related changes in the sutural morphology of humans. They found no statistically significant relationship between age and sutures morphology. They also inferred from their results that the product of the coronal suture and sagittal suture fractal dimensions and age were statistically insignificant.

The use of cranial suture complexity (fractal dimensions) has been investigated in pigs, deer, and alligators to associate complexity with diet, mastication, and phylogenetic relationships. Rafferty and Herring (1999), support that suture strains are correlated with sutural interdigitation in *Sus scrofa.* A study of sutural complexity of *Caiman* species, Monteiro and Lessa (2000) find that *C. latirostris* exhibits higher interdigitation in braincase sutures than its sister species. They inferred that that the harder dietary items of *C. latirostris* applies stronger longitudinal stress on the braincase than do the dietary items of its sister taxa. Burn et al., (2010) investigate the interdigitation ratios in pigs that were fed a soft diet and found that ratios did not decrease when compared to pigs fed harder diets.

These studies indicate that cyclic loads impact sutural interdigitation. These influences are reflected through phylogenetic history, as seen in the genus *Caiman.* Although there is strong support that cyclic loading influences sutural interdigitation in various mammalian species, the sutures in question and methodologies are often different. Other researchers have addressed how impact and quasi-static loads influence sutural morphology.

It is unlikely that the mammalian skull has adapted specifically for impact loading because impact loading does not occur until the suture is formed (Herring, 2008). Cranial sutures do not undergo impact loading until after birth, suggesting that impact loading has little pressure on cranial development. Jaslow and Biewener (1995), investigate how cranial sutures dissipate the stress applied to the skull in goats, indicating that impact loads on one horn exhibits increased strains on the bones, while forces applied to both horns undergo go less strain. The same results are found in cranial sutures themselves, indicating that sutures are likely to act as shock absorbers when undergoing impact loading. Nicolay and Vaders (2006) hypothesized that competition between males who wrestle, thus undergoing impact loading will have increased sutural complexity, but found no significant difference between suture complexity and sex. The presence of antlers had no effect on the sutural complexity in male white-tailed deer when compared to female deer. The amount of force produced by impact and cyclic loadings vary by species and are thought to be significantly higher than those created by quasi-static loads (Herring, 2008).

Quasi-static loads arise due to the development of adjacent tissues such as abutting sutures, growth rates and the expanding brain (Herring, 1993; Henderson et al, 2005). Using rat models Henderson et al., observed the geometric properties of the sagittal suture during development, suggesting that the morphology of the suture is age dependent, and that quasi-static loading is present in the suture. Herring (1993) suggested that the shape of and size of the skull are influenced by the size of the brain, combined with the age-related morphology of the sagittal suture in rats, it is likely that there is a developmental connection from diet to the morphology of the skull. The types of loads that the skull faces all impact cranial morphology in some way.

The interactions between the biomechanical pressures on the fontanelle to the development of the suture have yet to be explored. Now that we understand how biomechanics affect cranial suture morphology, it is plausible that the sutures at pterion undergo biomechanical influences. Its relationship to the middle meningeal arties, the temporalis, the cranial facial complex and the neuro-cranium put it in the position to undergo both cyclic and quasi-static loading. Further research into pterion and its complex components may elucidate the extent of ecological, dietary, intrinsic and extrinsic pressures on the pattern. The factors that make pterion a candidate for extensive biomechanical pressures are also its greatest weakness. Pterions relationship to the middle meningeal arties, optical canal, Broca's motor and the brain make developmental and strain studies difficult. Investigations into the biomechanical strains experienced by the vault indicate that most forces are absorbed by the cranio-facial complex (Lieberman, 2011). No studies have directly observed if pterion undergoes significant biomechanical influence caused by the temporalis or masseter muscle. One goal of this study is to identify the impacts of biomechanics on pterion.

Chapter 5: Phylogenetic Similarity

Comparative biologists, biological anthropologists, morphologists and paleontologists are often interested in traits related to various functional, ecological, molecular and phylogenetic aspects. A phylogeny is an evolutionary history of an organism often visually represented in a phylogenetic tree. A phylogenetic tree is a theoretical model of the relationships between organisms based upon genetic and morphological characteristics (Felsenstein, 1983; Felsenstein, 1985; Grandcolas & Grandcolas; 2001). The Linnaean classification of living organism is an example of an evolutionary history of all living organism that is based upon their morphological characteristics. When conducting a quantitative analysis of these traits it is important to account for the phylogenetic relationships of the species in question (Felsenstein, 1985; Harvey and Pagel, 1991). This is because species cannot be considered statistically independent when compared if they arise from a common ancestor. There are multiple methods used to account for phylogenetic similarity (Felsenstein, 1985; Stearns, 1983; Grafen, 1989), however, it is often unclear when to correct for phylogenetic similarity and which method to use (Bello et al., 2015). According to Harvey and Pagel (1991), there are two reasons why species are similar: phylogenetic niche conservatism and phylogenetic time lags.

Phylogenetic niche conservatism is the idea that traits within phylogenetically related taxa arise as a result of occupying similar ecological niches (Harvey & Pagel, 1991; Losos, 2008; Wiens et al., 2010). In other words, closely related species are likely to have the same traits if they occupy similar niches. According to Pagel and Harvey (1991), two points are critical to phylogenetic niche conservatism, one, if a vacant niche exists, species in a similar niche are likely to move into the vacant niche, and eventually diverging into a new species.

Second, some species may not be able to occupy a niche because other species are already occupying that niche. The species already occupying that niche is likely well adapted and a stronger competitor for the existing resources. This prevents species from moving into the niche and diverging into a new species.

Phylogenetic time lags are also another factor to consider when comparing phylogenetically related species. Phylogenetic time lags refer to the assumption that traits in related species that arise via natural selection or genetic drift will ultimately be lost given that there is enough genetic variation within a species, or variation arises through mutations. In other words, traits will be similar if there is low genetic variation or a lack of mutations across evolutionary time. Pagel and Harvey (1991), indicate that time lags may not be as significant as initially thought. This is because phylogenetically related species may have traits that have little to no adaptive significance and arise as a byproduct of natural selection or genetic drift (Gould and Lewontin, 1979).

5.1 – Non-Independence

Phylogenetic niche conservatism and phylogenetic time lags are just two reasons species share similar characteristics. These similarities create the problem of non-independence in statistical analysis (Felsenstien, 1985). Non-independence arises because species that are more closely related are more likely to be similar than species that are distantly related (Harvey & Pagel, 1991). Therefore, species that are closely related may share similar selective forces and responses to those selection forces. Not controlling for phylogenetic relationships, essentially assumes that species of a common ancestor radiated at the same time making their characteristics independent of each other. However, this view is not an accepted evolutionary concept, because evolution requires time and genetic constraint in order for speciation to occur. Figure 10, compares a single radiation event from a common ancestor (Box A) to the phylogenetic tree based on the radiation events of species used in this study (Box B).

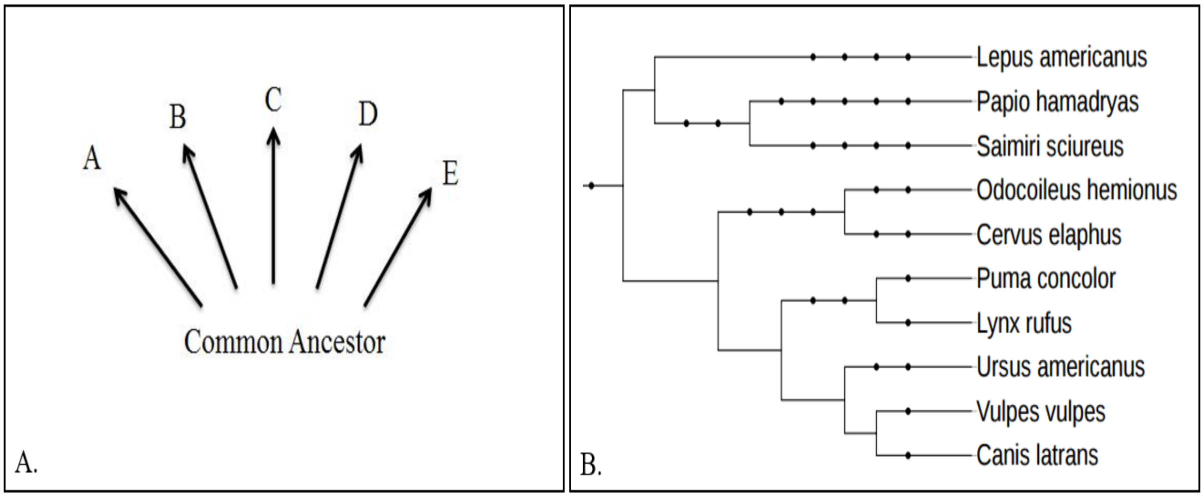

Figure 10. Box A: A single evolutionary radiation. Box B: Phylogenetic tree of sample used in analysis. Tree generated by PhyloT.

When making comparisons between related taxa without controlling for phylogenetic similarity, statistical tests are compromised because the degrees of freedom are overestimated which may inflate the probabilities associated with each test. This is because species are treated as independent units of analysis and the relationships between species are ignored (Felsenstien, 1985, Harvey & Pagel, 1991). Since species are phylogenetically similar and their relationships are hierarchical, the probability of character traits evolving independently as in Figure 10, is unlikely. By failing to control for these similarities two statistical assumptions are not met 1) species data is independent and 2) there exists a normal distribution with equality of variance and means. This occurs with both categorical and scale data. Multiple ways to control for these statistical issues including have been suggested, including, phylogenetic subtraction (Stearns, 1983), phylogenetic autocorrelation (Cheverud et al., 1985) and maximum likelihood (Lynch, 1991). In this study, species are the unit of analysis, therefore their phylogenetic similarities must be accounted for to meet the assumptions of independence and equal variances. Stearns phylogenetic subtraction method is discussed further in the methods section.

5.2 – Phylogenetic History of Species.

The ensuing discussion will address the phylogenetic history of the species used in this study. The sample in this study consists of species from the class of Mammalia. Characteristics that classify a species as mammals include the presence of hair, production of milk and being warm-blooded (Kardong, 2011; Foley et al., 2016). Mammals began to radiate from ancestral species during the Triassic period (Kardong, 2011) this radiation is believed to have occurred ~218mya (Meredith et al., 2011; Foley et al., 2016). The species in this study are members of infraclass Eutheria (Placental mammals), within Eutheria are four groups: Laurasiatheria, Euarchontoglires, Xenathra and Afrotheria.

The four orders found in this sample belong to Laurasiatheria and Eucharontoglires which are thought to have split ~74 to 97mya (Meredith et al., 2011; Foley et al., 2016). The orders carnivora and artiodactyla belong to Laurasitheria, while lagomorpha and primates belong to Eucharontoglires.

Chapter 6: Methods

The goal of this chapter is to clearly and concisely describe the methodologies used to test the following hypotheses, 1) pterion is phylogenetically conservative, 2) is pterion influenced by biomechanical pressures related to the mastication. Each of the hypotheses will be tested in species from four orders: artiodactyla, carnivora, lagomorpha and primates. These four orders represent differences in selective pressures such as diet, which should reflect through their masticatory apparatus, their sizes, and genetic make-up. These differences are key in identifying if one or more of the hypotheses accounts for pterions articulations. The proceeding sections will discuss the study design beginning with species selection, species and specimen selection, data collection methods, and quantitative methods. Each of these needs to be explicit to assure replicability of the study in order to disprove or confirm the results presented.

6.1 – Variables.

The collected variables were selected to represent overall cranial dimensions, and to serve as proxies for biomechanical influences, prognathism and neuro-cranium size. The first hypothesis is that pterion patterns are phylogenetically conservative. Variables necessary to test to test the hypothesis include the nominal categories of pterion pattern and taxonomic relationships. The second hypothesis is that biomechanical forces influence pterion. One way biomechanics influences cranial sutures is through mastication, therefore, variables related to mastication were obtained. The largest muscles responsible for mastication are the temporalis and the masseter as indicated by (**). Various measures related the temporalis and the masseter can be found in Table 3. Data on sutural complexity was collected to identify the influence of biomechanics on the pterion suture. This ordinal measure is not shown in Table 3, but is discussed in section 6.2. Except for measurements 16 – 21 all measurements were taken on the left side of the skull, unless there was significant damage.

Table 3. Variables adapted from Maynard-Smith and Savage (1959), Nogueira et al., (2005), Ilknur et al., (2009). Note that morphology varies from species to species therefore special attention was made to keep measures comparable. (**) indicates masticatory variables.

Variables:	**Abbreviation:**	**Description:**
1. Cranial Length	CL	Maximum distance from the most posterior portion of the skull to the most anterior portion of the skull.
2. Cranial Height	CH	Maximum distance from the most inferior position on the skull to the most superior position on the skull.
3. Cranial Width	CW	Maximum distance from the lateral portion of the zygomatics.
4. Orbital Height	OH	Maximum distance from the most inferior position of the orbit to the most superior portion of the orbit.
5. Inter-Orbital Breadth	IOB	Maximum distance between the two eye orbits.
6. Temporal Length**	TL	The length of the temporalis muscle insertion.
7. Temporal Height**	TH	The height of the temporalis muscle insertion.
8. Temporal Width	TW	Taken as the difference between the POC and CW.
9. Temporal Volume	TV	Taken as TL x TH x TW.
10. Post-Orbital Constriction**	POC	Maximum distance behind the eye orbits.
11. Masseter Arm**	MA	Maximum height of the masseter arm or maximum width of the ascending ramus.
12. Masseter Origin**	MO	The length of the masseter muscle insertion.
13. Masseter Depth	MD	Taken as the difference between the BFD and CW.
14. Masseter Volume	MV	Taken as MA x MO x MD.
15. Bilingual Foramina Distance	BFD	Maximum distance between the lingual foramina.
16. Left Suture Length	LSL	Maximum length of the left pterion suture.
17. Right Suture Length	RSL	Maximum length of the right pterion suture.
18. Left Pterion to Posterior Portion**	LP to PP	Maximum distance from the left anterior junction of pterion to the most posterior portion of the skull.
19. Right Pterion to Posterior Portion**	RP to PP	Maximum distance from the right anterior junction of pterion to the most posterior portion of the skull.
20. Left Pterion to Anterior Portion**	LP to AP	Maximum distance from the left anterior junction of pterion to the most anterior portion of the skull.
21. Right Pterion to Anterior Portion**	RP to AP	Maximum distance from the right anterior junction of pterion to the most anterior portion of the skull.
Total Variables: 21		

6.2 – Species and Specimen Selection.

The sample is a sample of convenience, representative of species present at the Burke Museum of Natural History. The Burke Museum includes, represented by 28 out of 29 mammalian orders with 892 mammalian species from almost every geographic location. Species selection is based on two major factors 1) degree of phylogenetic relatedness i.e. order, family and genus and 2) dietary categorizations. Phylogenetic relatedness is a criterion because it may identify if variations of pterion patterns are a result of being similar or influenced by factors such as mastication. The diet of each species was considered because the various diets influence masticatory apparatuses, for example, carnivore dentition is adapted to kill and eat meat, whereas herbivores are adapted to breaking down rough plant materials. The presence of pterion also influenced the selection of species, if a species did not exhibit pterion i.e. visible sutures, they were excluded. Most the sample is comprised of carnivores but includes omnivores and herbivores. See Table 4, for the species represented in the sample. The primary factor for selecting specimen is the presence/absence of pterion. Therefore, specimen with obliterated sutures at pterion are excluded. Relative completeness of the skull was also a factor, damaged skulls would not yield enough data for accurate comparisons. Number of specimen in a species also influenced selection.

Table 4. Species sample size.

Order	Family	Genus	Species	Sample Size (n)
Carnivora	Canidae	*Canis*	*latrans*	30
		Vulpes	*vulpes*	30
		Ursus	*americanus*	30
	Felidae	*Puma*	*concolor*	18
		Lynx	*rufus*	30
Primates	Cercopithecidae	*Papio*	*hamadryas*	8
	Cebidae	*Saimiri*	*sciureus*	8
Artiodactyla	Cerviade	*Odocoileus*	*hemionus*	14
		Cervus	*elaphus*	4
		Oreamnos	*americanus*	3
Lagomorpha	Leporidae	*Lepus*	*americanus*	21
Total: n=4	**n=6**	**n=11**	**n=11**	**n=196**

6.3 – Pterion Identification and Complexity Scale.

The identification of pterion in critical to this study there for pterion location and sutures must be easily identifiable. Pterion lies on the lateral vault of the skull in humans, this location might change based on species specific morphology. For example, in the deer, pterion was located on the lateral vault but is located inferior to the zygomatic arc. This made data collection difficult to make with traditional sliding calipers as the jaws were too thick to access pterions location. It is critical to the study that the sutures that make up pterion are present. That indicates that none of the sutures can be completely obliterated. Recall that age is a factor that influences the obliteration of a suture, thus, juveniles and older skulls are excluded. Juveniles are excluded to reduce the variation explained by developmental constraints which may influence the results of any statistical examinations. The pterion types presented by Murphy (1956) were used in this study, see Figure 11 for pterion types. As discussed in chapter 2, there is difficulty when identifying epipteric types. The difficulties arise due to number, size, and location within a suture. Therefore, when an epipteric bone prevented the frontal, sphenoid, parietal and temporal from articulation it was classified as an epipteric bone (see Figure 1.) However, if there was an epipteric bone located in the spheno-parietal or fronto-temporal suture it was classified as an epipteric bone of the spheno-parietal pattern (SPE) or the fronto-temporal pattern (FTE), see Table 6 for the patterns encountered in this study.

Although it might seem useful to use the 16 patterns presented by Montagu, there is little justification to support his classification. Pterion types have yet to be explored in vertebrates beyond human and non-human primates, meaning that there may be types that have yet to be encountered. In this case, types will be identified only be the bones that articulate together regardless of variations in suture length. The categories for pterion types are nominal and can be found in Table 5. As indicated in chapter 2, pterion occurs bilaterally on the skull but occasionally unilaterally by pattern. Therefore, data on pterion pattern is collected by side and not a single skull. Scale level data is generated by taking the length of the pterion suture as the distance between anterior junction and posterior junction see measurements 16 and 17 in Table 3. This measurement is also predicated on the pterion pattern found. The X pattern is the convergence of four separate sutures at a single point see Table 5, making it difficult to generate any scale data and for this reason will be excluded from the analysis.

Table 5. Pterion types adapted from Murphy (1956), no additional types were encountered.

Pterion Type	Number
Spheno-Parietal (SP)	1
Fronto-Temporal (FT)	2
Epipteric (E)	3
Stellate (X)	4
Spheno-Parietal-Epipteric (SPE)	5

Sutural complexity was defined on an ordinal scale. 0 = no complexity, 1 = little complexity, 2 = complex and 3 = highly complex. However, there were not enough cases in each category to run chi-squares. A new scale was created by combing 0 and 1 from the original scale. This category is now 1 with 1 = little complexity. Groups 2 and 3 were combined to great a category of 2 = complex.

6.4 – Preparing for and Collecting Data.

Data were collected using Paleo-Tech Rod Digital Calipers on 21 variables related to overall cranial size, the temporalis muscle, the masseter muscle, craniofacial size and neurocranium size descriptions, can be found in Table 5. To test the assumption of accuracy and repeatability of my measurements, data were collected repeatedly on a single bobcat from the collection of Dr. Sarah Campbell. Over the course of one week each measurement excluding TW, TV, MD, MV were taken three times and then averaged. To assure accuracy and repeatability, repeated measures analysis of variance was calculated. Once replicability testing was complete and verified, measurements were taken on each of the species from September 1st 2015 through April 1st 2016 at The Burke Museum in Seattle, Washington. Data were collected every Tuesday and Friday from 10 a.m. to 4 p.m. in the Mammalogy Department under the Collections Manager Jeff Bradley. I was given a generous workspace with available resources including a large magnifying glass and a reference library. My own tools consisted of the Paleo-tech digital rod calipers and hand lens, extra batteries and my data collection forms.

6.5 – Stearns Approach and Hypothesis Testing.

In 1983, Stearns investigated two questions, 1) do size and phylogeny affect the patterns of covariation in mammalian life-history traits and 2) do phylogenetic constraints on these traits differ from lineage to lineage? Stearns' analysis assumed that the total variation associated with differences among higher nodes (order/family) is representative of variation due to phylogenetic relatedness, therefore making species level data unsuitable for analysis. Stearns first calculates the correlation and regression on each of the life-history traits on adult weight, this is done with the effects of weight added and removed. Second, a two-level ANOVA for each trait is used to identify which levels (order/family) account for most of the variation with each trait. A factor and cluster analysis is then run on the data. Stearns then calculates the mean of each trait in a family and runs a factor and cluster analysis. This step is repeated at the order level. Finally, the order mean for each trait is subtracted from the value of each species in the order, this is also done at the family level. A second analysis is done on the values after variation due to order and family is removed. By analyzing this data, the impact of order and family on life history traits may be revealed; see Stearns (1983) for a full review of methods. Species are thought to reflect variation due to phylogenetic relatedness and by subtracting the mean values of order and family from each trait the influence of the order and family is removed. Stearns concluded that with the effects of order and family removed, there is lineage-specific variation among the traits. With the effects of weight (size) removed. order and family effects still impacted the covariation of the traits. This led Stearns to conclude that morphology and size may constrain the evolution of life history traits.

In this analysis, the goal is not to identify the influence of order and family on the variables used, but to control for the assumption of non-independence and unequal variances. To control for the effects of order on the data the mean value for each trait is calculated then subtracted from the raw data. For example, the mean value for order cranial length is 177.93mm, and the species value is 173.33 mm. The species data are subtracted from the order mean for a value of -4.6 mm. The -4.6 mm value is representative of data free of variation due to the order. This process is then repeated to remove family level variation (193.13 mm – 173.33 mm = -19.8 mm). To analyze data free of the effects of order and family, the data free of order variation is subtracted from the data free of family variation (-4.6 mm -19.8 mm = -24.4 mm). Hypothesis testing was conducted on data that is free of the effects of both order and family.

<u>Hypothesis One:</u> Pterion is phylogenetically conservative.

Chi-squares were employed to compare species to pterion pattern to identify if species and pterion pattern are dependent. Combining groups would not have worked given each pattern was significantly different with the possible exception of SP and SPE. Fisher's Exact Test values are reported when expected values do not meet the assumption of the chi-square test.

<u>Hypothesis Two</u>: Pterion Patterns are under biomechanical influence.

<u>Test One:</u> Chi-Square Analysis/Fishers Exact Test

To identify it pterion is under biomechanical influence; chi-square analyses were used to determine if pterion pattern and sutural complexity are independent. Fisher's Exact Test values are reported when expected values do not meet the assumption of the chi-square test.

<u>Test Two:</u> Stepwise Linear Regression

Stepwise Linear Regression are employed to determine the effects of masticatory variables on suture length. Before running the regressions, paired t-tests were used to identify a difference in suture length between the left and right sides. If the paired t-test yields no significant difference between sides than Combined Suture Length (CSL) will be used as the dependent variable. CSL is the average suture length of both sides. Treating each side as an individual data point will reduce the number tests that need to be ran. Treating each side as an individual data point may identify symmetrical variation however, that is not the goal of this analysis.

Chapter 7. Results

The following chapter will present the results of testing each hypothesis, following a description of the results of repeated measurements test to establish measurement reliability. Some tests required analysis at each taxonomic level and are identified as so.

Repeated Measures ANOVA

Null Hypothesis: There is no difference between the mean of each measurement made over the course of one week.

As described in the methods chapter, 14 measurements were taken repeatedly on a *Lynx rufus* skull to determine the repeatability of the measures before beginning actual data collection. Based on the results of the ANOVAs, the null hypothesis is rejected if the F-value is below the critical value, indicating that the mean measurements did not differ significantly each day. This null hypothesis was rejected for all of the measures except temporal height (Table 6), indicated that these are accurate and repeatable measures. Locating the temporal muscle insertion scar in *Lynx rufus* provided some difficulty.

Table 6. Repeated Measures ANOVA results. Suture Length,TV,TW,MD,MV not included in original measurements. Measurements taken on *Lynx rufus*.

Variable	df_{error}	$df_{between}$	MS_{error}	$MS_{between}$	F	C.V.
Cranial Length	12	6	8.03	.65	.081	4.0
Cranial Height	12	6	-5.21	3.95	-0.75	3.0
Cranial Width	12	6	1.09	.103	.094	3.0
Masseter Arm	12	6	.103	2.17	-21.07	4.0
Masseter Origin	12	6	.59	.33	0.56	4.0
Bilingual Foramina Distance	10	5	3.86	1.22	.32	4.74
Temporal Length	12	6	-8.49	2.16	-0.25	4.0
Temporal Height	6	3	.49	15.65	31.94	8.94
Post-Orbital Construction	12	6	5.5	.035	.0064	4.0
Inter-Orbital Breadth	4	2	.68	.011	.0165	9.28
Left Pt to AP	2	1	-24.90	-.15	.0053	199.5
Right Pt to AP	2	1	1.21	.0096	.0079	199.5
Left Pt to PP	2	1	9.02	.4128	.0457	199.5
Right Pt to PP	2	1	84.34	.0294	.0003	199.5

Hypothesis One:

Biological Hypothesis: Pterion is phylogenetically conservative.

Test One: Pattern Frequency by Taxonomic Level.

To determine if pterion is under phylogenetically conservative, I first identified the frequency of the nominal patterns for each species. The frequencies for each species suggests that there is one dominant pattern. In coyotes, foxes, black bears, bobcats, goats, deer and squirrel monkey the dominant pattern is the SP pattern. In baboons, and snowshoe hares the dominant pattern is the FT type, see Figure 12 for pattern percentages. There are two cases of the SPE pattern in coyotes, two cases of the FT pattern in foxes, two cases of the SPE pattern in black bears. Bobcats exhibit three cases of the SPE pattern and one of the FT pattern. There is one case of the FT pattern in the mule deer and the red deer.

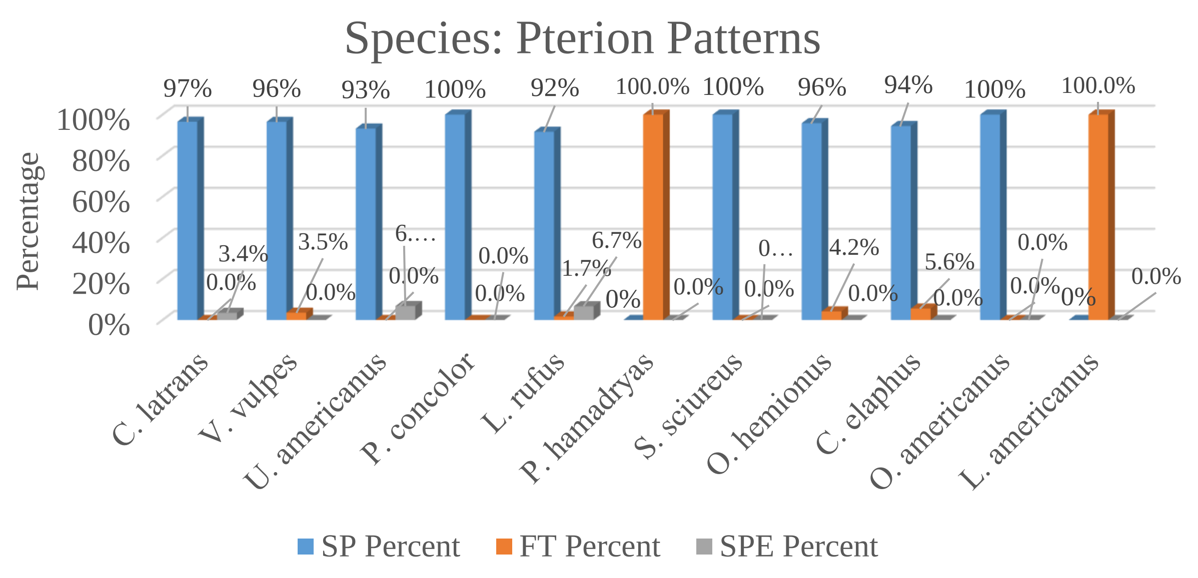

Figure 12. Percentage of pterion patterns in each species.

In the Canidae specimens examined, there are 166 incidences of the SP pattern, 84 of which are on the left side and 82 of which are found on the right side. There are six cases of the SPE pattern, three on each side. The FT pattern was found once on the right and on the left side. This indicates that at the familial level, the SP pattern occurs most frequently in Canidae. In regards to Felidae, there are 87 cases of the SP pattern, 44 of which are found on the left side and 43 on the right. There is only one occurrence of the FT pattern in Felidae, which is found on the left side. Four SPE patterns were found, three on the left and one on the right. In Felidae, the SP pattern occurs most frequently, see Figure 13 for pattern percentages. In Cercopithecidae, the only pattern that occurs is the FT pattern, with 14 cases, seven on each side. In Cebidae, there are 15 cases of the SP pattern, eight on the left and seven on the right. In both Cervidae and Bovidae, the SP pattern is the dominant pattern. There are 31 cases in Cervidae 16 of which are found on the left and 15 on the right. In Bovidae, there are three cases, one on the left and two on the right. In Leporidae, there are 42 cases of the FT pattern, split evenly between the left and right side.

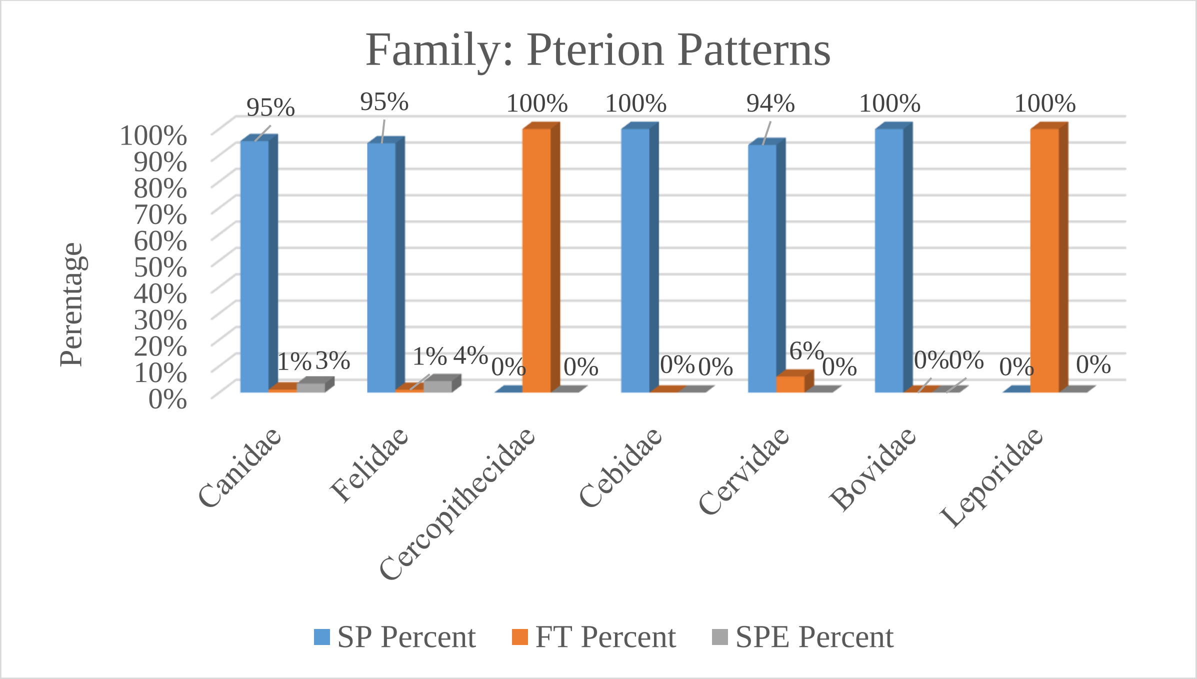

Figure 13. Percentage of pterion patterns at the family level.

In the order carnivora, there are 253 total cases of the SP pattern, 128 occur on the left side and 125 occur on the right side, pattern percentages can be found in Figure 14. There are three cases of the FT pattern in carnivora, one on the left and two on the right. In Primates, there are 15 cases of the SP pattern and 14 of the FT pattern. In artiodacytla there are 34 cases of the SP pattern, 17 found on each side. On the left side, there are two cases of the FT pattern in artiodactlya. In lagomorpha there are again 42 cases of the FT pattern, 21 found on each side.

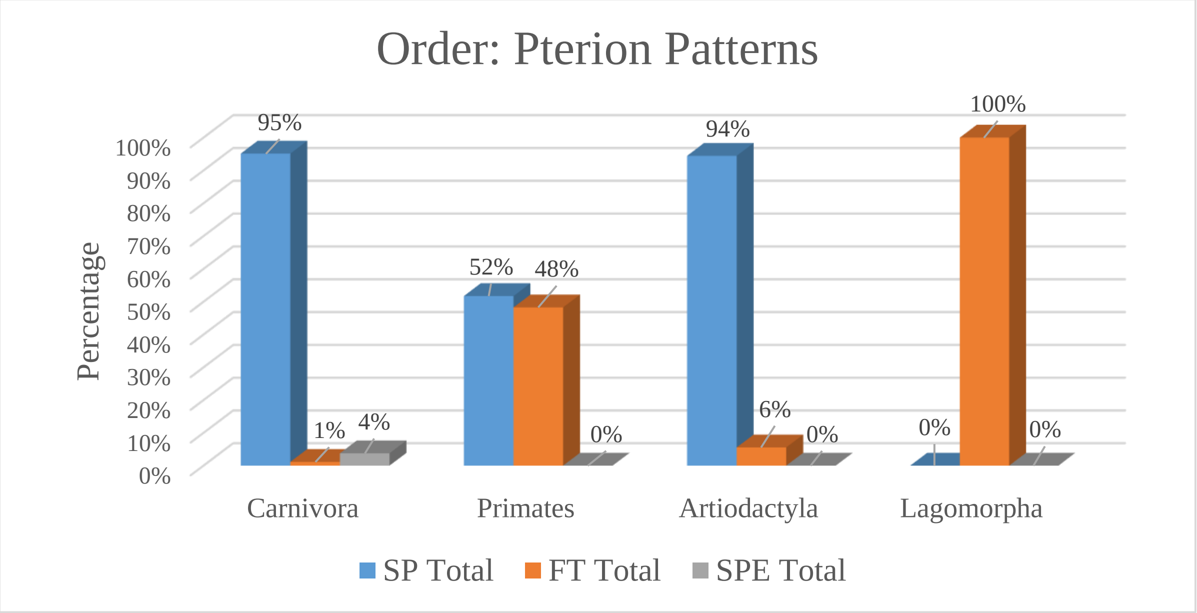

Figure 14. Percentage of pterion patterns at the order level.

<u>Test Two:</u> Chi-Square Analysis/Fishers Exact Test.

To investigate whether pterion patterns and taxonomic level are independent, a chi-square analysis was conducted. Results of the Chi-square test can be found in Table 8. All p values were less than α = .05 indicating that we reject our null hypothesis in favor of the alternative hypothesis, that pterion patterns and species are not independent (Right: X^2 = 173.73, df = 20, n = 177, P = .000; Left: X^2 = 178.42, df = 20, n = 185, P = .000). This trend continues at the family and order level. See Table 8. The assumption of no more than 20% of cells having an expected value of five or greater is not met. The chi-square test summary can be found in Appendix A.

Table 8. Chi-Square test results for each taxonomic level. Each Genus is comprised of one species making species and genus level data the same.

Chi-Square Test	n	X^2 Value	df	Sig
Species and Right Pterion	183	173.73	20	P = .000
Species and Left Pterion	185	178.42	20	P = .000
Family and Right Pterion	183	169.77	12	P = .000
Family and Left Pterion	190	171.91	12	P = .000
Order and Right Pterion	183	143.89	6	P = .000
Order and Left Pterion	190	143.41	6	P = .000

Hypothesis Two:

Biological Hypothesis: Pterion patterns in mammals are influenced by biomechanical forces.

Test One: Paired t-test:

H_o: There is no significant difference in suture length on the left and right sides of the skull.

H_a: There is a significant difference in suture length on the left and right sides of the skull.

To investigate the effects of masticatory variables on suture length, a paired t-test was employed to identify a significance difference between suture length on the left and right side of the skull. This is done in order to reduce the number of tests that will be required be treating each side as separate variables. Results of the paired t-test indicate there is no significant differences between the left and right side. All species had a significance value greater than $\alpha = .05$, indicating a failure to reject the null hypothesis. Results of the test can be found in Table 9. The summary statistics can be found in Appendix A.

Table 9. ANOVA results

Species	n	t	df	Sig.
C. latrans	28	-1.22	27	.231
V. vulpes	9	1.08	8	.309
U. americanus	30	1.86	29	.072
P. concolor	13	1.62	12	.131
L. rufus	29	.060	28	.952
S. sciureus	6	.375	5	.723
P. hamadryas	6	-1.42	5	.213
O. hemionus	8	-3.42	7	.742
C. elpus	4	.484	3	.661
L. americanus	20	.601	19	.555

Stepwise Regression:

After completing a paired t-test the variable Combined Suture Length (CSL) was created by adding the left and right suture sides and dividing by two. Using CSL as the dependent variable, stepwise regressions were run against the masticatory variables found in Table 3. Model Summaries for each taxonomic level can be found in Appendix A.

Species Level Stepwise Regression:

Stepwise multiple regressions at the species level were conducted to investigate the masticatory variables that best predict combined suture length. In *U. americanus*, left pterion to the most posterior portion of the skull (neurocranium) and post-orbital constriction were found to be significant predictor variables F(2,22) = 15.96, p = .000. In *L. rufus* (bobcat), the significant predictors of combined suture length include right pterion to the most posterior portion of the skull (neurocranium), masseter origin and post-orbital constriction, F(3,25) = 13.42, p = .000. See Table 10 for the ANOVA results.

Table 10. Species Level ANOVA table for Combined Suture Length versus masticatory variables.

ANOVA[a,j]

Species	Model		Sum of Squares	df	Mean Square	F	Sig.
Ursus americanus	2	Regression	1.107	2	.554	15.963	.000[f]
		Residual	.763	22	.035		
		Total	1.870	24			
Lynx rufus	3	Regression	10.208	3	3.403	13.425	.000[i]
		Residual	6.337	25	.253		
		Total	16.545	28			

Results indicate masticatory predictor variables predict the combined suture length. In black bears, the $R^2 = .59$, indicating that 59% of the variation in suture length can be predicted by the left pterion to the most posterior portion of the skull and the post-orbital constriction. In Bobcats, the $R^2 = .61$, indicates that 61% of the variation in suture length can predicted by right pterion to the most posterior portion of the skull, masseter origin, and post-orbital constriction, see Table 11 for the model summary. See Figures 15 and 16 for the scatterplots of black bears and bobcats respectively. Variable coefficients can be found in Appendix A.

Table 11. Model Summary

Species Model Summary Table

Species	Model	R	R Square	Adjusted R Square	Std. Error of the Estimate
Ursus americanus	2	.769[f]	.592	.555	.18624
Lynx rufus	3	.786[i]	.617	.571	.50345

f. Predictors: (Constant), lnSpcsLPtoPP, lnSpcsPOC

i. Predictors: (Constant), lnSpcsRPtoPP, lnSpcsMO, lnSpcsPOC

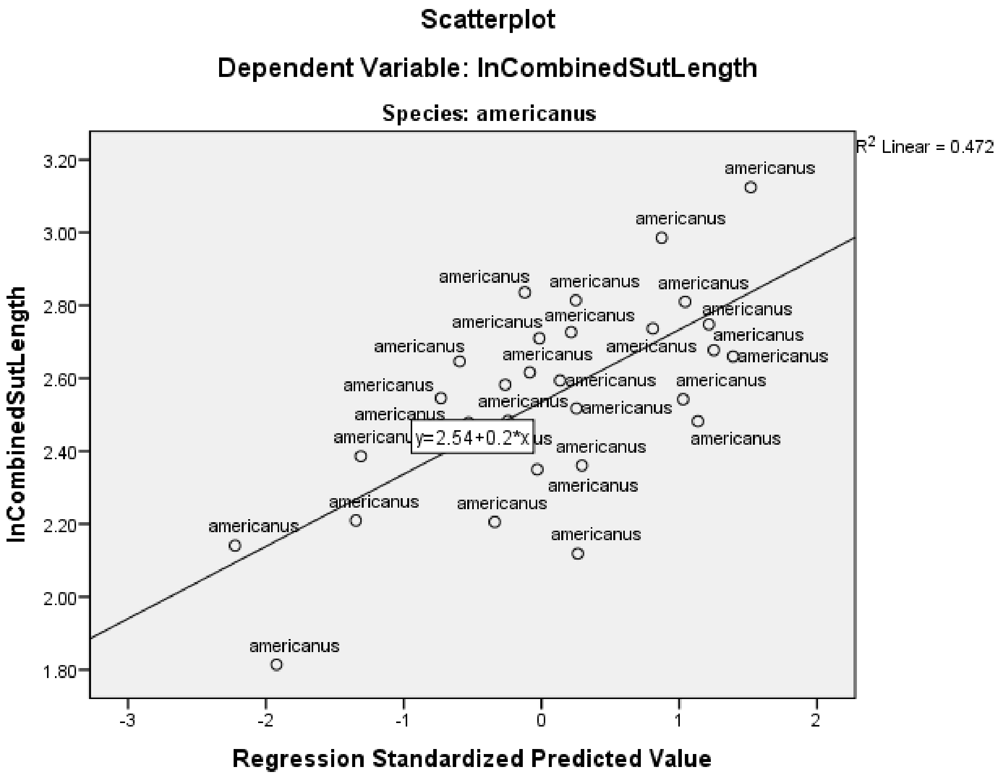

Figure 15. Blackbear Scatterplot of Model Summary two.

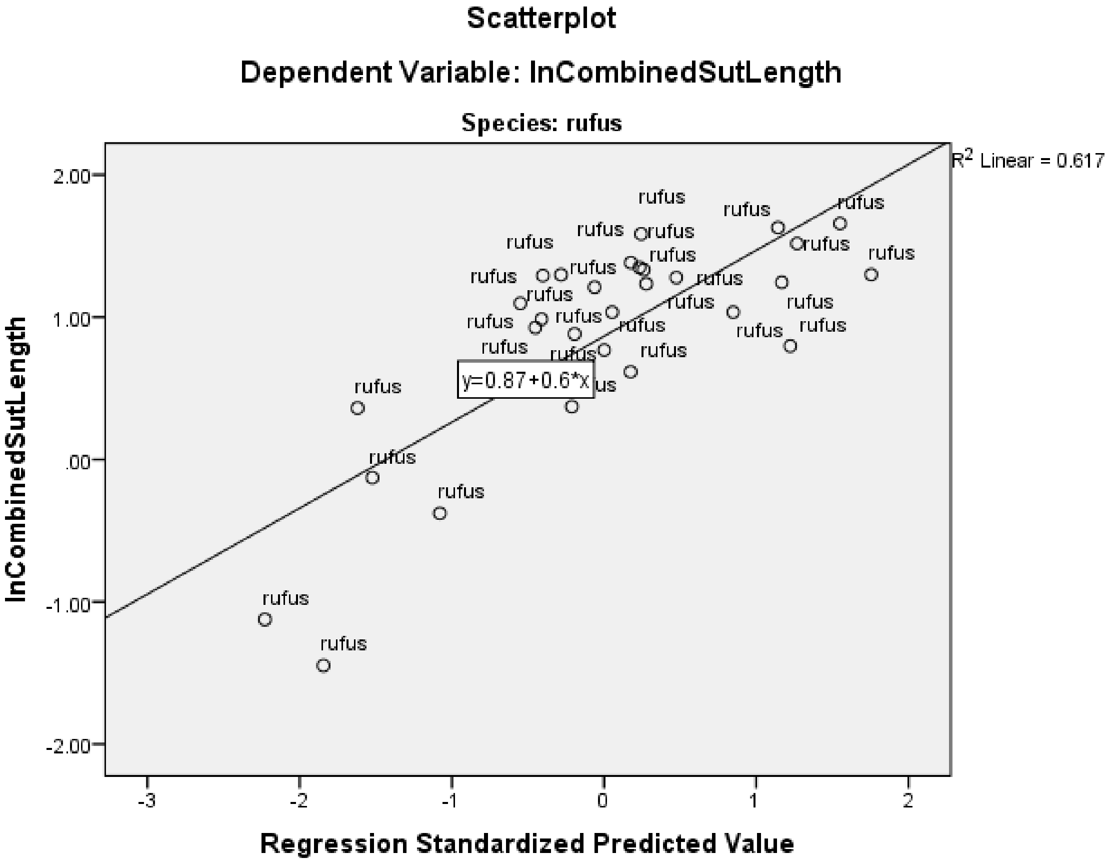

Figure 16. Bobcat Scatterplot of Model Summary three.

Family Level Stepwise Regression:

Stepwise regressions were then run at the family level to identify the significant predictors of cranial suture length. In the family Canidae, left pterion to the most posterior portion of the skull, temporal length and post-orbital constriction, were found to be significant predictors of cranial suture length F(3,52) = 33.74, p = .000. In Felidae, right pterion to the most posterior portion of the skull, right pterion to the most anterior portion of the skull and post-orbital constriction, were found to be significant predictors of cranial suture length F(3,33) = 9.60, p = .000. Post-orbital constriction, neurocranium size and prognathism are also significant predictors at the species level. See Table 12 for ANOVA results.

Table 12. Family level regression ANOVA results.

ANOVA[a,h]

Family	Model		Sum of Squares	df	Mean Square	F	Sig.
Canidae	3	Regression	3.034	3	1.011	33.474	.000[d]
		Residual	1.571	52	.030		
		Total	4.605	55			
Felidae	3	Regression	8.826	3	2.942	9.606	.000[g]
		Residual	10.107	33	.306		
		Total	18.934	36			

Regression Analyses indicate that masticatory variables predict the cranial suture length at the family level. In canids the third model $R^2 = .65$ indicating that 65% of the variation in suture length can be explained by, left pterion to the most posterior portion of the skull, temporal length and post-orbital constriction. In Felids 46% of the variation in suture length can be explained by, right pterion to the most posterior portion of the skull, right pterion to the most anterior portion of the skull and post-orbital constriction, see Table 13 for the model summary. See Figures 17 and 18 for Canidae and Felidae scatterplots.

Table 13. Family level regression model summary.

Model Summary[d,h]

Family	Model	R	R Square	Adjusted R Square	Std. Error of the Estimate
Canidae	3	.812[c]	.659	.639	.17382
Felidae	3	.683[g]	.466	.418	.55342

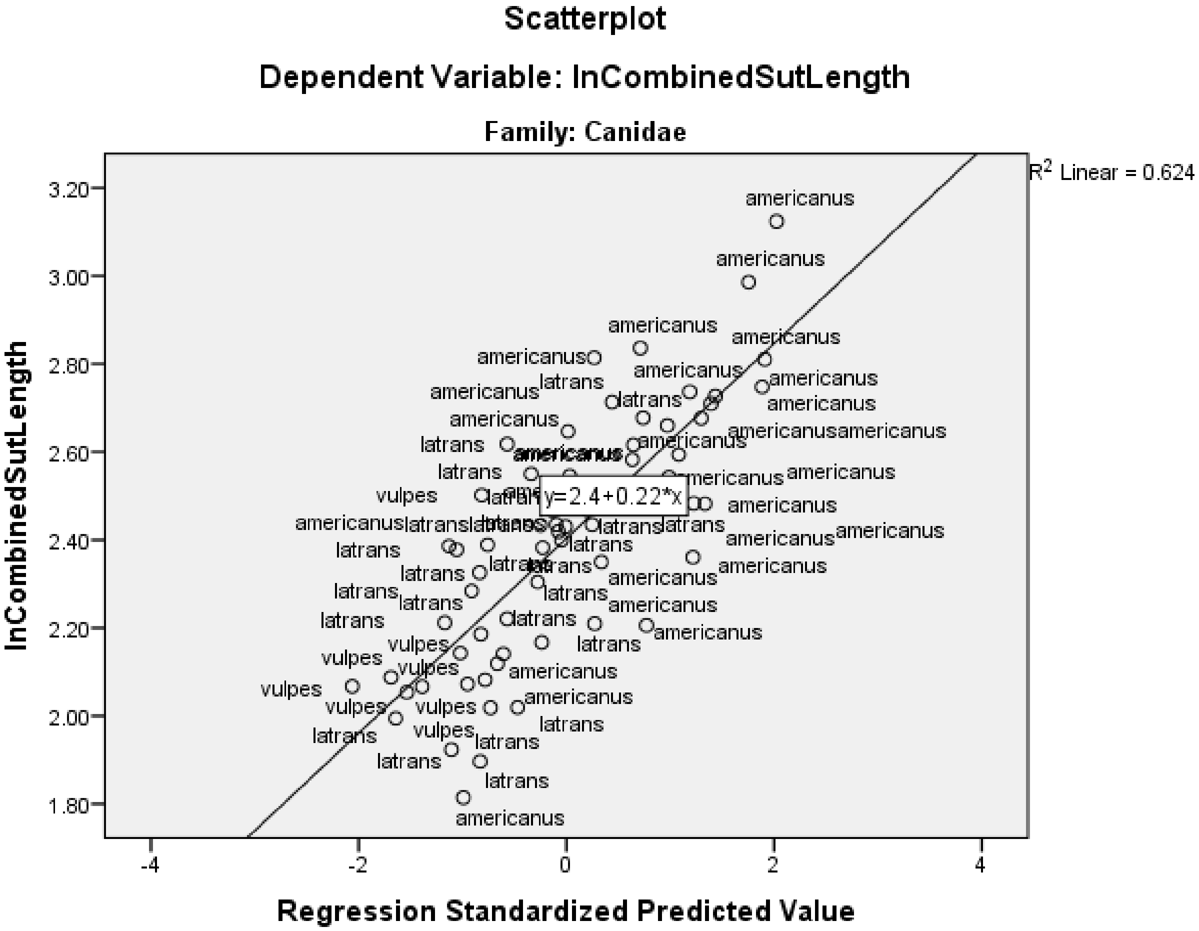

Figure 17. Canidae Scatterplot model summary three.

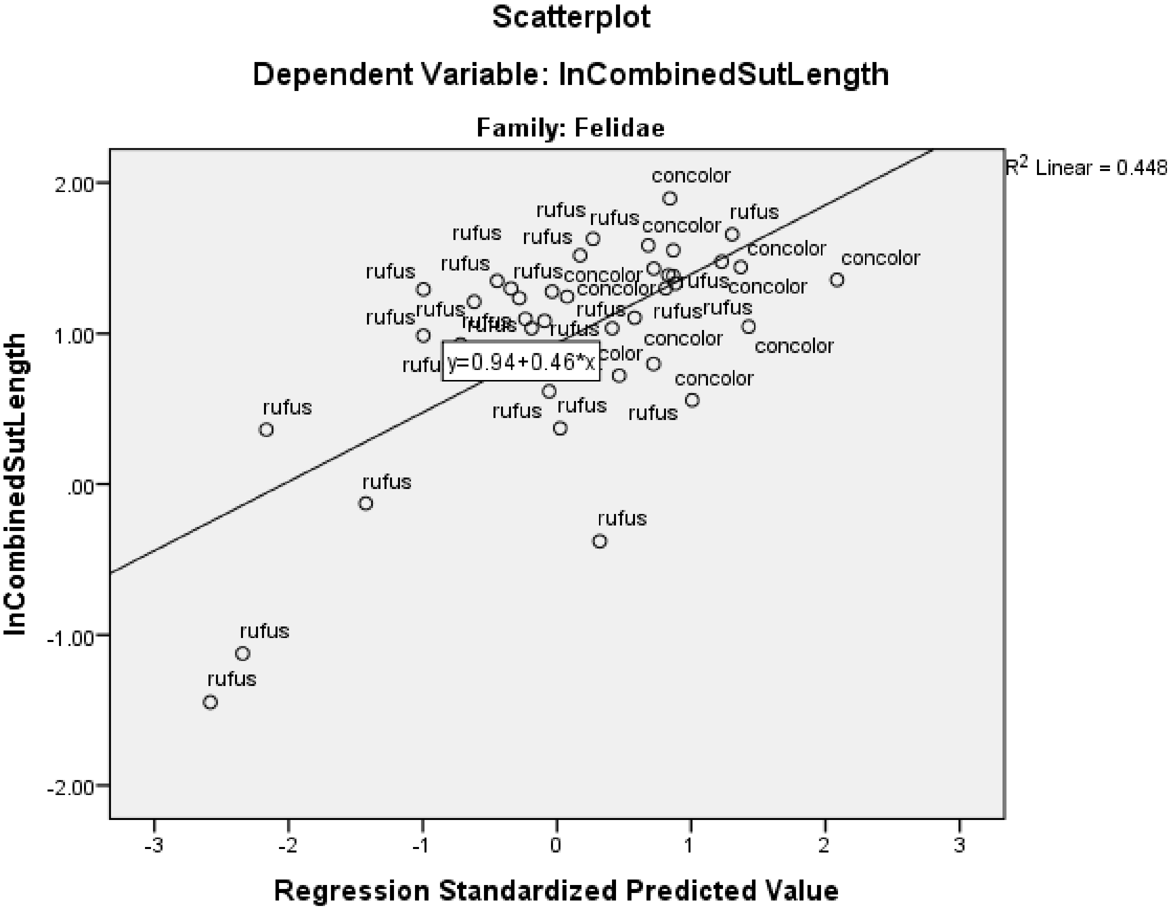

Figure 18. Felidae Scatterplot: Model Summary three.

<u>Order Level Stepwise Regression:</u>

Stepwise regressions were run at the order level to identify significant predictors of cranial suture length. In Carnivora, left pterion to the most anterior portion of the skull, left pterion to the most posterior portion of the skull and temporal length are significant predictors of cranial suture length F(3,89) = 87.49, p = .000, see Table 14.

Table 14. Order level ANOVA results.

ANOVA[a,g]

Order	Model		Sum of Squares	df	Mean Square	F	Sig.
Carnivora	4	Regression	52.495	4	13.124	66.082	.000[e]
		Residual	17.477	88	.199		
		Total	69.971	92			

The results of the analysis indicate that the slope of the regression line is not zero, allowing the conclusion that in carnivora, masticatory variables do predict the combined suture length. In the order carnivora, the fourth model $R^2 = .75$ indicating that LP to AJ left pterion to the most anterior junction of the skull, masseter origin, right pterion to the most posterior portion of the skull and temporal length successfully predict 75% of the cranial suture length, see Table 15. See Figure 19 for carnivora scatterplot.

Table 15. Order level model summary.

Model Summary[f,g]

Order	Model	R	R Square	Adjusted R Square	Std. Error of the Estimate
Carnivora	4	.866[d]	.750	.739	.44564

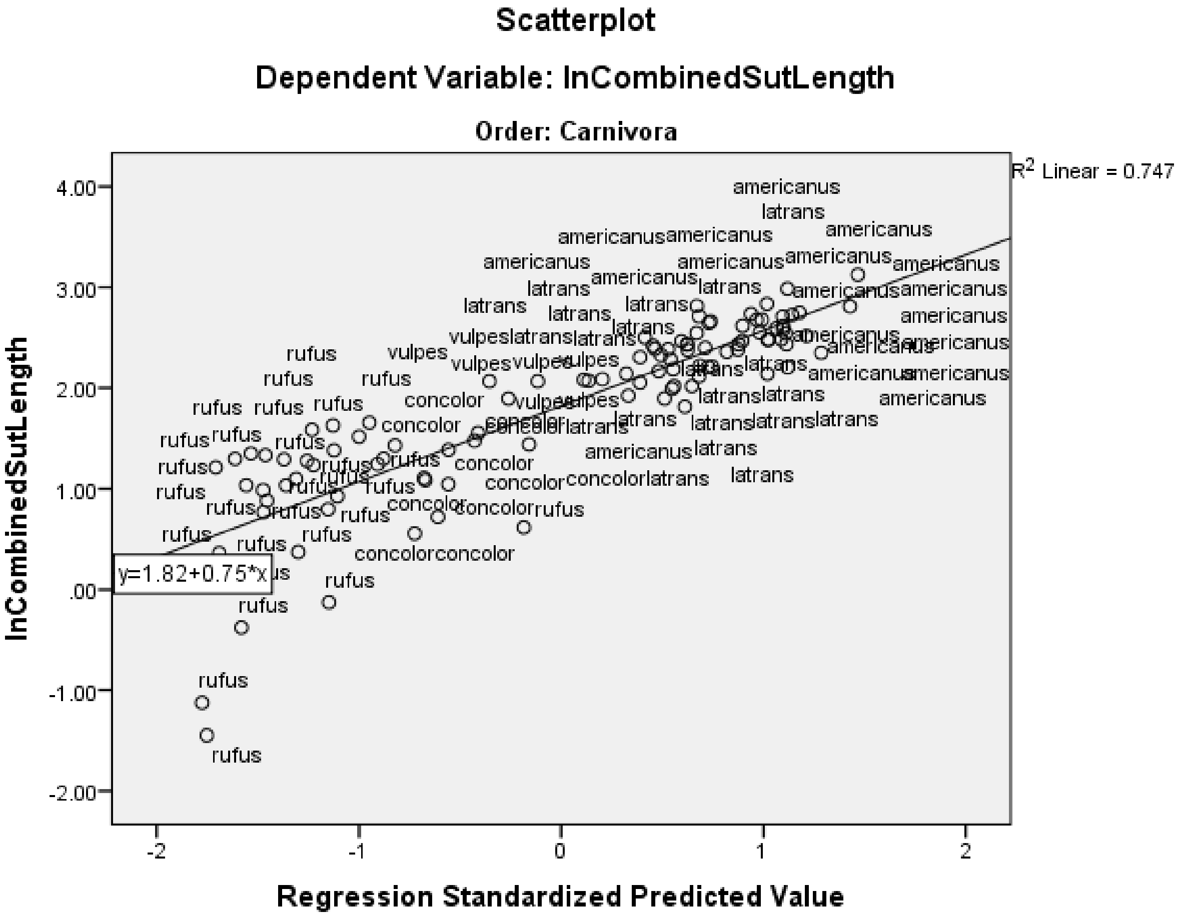

Figure 19. Carnivora Scatterplot.

<u>Test Two:</u> Chi-Square Analysis/Fishers Exact Test

To investigate if pterion pattern and sutural complexity are independent, a chi-square analysis was conducted. See Table 9 for the results of the Pearson’s Chi-square test. Results indicate that pterion pattern and sutural complexity are independent Right: X^2 = .172, df = 2, n = 163, p = .917; Left: X^2 = 3.83, df = 2, n = 169, p = .147). Both p-values were greater than α = .05, indicating a failure to reject the null hypothesis that pterion pattern and sutural complexity are independent (See Table 16.). The assumption of no more than 20% of cells having an expected value of five or greater is not met. The chi-square test summary can be found in Appendix A.

Table 16. Results of the Chi-Square test.

Chi-Square Test	n	X^2 Value	df	Sig
Right Pterion Pattern and Complexity	163	.172	2	P = .917
Left Pterion Pattern and Complexity	169	3.83	2	P = .147

Chapter 8: Discussion

The aim of this study was to investigate two main hypotheses. First, is pterion phylogenetically conservative? Second, is pterion under biomechanical influence? These hypotheses have been repeatedly proposed as possible mechanisms that influence pterions patterns (Murphy, 1956; Saxena et al., 1988; Wang et al., 2006; Ilknur et al., 2009, Halenar, 2015). Humans and non-human primates have been the units of analyses when investigating pterion and few have used vertebrate models. The shared history of human and non-human primate species make it difficult to identify how pterion may be influenced by biomechanics via mastication. The advantage of examining non-primate vertebrates is that the influences on pterions patterns may be exaggerated because the species in this study have evolved in different settings.

8.1 – Discussion.

The first hypothesis investigated was that pterion is phylogenetically conservative. The SP pattern dominates each species analyzed in this study with the exception of hamadryas baboons and snowshoe hares, which are dominated by the FT pattern. According to Topinard as in Montagu (1933), the SP pattern has been found to occur in dogs, foxes, raccoons, cats, goats and sheep. The results presented here support Topinards observations that the SP pattern occurs frequently amongst Felids and Canids (foxes, dogs and cats) as well as in Artiodactyla (goats and deer). However, Topinard suggests that the SP pattern of goats and deer differs from those in dogs and cats. This study did not attempt to discern any variations within patterns. To my knowledge, there are no reports that identify pterion patterns in hares.

The primates in the study sample exhibit, two patterns the SP and the FT. The SP pattern occurred in 100% of the cases observed in the squirrel monkeys, this observation is also reported by Montagu (1933) in six saimiri species. In hamadryas baboons, the FT occurs most frequently; Montagu found the same in eight baboon species found in his study. Montagu however, finds eight cases of the SP pattern amongst his eight species, this study does not find any additional patterns. Second, that as we identify the frequency of patterns at each taxonomic level i.e. family and order, there is little variation among the patterns. Chi-square results comparting qualitative pattern frequencies to taxa at multiple levels indicate that species, family and order are not independent of pattern. Therefore, we can infer that there is one primary pattern found at each taxonomic level. However, my sample does not completely reflect the entirety of species represented in artiodactyla, carnivora, primates and lagomorpha. This study does identify that there is variation within placental mammals, however, there is more conservativism within closely related species; pterion is highly conservative in carnivora (SP), artiodactyla (SP) and lagomorpha (FT). One species from Catarrhini (Baboon) and one from Platyrrhini (Squirrel Monkey) exhibit two different patterns FT and SP respectively.

The results of the stepwise regression at the species level indicate that some of the masticatory variables do successfully predict the combined suture length. In black bears, left pterion to the most posterior portion of the skull and the post-orbital constriction predicts 55% of the combined suture length. Left pterion to the most posterior portion (LP to PP) of the skull is a proxy for neurocranium size, when combined with post-orbital constriction (POC) would indicate that the temporalis has influence on the combined suture length. A longer neurocranium and narrow post-orbital constriction would likely indicate a larger temporal fossa. Research suggests that the larger the temporal fossa the larger the temporalis muscle (Maynard-Smith and Savage, 1959; Radinsky 1981a; Samuels, 2009). The larger size of the temporalis suggests enhanced bite force and larger gape size (Christianson and Wroe, 2007; Slater and Van Valkenburg, 2009), therefore making it plausible that temporalis has influence on the sutures at pterion.

In the bobcat 57% of the variance in suture length is predicted by right pterion to the most posterior portion of the skull (RP to PP), masseter origin (MO) and post-orbital constriction (POC). RP to PP is a proxy measure for the size of the neurocranium, in Felids, the skull is shorter and wider relative to canids (Radinsky, 1981). In the case of the Bobcat (*L. rufus)*, the skull is described as having the largest zygomatic breadth among other felid lineages, and it's described as being broad and robust (Sicuro and Oliveira, 2011). These characteristics are consistent within the lynx lineage with increased size of the neurocranium being a significant indicator of cranial suture length. The masseter origin (MO) is also a proxy for the masseter muscle, the forces generated by the masseter have been discussed above, it is likely that the MO is a significant predictor variable. Bobcats also show higher post-orbital constriction (POC) ratios when compared to other felid species supporting that the skull of the bobcat being broader. The Stepwise regression model predicts that the size (RP to PP) and width of the neurocranium (POC), as well as the masseter origin (MO) influence the size of the combined suture length.

In Canids, 63% of the variance in suture length is predicted by left pterion to the most posterior portion of the skull (LP to PP), temporal length (TL) and post-orbital constriction (POC), in Felids 41% is explained by right pterion to the most posterior portion of the skull (RP to PP), right pterion to the most anterior junction of the skull (RP to AJ) and post-orbital constriction (POC). These three predictor variables in canids confirm that size of the neurocranium, temporal muscle and post-orbital constriction predict some of the variance in combined suture length. These variables are similar to those in bobcats, further supporting that neurocranium and post-orbital constriction influence cranial suture length. The fact that these variables remain significant at the familial level indicates that RP to PP and POC are phylogenetically conservative traits within Felids. The POC remains a significant variable at the family level, however, Sicuro and Oliveira, (2011), find that post-orbital constriction ratios differ significantly at the family level.

At the order level 73% of the variance in Carnivora is explained by LP to AJ, RP to PP and TL. LP to AJ is a proxy for the length of the facial skeleton, indicating that the rostrum (snout) and neurocranium (RP to PP) significantly influenced the combined suture length. Canids, lack significant bite force when compared to felids (Christiansen and Adolfssen, 2005), but the combination of a longer rostrum and feeding behavior account for weaker bite force in canids (VanValkenburg and Ruff, 1987; Christiansen and Adolfssen, 2005; Christiansen and Wroe, 2007). Overall, these findings support the hypothesis that predictor variables related to mastication do predict some of the variance in combined suture length.

A chi-square analysis was used to test the pterion patterns against sutural complexity defined as two ordinal categories, non-complex versus complex. Cranial sutures do reflect different levels of interdigitation however, there are not enough cases to association interdigitation with a specific pattern. This differs from the findings of Rafferty and Herring (1999) who found that sutural interdigitation was associated with compressive strain. However, their study is investigated the sutural interdigitation in craniofacial sutures;

whereas pterion is a vault suture. Sutural complexity is investigated among white tailed deer (Nicolay and Vaders, 2006), who hypothesized that there will be dimorphic variation in suture morphology because male deer compete for mates via headbutting. They expected that males would exhibit higher suture complexity but found that this was not the case. This suggests that the sutures are less influenced by extrinsic impact loading or that the forces generated upon the sutures are not enough to impact the sutural morphology. It is therefore plausible that any biomechanical influences at pterion do not affect the suture morphology. This is the first study attempting to identify if there are varying levels of sutural interdigitation at pterion.

8.2 – Study Limitations

One of the limitations faced was that of sample size. Sample size is critical because the population in question needs to be represented in the sample. A small sample size may result in misrepresentation of the population characteristics. The total sample size in this study N=198, among carnivore n=30 was the exception excluding *Puma concolor*. Lagomorpha was represented by *Lepus. americanus* (n=21). The order of primates was represented by n=8 for both *P. hamadryas* and *S. sciureus.* The sample size of Artiodactyla ranged from n=14 in *Odocoileus hemionus* and n=3 in *Oreamnos americanus*. The small representation of each order, family and genera made it difficult to identify the effects of phylogenetic similarities on species level data, it was even impossible to do so in *Lepus. americanus*. Initial observations of overall Lagomorph cranial morphology (rostrum, vault and orbits) indicate shared cranial morphology indicating that the FT pattern maybe present in other lagomorph species. However, sample size and time constraints prevented further observations. The small representation of mammals can lead to the over/underestimation of statistical information thus skewing the interpretations of each test.

Proxies for proganthism (LP/RP to AJ) and neurocranium (LP/RP to PP) provide some difficulty when assessing the impacts of biomechanics on suture length. Although there is evidence to support that the size of the rostrum impacts hunting behavior and bite force amongst felids and canids, in this study it is difficult to say definitively that they reflect biomechanical impacts over size impacts. It would have also benefited the study had I ran paired t-tests between the left and right side as to eliminate the asymmetrical variation in biomechanical influences on suture length. Scale data on pterion is generated by taking the length of the suture (size), this also makes to it difficult to identify if all these variables (TL, TH, MO, MA) are indicators of biomechanical influence or of size. In future studies size influence, must be accounted for. Controlling for phylogenetic similarity also provided some difficulty in the sample design. The goal of this analysis was not to establish phylogenetic relationships based on the pterion articulations, therefore it was unclear which method is suitable.

This analysis identifies the impact of masticatory variables on cranial suture length. Unfortunately, this sample is dominated by the SP pattern. If there were enough cases of the FT pattern to analyze the impacts of masticatory variables on cranial suture length, then a comparison of the influence of masticatory variables of the SP vs FT patterns could have been made. This comparison could potentially identify if biomechanics influences one pattern over another.

Chapter 9: Conclusion.

In summary, I have two new contributions to the understanding of pterion. First, pterion is phylogenetically conservative. This is exemplified by the lack of diversity of patterns amongst species that are phylogenetically related, thus, it is likely that this location has remained relatively unchanged throughout evolution. My conclusion that pterion is phylogenetically conservative may be refuted by future studies that include a larger sampling of species that are phylogenetically similar. My second contribution is that the pterion suture length is influenced by biomechanical stressors related to mastication. It is unclear how biomechanically generated forces influence pterion suture morphology. It is also unclear how size impacts the length of pterions suture. Finally, future studies should begin to identify if there is any allelic variation in the genes that influence suture morphology. Identifying allelic variation would bring forth new hypotheses in regards to cranial suture morphology, hypotheses such as the role of environmental/epigenetic would provide further understanding of the importance of environment throughout ontogeny.

This study highlights the impacts of biomechanics on pterions suture morphology, while simultaneously highlighting the importance of cranial vault sutures on the skull. It is difficult to identify at what stages the lateral vault sutures begin to close in all species and if their closure is influenced by biomechanics. Although the lateral vault is a medically significant location (thinnest part on the skull, meningeal arteries, brocas motor), future studies should try to identity what role biomechanics plays on these sutures.

References Cited

Aiello, L., Dean, C.
1990 An Introduction to Human Evolutionary Anatomy. New York: Academic Press.

Adejuwon, S. Olopade, F. Bolaji, M.
2013 Study of the Location and Morphology of the Pterion in Adult Nigerian Skulls. Hindawi Publishing Corporation. *ISRN Anatomy,* 1-4.

Agarwal, A. Singh, P. Gupta, S. Gupta, C.
1980 Pterion formation and its variations in the skull of Northern India. *Anthroplogischer Anzeigher*, 265-269.

Alaqeel, S.M. Hinton, R.J. Opperman, L.A.
2006 Cellular response to force application at craniofacial sutures. *Orthod Craniofacial Res,* 9:111-112.

Aksu, F. Akyer, P. Kale, A. Geylan, S. Gayretli, O.
2014 The Localization and Morphology of Pterion in Adult West Anatolian Skulls: *Journal of Craniofacial Surgery*, 25(4):1488–1491.

Anderson, R. McBrayer, L. Herrel, A.
2008 Bite force in vertebrates: opportunities and caveats for use of a nonpareil whole-animal performance measure. *Biological Journal of the Linnean Society,* 93:709-720.

Anton, S. Jaslow,C. Swartz, S.
1992 Sutural complexity in artificially deformed human (*Homo sapiens*) crania. *Journal of Morphology*, 214(3):321-332.

Apinhasmit,W. Chompoopong, S. Chaisuksunt, V. Thiraphatthanavong, P. Phasukdee, N.
2011 Anatomical consideration of pterion and its related reference in dry Thai dry skulls for pterional surgical approach. *Journal of Medical Association of Thailand*, 94(2):205-214.

Asala, S. Mbajiorgu, F.
1996 Epigenetic variation in the Nigerian skull: suture pattern at the pterion *East African Medical Journal*, 73:484-486.

Bellary, S. Steinberg, A. Mirzaya, N. Shirak, M. Tubbs, S. Cohen-Gadol, A. Loukas, M.
2013 Wormian Bones: A Review. *Clinical Anatomy,* 26:922-927.

Bello, F. Berg, P. Andre, T.
2015 On the need for phylogenetic ‘corrections in functional trait-based approaches. *Folia Geobot*, 50:349-357.

Behrents, R. Carlson, D. Abdelnour, T.
1978 *In Vivo* Analysis of Bone Strain about the Sagittal Suture in *Macaca mulatta* during Masticatory Movements. *J. Dent Res,* 57(9-10): 904-908.

Berger, L. de Ruiter, D. Churchill, S. Schmid, P. Carlson, K. Dirks, P. Kibii, J.
2010 *Australopithecus sediba*: A New Species of *Homo*-Like Australopith from South Africa. *Science* 328:195-204.

Berger, L. Hawks, J. de Ruiter, D. Churchill, S. Schmid, P. Delezene, L. et al.,
2015 *Homo naledi*, a new species of the genus *Homo* fromm the Dinaledi Chamber, South Africa. *Genomics and evolutionary biology*, 1-35.

Berry, C. Berry, R.
1967 Epigenetic variation in the human cranium. *Journal of Anatomy*, 1101(2):361-379.

Boas, F.
1912 Changes in the Bodily Form of Descendants of Immigrants. *American Anthropologist*, 14(3):530-562.

Broadfield, D. Holloway, R. Mowbray, K. Silvers, A. Yuan, M. Marquez, S.
2001 Endocast of Sambungmacan 3 (Sm3) A New *Homo erectus* from Indonesia. *The Anatomical Record,* 262:369-379.

Burn, A.K. Herring, S.W. Hubbard, R. Zink, K. Rafferty, K. Lieberman, D.E.
2010 Dietary Consistency and the midline sutures in growing pigs. *Orthod Craniofac Res,* 13(2):106-113.

Byron, D. C. Borke, J. Yu, J. Pashley, D. Wingard, J. Hamrick, M.
2004 Effects of Increased Muscle Mass on Mouse Sagittal Suture Morphology and Mechanics. *THE ANATOMICAL RECORD PART A,* 279A:676-684.

Cheverud, J.
1982 Phenotypic, Genetic, and Environmental Morphological Integration in the Cranium. *Evolution,* 36(3):499-516.

Cheverud, J. Dow, M. Leutenegger, W.
1985 The quantitative assessment of phylogenetic constrains in comparative analyses: sexual dimorphism in body weight among primates. *Evolution*, 93:1335-1351.

Christiansen, P. Adolfssen, J.
2005 Bite forces, canine strength and skull allometry in carnivores (Mammalia, Carnivora). *Journal of Zoology,* 266(2):133-151.

Christiansen, P. Wroe, S.
2007 Bite forces and evolutionary adaptations to feeding ecology in carnivores. *Ecology* 88(2):347-358.

Chou, H. Satpute, D. Müftü, A. Mukundan, S. Müftü, S.
2015 Influence of mastication and edentulism on mandibular bone density. *Computer Methods in Biomechanics and Biomedical Engineering*, 18(3):269-281.

Collins, H.
1925 The pterion in primates. *American Journal of Physical Anthropology,* 8(3):261-274.

Collins, H.
1926 The temporo-frontal articulation in man. *American Journal of Physical Anthropology*, 9(3):343-348.

Collins, H.
1930 Notes on the pterion. *American Journal of Physical Anthropology,* 14(1):41-44.

Cornette, R. Tresset, A. Herrel, A.
2015 The Shrew Tamed by Wolff's Law: Do Functional Constraints Shape the Skull Through Muscle and Bone Covariation? *Journal of Morphology*, 276:301-309.

Corruccini, R.
1974 An examination of the meaning of cranial discrete traits for human skeletal biological studies. *American Journal of Physical Anthropology,* 40(3):425-445.

Cray, J. Meindl, R. Sherwood, C. Lovejoy, O.
2008 Ectocranial Suture Closure in *Pan troglodytes* and *Gorilla gorilla*: Pattern and Phylogeny. *American Journal of Physical Anthropology,* 136:394-399.

Cray, J. Cooper, G. M. Mooney, M.P. Siegel, M.I.
2012 Ectocranial suture fusion in primates: as related to cranial volume and dental eruption. *J Med Primatol,* 41:356-363.

Cremin, B. Goodman, H. Spranger, J. Beighton, P.
1982 Wormian bones in osteogenesis imperfect and other disorders. *Skeletal Radiology,* 8:35-38.

Dixon, M. Marazita, ML. Beaty, TH. Murry, JC.
2011 Cleft lip and palate: understanding genetic and environmental influences. *Nature Reviews Genetics*, 12(3):167-178.

Eboh, D. Obaroefe, M.
2014 Morphometric Study of Pterion in Dry Human Skull Bones of Nigerians. *International Journal of Morphology*, 32(1):208-213.

Elftman, H. Manter, J.
1935 The Evolution of the Human Foot, with Especial Reference to the Joints. *Journal of Anatomy*, 70(1):56-67.

Esteve-Altava, B. Rasskin-Gutman, D.
2014 Theoretical morphology of tetrapod skull networks. *Comptes Rendus Palevol*, 13(1):41-50.

Esteve-Altava, B. Boughner, J. Diogo, R. Villmoare, B. Rasskin-Gutman, D.
2015 Anatomical network analysis shows decoupling of modular lability and complexity in the evolution of the primate skull. *PloS one*, 10(5):e0127653.

Esteve-Altava, B. Diogo, R. Smith, C. Boughner, J. C. Rasskin-Gutman, D.
2015 Anatomical networks reveal the musculoskeletal modularity of the human head. *Scientific Reports*, 5:8298.

Falk, D. Konigsberg, L. Helmkamp, C. Cheverud, J. Vannier, M. Hildebolt, C.
1989 Endocranial Suture Closure in Rhesus Macaques (*Macaca mullata*). *American Journal of Physical Anthropology,* 80:417-428.

Felsenstein, J.
1985 Phylogenies and the comparative method. *The American Naturalist*, 123(1):1-15

Finarelli, J.
2006 Estimation of Endocranial Volume Through the use of External Skull Measurements in Carnivora (Mammalia). *Journal of Mammalogy*, 87(5):1027-1036.

Fleagle, J. G. Stern, J. Jungers, W. Susman, R.
1981 Climing: A Biomechanical Link with Brachiation and with Bipedalism. *Symp. Zool. Soc. Lond. 48:359-375.*

Fleagle, J.G.
2013 Primate Adaptations and Evolution, 3rd edition. New York: Academic Press.

Frost, H.
2003 A 2003 Update of Bone Physiology and Wolff's Law for Clinicians. *Angle Orthodontist.* 74(1):3-15.

Foley, N. Springer, M. Teeling, E.
2016 Mammal madness: is the mammal tree of life not yet resolved? *Phil. Trans. R. Soc. B*, 371: 20150140.

Gans, C. De Vree, F. Gorniak, G.
1978 Analysis of Mammalian Masticatory Mechanisms: Progress and Problems. *Zbl. Vet. Med. C. Anat. Histol. Embryol*, 7:226-244.

Gerstner, G. Goldberg, L.
1994 Species-Specific Morphology of Masticatory Jaw Movements. *Behavior*, 128:3-4.

Gittleman, J.
1985 Carnivore body size: Ecological and taxonomic correlates. *Oecologia*, 67:540-554.

Goswami, A. Milne, N. Wroe, S.
2011 Biting through constraints: cranial morphology, disparity and convergence across living and fossil carnivorous mammals. *Proc. R. Coc. B.*, 278:1831-1839.

Goswami, A. Foley, L. Weisbecker, V.
2013 Patterns and implications of extensive heterochrony in carnivoran cranial suture closure. *Journal of Evolutionary Biology*, 26:1249-1306.

Grafen, A.
1989 The Phylogenetic regression. *Phil. Trans. R. Soci. Lond*. 326:119-157.

Grancolas, P. Deleporte, P. Desutter-Grandcolas, L. Daugeron, C.
2001 Phylogenetics and Ecology: As Many Characters as Possible Should Be included in the Cladistic Analysis1. *Cladistics*, 17(1):104-110.

Gravlee, C. Bernard, R. Leonard, W.
2003 Boas's Changes in Bodily Form: The Immigrant Study, Cranial Plasticity, and Boas's Physical Anthropology. *American Anthropologist*, 105(2):326-332.

Grüneberg, H.
1952 Genetical studies on the skeleton of the mouse. IV. Quasi-continuous variations. *J. Genetics*, 51:95-114.

Ha, R. Ha, J.
2012 Integrative Statistics for the Social and Behavioral Sciences. Sage Publications, Thousand Oaks California.

Halenar, J.
2015 Investigating the variation at pterion across platyrrhines, with special attention to *Alouatta.* American Journal Physical Anthropololgy Suppl, in press.

Hallgrímsson, B. Lieberman, D. Liu, W. Ford-Hutchinson, A. Jirik, F.
2007 Epigenetic interactions and the structure of phenotypic variation in the cranium. *Evolution and Development*, 9(1):76-91.

Harcourt-Smith, W. Aiello, L.
2004 Fossils, feet and the evolution of human bipedal locomotion. *Journal of Anatomy*, 204(5):403-416.

Harvey, P. Pagel, D.
1991 *The comparative method in evolutionary biology*. Oxford: Oxford university press.

Hauser, G. De Stefano, G.
1989 Epigenetic variants of the human skull. *E. Schweizerbart'sche Verlagsbuchhandlung, Nägele U. Obermiller, Stuttgart.*

Henderson, J. Chang, J. Song, H. Longaker, M. Carter, D.
2005 Age-dependent properties and quasit-static strain in the rat sagittal suture. *Journal of Biomechanics*, 38(11):2294-2301.

Herring, S. Herring, S.
1974 The Superficial Masseter and Gape in Mammals. *The American Naturalist*, 108(962):561-576.

Herring, S.
1985 The Ontogeny of Mammalian Mastication. *American Zoologist*, 25(2):339-349.

Herring, S. Mucci, R.
1991 In Vivo Strain in Cranial Sutures: The Zygomatic Arch. *Journal of Morphology*. 207(3):225.

Herring, S.
1993 Formation of the Vertebrate Face: Epigenetic and Functional Influences. *American Zoology*, 33:472-483.

Herring, S. Shengyi, T.
2000 Strain in the Braincase and its Sutures during Function. *American Journal of Physical Anthropology, 112*(4):575.

Herring, S. Rafferty, Liu, Z.J. Marshall, C.
2001 Jaw muscles and the skull in mammals: The biomechanics of mastication. *Comparative Biochemistry and physiology A, Molecular and Integrative Physiology*, 131(1)203-219.

Herring, S.
2007 Masticatory Muscles and the Skull: A comparative Perspective. *Arch Oral Biol*, 52(4):296-299.

Herring, S.
2008 Mechanical Influences on Suture Development and Patency. *Front Oral Biol*, 12:4156.

Hylander, W. Johnson, K. Crompton, A.W.
1992 Muscle Force Recruitment and Biomechanical Modeling: An Analysis of Masseter Muscle Function During Mastication in *Macaca fascicularis. American Journal of Physical Anthropology* 88:365-387.

Hylander, W.
2006 Functional Anatomy of the TMJ. *In* Laskin, D. Greene,C. Hylander, W. Temporormandibular Disorders: An Evidenced-Based Approach to Diagnosis and Treatment. Quintessence Publishing Co. 3-34.

Holloway, R.
1981 Volumetric and Asymmetry Determinations on Recent Hominid Endocasts: Spy I and II, Djebel Ihroud I, and the Sale *Homo erectus* Specimens, With Some Notes on Neandertal Brain Size. *American Journal of Physical Anthropology*, 55:385-393.

Hoshi, H.
1971 Comparative Morphology of the mammalian mandible in relation to food habit. *Okajimas Folia Anat Jpn.* 48(5):333-345.

Howells, W.W.
1973 Cranial variation in man. A study by multivariate analysis of patterns of difference. Among recent populations. *Papers of the Peabody Museum of Archaeology and Ethnology*. 67:1-259.

Howells, W.W
1989 Skulls shapes and the map: craniometric analyses in the dispersion of modern Homo. Cambridge. *Peabody Museum of Archaeology and Ethnology,* 79

Ilknur, Ari, Mustafa, K. and Sinan, B.
2009 A Comparative Study of Variation of the Pterion of Human Skulls from 13th and 20th Century Anatolia. *International Journal Morphology,* 27(4):1291–1298.

Jahan, E. Matsumoto, A. Udagawa, J. Rafiq, A. Hasimoto, R. Rahman, O. Habib, H. Sekine, J. Otani, H.
2010 Effects of restriction of the fetal jaw movement on prenatal development of the temporalis muscle. *Archives of Oral Biology,* 55:919-927.

Janis, C.
1990 Correlations of Cranial and Dental Variables with Dietary Preferences in Mammals: A Comparison of Macropodoids and Ungulates. *Mem. Qd Mus.*, 28(1):349-366.

Jaslow, C.
1990 Mechanical Properties of Cranial Sutures. *Journal of Biomechanics,* 23(4):313-321.

Jaslow, C. Biewener, A.
1995 Strain patterns in the horncores, cranial bones and sutures of goats (Capra hircus) during impact loading. *Journal of Zoology*, 235(2):193-210.

Jayaprakash, P. Srinivasan, GJ.
2013 Skull sutures: Changing morphology during preadolescent growth and its implications in forensic identification. *Forensic Science International,* 229(1):166.e1-166.e13.

Jungers, W. Cartmill, M.
2003 Hypoglossal Canal Size in Living Hominoids and the Evolution of Human Speech. *Human Biology*, 75(4):473-484.

Klingenberg, C.
2008 Morphological integration and the developmental modularity. *Annual review of ecology,evolution, and systematics,* 115-132.

Kardong, K.
2011 Vertebrates: Comparative Anatomy, Function, Evolution. McGraw-Hill, New York City, New York.

Kumar, S. Anurag, M. Chauhan, P. Chaudary, A. Jain, S.
2013 Pterion its location and clinical implications-A Study Compared. *Journal of Evolution of Medical and Dental Sciences*, I2(25):4599-4608.

La Croix, S. Zelditch, M. L. Shivik, J. A. Lundriga, B.L. Holekamp, K.E.
2011 Ontogeny of feeding performance and biomechanics in coyotes. *Journal of Zoology* 285:301-315.

Lee, U. Park, D. Kwon, S. Paik, D. Han, S.
2001 Morphological analysis of the Pterion in Korean. *Korean Journal of Physical Anthropology*, 14:281-289.

Lieberman, D.
2011 The Evolution of the Human Head. The Belknap Press of Harvard University Press, Cambridge, Massachusetts.

Logan, C. Clutton-Brock, T.
2013 Validating methods for estimating endocranial volume in individual red deer (*Cervus elphus). Behavioural Processes*, 92:143-146.

Long, CA.
1985 Intricate sutures as fractal curves. *Journal of Morphology,* 185:285-295.

Lovejoy, C. Meindl, R. Ohman, J. Heiple, K. White, T.
2002 The Maka Femur and Its Bearing on the Antiquity of Human Walking: Applying Contemporary Concepts of Morphogenesis to the Human Fossil Record. *American Journal of Physical Anthropology.* 119:91-133

Luca, F. Perry, G. Di Rienzo, A.
2010 Evolutionary adaptations to dietary changes. *Annual Review of Nutrition*, 30:291-314.

Lynch, M.
1991 Methods for the analysis of comparative data in evolutionary biology. *Evolution*, 1065-1080.

Lynnerup, N. Jacobsen, J.C.
2003 Brief Communication: Age and Fractal Dimensions of Human Sagittal and Coronal Sutures. *American Journal of Physical Anthropology*, 121:332-336.

Ma, S. Louisa, B. Stringer, M.
2012 Reappraising the surface anatomy of the pterion and its relationship to the middle meningeal artery. *Clinical Anatomy*, 25(3):330-339.

Mattson, D.
1998 Diet and Morphology of Extant and Recently Extinct Northern Bears. *Ursus*, 10:479-496.

Maynard-Smith, J. Savage, J.
1959 The mechanics of mammalian jaws. *Sch Sci Rev*, 40:289-301.

McLaughlin, N. Cutler, A. Martin, N.
2013 Technical nuances of temporal muscle dissection and reconstruction for the pterional keyhole craniotomy: Technical Note. *Journal of neurosurgery*, 118(2):309-314.

McPherson, G. Kriewall, T.
1980 The Elastic Modulus of Fetal Cranial Bone: A First Step Towards an Understanding of the Biomechanics of Fetal Head Molding. *Journal of Biomechanics* 13:9-16.

Meredith, R. Janečka, J. Gatesy, J. Ryder, O. Fisher, C. Teeling, E. Goodbla, A et al.
2011 Impacts of the Cretaceous Terrestiral Revolution and KP_g Extinction on Mammal Diversification. *Science*, 334:521-524.

Miendl, R. Loveyjoy, O.
1985 Ectocranial Suture Closure: A revised Method for the Determination of Skeletal Age at Death Based on the Lateral-Anterior Sutures. *American Journal of Physical Anthropology*, 68:57-66.

Miura, T. Perlyn, C. Kinboshi, M. Ogihara, N. Kobayashi-Miura, M. Morris-Kay, G. Shiota, K.
2009 Mechanism of Skull suture maintenance and interdigitation. *Journal of Anatomy,* 215:642-655.

Moa, J. Wang, X. Kopher, A.
2003 Biomechanics of Craniofacial Sutures: Orthopedic Implications. *Angle Orthodontist*, 73(2):128-135.

Montagu, A.
1930 A Note on a Rare Type of Pterion in the Gorilla. *Journal of Anatomy* 64(2):247-9.

Montagu, A.
1933 The Anthropological Significance of Pterion in Primates. *American Journal Physical Anthropology* 18:159–336.

Monteiro, L. R. Lessa, L. G.
2000 Comparative Analysis of Cranial Suture Complexity in the Genus *Caiman* (*Crocodylia, alligatoridae). Re. Brasil. Biol*, 60(4):689-694.

Moss, M.
1954 Growth of the calvaria in the Rat. The determination of osseous morphology. *American Journal of Anatomy,* 94(36): 333-361.

Moss, M. Young, M.
1960 A Functional Approach to Craniology. *American Journal of Physical Anthropology*, 18(4): 281-292.

Moss, M.
1968 A Theoretical Analysis of the Functional Matrix. *Acta Biotheoretica*, 18(1):195-202.

Moss, M. Rankow, M.
1968 The Role of the Functional Matrix Hypothesis in Mandibular Growth. *The Angle Orthodontist*, 38(2):95-103.

Moss, M. Salentijn, L.
1969 The primary role of functional matrices in facial growth. *American Journal of Orthodontics,* 55(6): 566-577.

Moss, M.
1975 Functional Anatomy of Cranial Synostosis. *Childs Brain*, 1(1):22-33.

Moss, M.
1997a The functional matrix hypothesis revisited. 1. The role of mechanotransduction. *American Journal of Orthodontics and Dentofacial orthopedics,* 112(1):8-11.

1997b The functional matrix hypothesis revisited. 2. The role of an osseous connected cellular network. *American Journal of Orthodontics and Dentofacial orthopedics,* 112(2):221-226.

1997c The functional matrix hypothesis revisited. 3. The genomic thesis. *American Journal of Orthodontics and Dentofacial orthopedics,* 112(3):338-342.

1997d The functional matrix hypothesis revisited. 4. The epigenetic antithesis and the revolving synthesis. *American Journal of Orthodontics and Dentofacial orthopedics,* 112(4):410-417.

Moss, M.
2007 The differential roles of periosteal and capsular functional matrices in orofacial growth. *The European Journal of Orthodontics*, 29(1):i96-i101.

Murphy, T.
1955 The spheno-ethomoidal articulation in the anterior cranial fossa of the Australian aboriginie. *American Journal of Physical Anthropology*, 13(2):285-300.

Murphy, T.
1956 The pterion in the Australian aborigine. *American Journal of Physical Anthropology*, 14:225–244.

Mwachaka, P. Hassanali, J. Odula, P.
2008 Sutural morphology of the pterion and asterion among adult Kenyans. *Brazilian Journal of Morphological Science,* 26:4-7.

Mwachaka, P. Hassanali, J. Odula, P.
2009 Anatomic Position of the Pterion among Kenyans for the Lateral Skull Approaches. *International Journal of Morphology*, 26(4):931-933.

Nicolay, C.W. Vaders, M. J.
2006 Cranial Suture Complexity in White-Tailed Deer (*Odocoileus virginianus)*. *Journal of Morphology*, 267:841-849.

Nogueira, M. Monteiro, L. Peracchi, A. de Araújo, A.
2005 Ecomorphological analysis of the masticatory apparatus in the seed-eating bats, genus *Chiroderma* (Chiroptera: Phyllostomidae). *J. Zool. Lond.* 266:355-364.

Oguz, O. Sanli, S. Bozkir, M. Soames, R.
2004 The pterion in Turkish male skulls. *Surgery Radiol Anat* 26:220-224.

Opperman, L. A.
2000 Cranial Sutures as Intramembranous Bone Growth Sites. *Developmental Dynamics,* 219:472-485.

O'Rahilly, R. Müller, F.
1996 Human Embryology and Teratology. New York: Wiley-Liss.

Parker, C.
1905 Wormian Bones. Roberts Press.

Paschetta, C. de Azebedo, S. Castillo, L. Martínez-Abadías, N. Hernàndez, M. Lieberman, D. Gonzàlez-José, R.
2010 The Influence of Masticatory Loading on Craniofacial Morphology: A Test Case Across Technological Transitions in the Ohio Valley. *American Journal of Physical Anthropology*, 141:297-314.

Pearson, O. Lieberman, D.
2004 The Aging of Wolff's "Law": Ontogeny and Responses to Mechanical Loading in Cortical Bone. *Yearbook of Physical Anthropology*, 47:63-99.

Perelman, P. Johnson, W. Roos, C. Seuánez, H. Horvath, J. Moreira, M et al.
2011 A Molecular phylogeny of Living Primates. *PLoS Genet*, 7(3): e1001342.

Pérez-Berberia, J. Gordon, I.
1999 The functional relationship between feeding type and jaw and cranial morphology in ungulates. *Oecologia*, 118:157-165.

Pucciarelli, H. Dressino, V. Niveiro, M.
1990 Changes in Skull Components of the Squirrel Monkey Evoked by Growth and Nutrition: An Experimental Study. *American Journal of Physical Anthropology*, 81:535-543.

Radinsky, L
1981a Evolution of Skull Shape In Carnivores. 1. Representative modern carnivores. *Biological Journal of the Linnean Society*, 15(4):369:388.

1981b Evolution of Skull Shape in Carnivores. 2. Additional Modern Carnivores. *Biological Journal of the Linnean Society*, 16(4):337-355.

Radinsky, L.
1982 Evolution of Skull Shape in Carnivores. 3. The Origin and Early Radiation of the Modern Carnivore Families. *Paleontological Society*, 8(3):177-195.

Rager, L. Hautier, L. Forasiepi, A. Goswami, A. Sanchez-Villagra, M.
2014 Timing of Cranial Suture Closure in Placental Mammals: Phylogenetic Patterns, Intraspecific Variation, and Comparison With Marsupials. *Journal of Morphology*, 275:125-140.

Rafferty, K. L. Herring, S.W.
1999 Cranial Sutures: Morphology, Growth, and In Vivo Masticatory Strains. *Journal of Morphology*, 242(2):167.

Rasskin-Gutman, D. Esteve-Altava, B.
2014 Connecting the dots: anatomical network analysis in morphological EvoDevo. *Biological Theory*, 9(2):178-193.

Rice, D. P.
2008 Developmental anatomy of craniofacial sutures. Frontiers of Oral Biology, 12:1-21.

Richtsmeier, J. Aldridge, K. Deleon, V. Panchal, J. Kane, A. Marsh, J. Yan, P. Cole III, T.
2006 Phenotypic Integration of the Neurocranium and Brain. *J Exp Zool B Mol Dev Evol.* 306(4):360-378.

Saladin, K.
2010 Anatomy and Physiology: The Unity of Form and Function. New York, NY, McGraw-Hill Companies.

Samuels, J.
2009 Cranial morphology and dietary habits of rodents. *Zoological Journal of the Linnean Society*, 155:864-888.

Sanchez-Lara, P. Graham, J. Hing, A. Lee, J. Cunningham, M.
2007 The morphogenesis of Wormian Bones: A Study of craniosynostosis and purposeful cranial deformation. *Am J Med Genet A*, 143:3243-3251.

Sardi, M. Novellino, P. Pucciarelli, H.
2006 Craniofacial morphology in the Argentine center-west: Consequences of the transition to Production. *American Journal of Physical Anthropology,* 130(3):333-343.

Satpute, C. Wahane. A.
2015 To Study the Morphology of Pterion in Dry Human Skull in Vidarbha Region. *Internat J Sci Res*, 4(1):2171-2173.

Saxena, S. Jain, S. Chowdhary, D.
1988 A Comparative study of pterion formation and its variations in the skulls of Nigerians and Indians. *Anthropol Anz*, 48:75-82.

Schmitt, D.
2003 Insights into the evolution of human bipedalism from experimental studies of humans and other primates. *Journal of Experimental Biology,* 206(9):1437-1448.

Semler, O. Cheung, M. Glorieux, F. Rauch, F.
2010 Wormian bones in osteogenesis imperfecta: correlation to clinical findings and genotype. *Am. J. Med. Genet*, 152:1681-1687.

Slater, GJ. Van Valkenburgh, B.
2009 Allometry and performance: the evolution of skull form and function in felids. *Journal of Evolutionary Biology*, 22:2278-2287.

Sicuro, F. Oliveira, L.
2011 Skull morphology and functionality of extant Felidae (Mammalia: Carnivora): a phylogenetic and evolutionary perspective. *Zoological Journal of the Linnean Society*, 161(2):414-462.

Stearns, S.
1983 The Influence of Size and Phylogeny on Patterns of Covariation among Life-History Traits in the Mammals. *Oikos,* 41(2):173-187.

Stearns, S.
1985 Trade-Offs in Life-History Evolution. *Functional Ecology* 3(3):259-268.

Som, P. M. Naidich, T.P
2013 Development of the Skull Base and Calvarium: An overview of the Progression from Mesenchyme to Chondrification to Ossification. *Neurographics.* 3:169-184.

Sun, Z. Lee, E. Herring, S.
2004 Cranial Sutures and Bones; Growth and Fusion in Relation to Masticatory Strain. *The Anatomical Record Part A,* 267A:150-161.

Todd, W. T. Lyon, D.W.
1925 Cranial Suture Closure Its Progress and Age Relationship Part III – Endocranial Closure in Adult Males of Negro Stock. *American Journal of Physical Anthropology,* 8(1)47-71.

Urzi, F. Iannello, A. Torrisi, A. Foti, P. Mortellaro N. Cavallaro, M.
2003 Morphological variability of pterion in the human skull. *Italian Journal of Anatomy and Embryology*. 108:83-117.

Van Lindert, E. Perneczky, A. Fries, G. Pierangeli, E.
1998 The supraorbital keyhole approach to supratentorial aneurysms: concept and technique. *Surgical neurology,* 49(5): 481-490.

Van Heteren, A.
2011 Masticatory Adaptations of Extant and Extinct Ursidae: an Assessment Using Three-dimensional Geometric Morphometrics. University of Roehampton.

Van Valkenburgh, B. Ruff, C. B.
1987 Canine tooth strength and killing behavior in large carnivores. *Journal of Zoology,* 212: 379–397.

Vannucci, R. Barron, T. Holloway, R.
2011 Craniometric ratios of microcephaly and LB1, Homo floresiensis, using MRI and endocasts. *Proceedings of the National Academy of Sciences,* 108(34):14043-14048.

Wang, Q. Opperman, L. Havill, L. Carlson, D. Dechow, P.
2006 Inheritance of Sutural Pattern at the Pterion in Rhesus Monkey Skulls. *The Anatomical Record Part A,* (288):1042-1049.

Wang, X. Luo, J. Li, P. Cheng, B. Li, Z. Cheng, H.
2016 The role of pterional keyhole approach in the microsurgical clipping of anterior circulation artery aneurysms: experiences with 26 cases and literature review. *International Journal of Clinical Experimental Medicine,* 9(3):5922-5931.

Wayne, R.
1986 Cranial Morphology of Domestic and Wild Canids: The Influence of Development on Morphological Change. *Society for the study of Evolution,* 40(2):342-261.

White, T. Folkens, P.
2012 Human Osteology. San Diego: Academic Press.

Whitlock, M. Schluter, D.
2014 The analysis of biological data. Greenwood Village, Colo: Roberts and Co. Publishers.

Wilson, D.
1971 Limited exposure in cerebral surgery: Technical note. *Journal of neurosurgery,* 34(1):102-106.

Xu, T. Moore, I. Gallant, J.
1993 Fractals, fractal dimensions and landscapes – a review. *Geomorphology,* 8:245-262.

Yaşargil, M.G. Antic, J. Laciga,R. Jain, KK. Hodosh, RM, Smtih, RD.
1976 Microsurgical pterional approach to aneurysms of the basilar bifurcation. *Surg Neurology,* 6:83-91

Yaşargil, M.G. Reichman, MV. Kubic, S.
1987 Preservation of the frontotemporal branch of the facial nerve using the interfacial temporalis flap for pterional craniotomy. Technical article. *J. Neurosurg,* 67:463-466.

Yasargil, M. G. Abernathey, C. Sarioglu, A.
1989 Micronuerosurgical treatment of intracranial dermoid and epidermoid tumors. *Neurosurgery,* 24(4):561-567.

Yu, J. Wright, R. Williamson, M. Braselton III, J. Abell, M.
2003 A Fractal Analysis of Human Cranial Sutures. *Cleft Palate-Craniofacial Journal,* 40(4):409-415.

Zalawadia, A. Vadgama, J. Ruparelia, S. Patel, S. Rathod, S. Patel, S.
2010 Morphometric study of pterion in dry skull of Gujarat Region. *National Journal of Integrated Research in Medicine,* 1(4):25-29.

Appendix A

Hypothesis: Pterion is Phylogenetically Conservative

Test One: Frequency Charts by Family

Statistics

Family			Left Pterion	Right Pterion
Canidae	N	Valid	88	86
		Missing	2	4
Felidae	N	Valid	47	45
		Missing	1	3
Cercopithecidae	N	Valid	7	7
		Missing	1	1
Cebidae	N	Valid	8	7
		Missing	0	1
Cervidae	N	Valid	18	15
		Missing	0	3
Bovidae	N	Valid	1	2
		Missing	2	1
Leporidae	N	Valid	21	21
		Missing	0	0

Left Pterion

Family			Frequency	Percent	Valid Percent	Cumulative Percent
Canidae	Valid	Spheno-Parietal	84	93.3	95.5	95.5
		Fronto-Temporal	1	1.1	1.1	96.6
		Spheno-Parietal-Epipteric	3	3.3	3.4	100.0
		Total	88	97.8	100.0	
	Missing	.00	2	2.2		
	Total		90	100.0		
Felidae	Valid	Spheno-Parietal	44	91.7	93.6	93.6
		Spheno-Parietal-Epipteric	3	6.3	6.4	100.0
		Total	47	97.9	100.0	
	Missing	.00	1	2.1		
	Total		48	100.0		
Cercopithecidae	Valid	Fronto-Temporal	7	87.5	100.0	100.0
	Missing	.00	1	12.5		
	Total		8	100.0		
Cebidae	Valid	Spheno-Parietal	8	100.0	100.0	100.0
Cervidae	Valid	Spheno-Parietal	16	88.9	88.9	88.9
		Fronto-Temporal	2	11.1	11.1	100.0
		Total	18	100.0	100.0	
Bovidae	Valid	Spheno-Parietal	1	33.3	100.0	100.0
	Missing	.00	2	66.7		
	Total		3	100.0		
Leporidae	Valid	Fronto-Temporal	21	100.0	100.0	100.0

Right Pterion

Family			Frequency	Percent	Valid Percent	Cumulative Percent
Canidae	Valid	Spheno-Parietal	82	91.1	95.3	95.3
		Fronto-Temporal	1	1.1	1.2	96.5
		Spheno-Parietal Epipteric	3	3.3	3.5	100.0
		Total	86	95.6	100.0	
	Missing	.00	4	4.4		
	Total		90	100.0		
Felidae	Valid	Spheno-Parietal	43	89.6	95.6	95.6
		Fronto-Temporal	1	2.1	2.2	97.8
		Spheno-Parietal Epipteric	1	2.1	2.2	100.0
		Total	45	93.8	100.0	
	Missing	.00	3	6.3		
	Total		48	100.0		
Cercopithecidae	Valid	Fronto-Temporal	7	87.5	100.0	100.0
	Missing	.00	1	12.5		
	Total		8	100.0		
Cebidae	Valid	Spheno-Parietal	7	87.5	100.0	100.0
	Missing	.00	1	12.5		
	Total		8	100.0		
Cervidae	Valid	Spheno-Parietal	15	83.3	100.0	100.0
	Missing	.00	3	16.7		
	Total		18	100.0		
Bovidae	Valid	Spheno-Parietal	2	66.7	100.0	100.0
	Missing	.00	1	33.3		
	Total		3	100.0		
Leporidae	Valid	Fronto-Temporal	21	100.0	100.0	100.0

Test One: Pterion Frequency by Order

Statistics

Order			Left Pterion	Right Pterion
Carnivora	N	Valid	135	131
		Missing	3	7
Primates	N	Valid	15	14
		Missing	1	2
Artiodactyla	N	Valid	19	17
		Missing	2	4
Lagomorpha	N	Valid	21	21
		Missing	0	0

Left Pterion

Order			Frequency	Percent	Valid Percent	Cumulative Percent
Carnivora	Valid	Spheno-Parietal	128	92.8	94.8	94.8
		Fronto-Temporal	1	.7	.7	95.6
		Spheno-Parietal-Epipteric	6	4.3	4.4	100.0
		Total	135	97.8	100.0	
	Missing	.00	3	2.2		
	Total		138	100.0		
Primates	Valid	Spheno-Parietal	8	50.0	53.3	53.3
		Fronto-Temporal	7	43.8	46.7	100.0
		Total	15	93.8	100.0	
	Missing	.00	1	6.3		
	Total		16	100.0		
Artiodactyla	Valid	Spheno-Parietal	17	81.0	89.5	89.5
		Fronto-Temporal	2	9.5	10.5	100.0
		Total	19	90.5	100.0	
	Missing	.00	2	9.5		
	Total		21	100.0		
Lagomorpha	Valid	Fronto-Temporal	21	100.0	100.0	100.0

Right Pterion

Order			Frequency	Percent	Valid Percent	Cumulative Percent
Carnivora	Valid	Spheno-Parietal	125	90.6	95.4	95.4
		Fronto-Temporal	2	1.4	1.5	96.9
		Spheno-Parietal Epipteric	4	2.9	3.1	100.0
		Total	131	94.9	100.0	
	Missing	.00	7	5.1		
	Total		138	100.0		
Primates	Valid	Spheno-Parietal	7	43.8	50.0	50.0
		Fronto-Temporal	7	43.8	50.0	100.0
		Total	14	87.5	100.0	
	Missing	.00	2	12.5		
	Total		16	100.0		
Artiodactyla	Valid	Spheno-Parietal	17	81.0	100.0	100.0
	Missing	.00	4	19.0		
	Total		21	100.0		
Lagomorpha	Valid	Fronto-Temporal	21	100.0	100.0	100.0

Test Two: Chi-Squares Species Level

Case Processing Summary

	Cases					
	Valid		Missing		Total	
	N	Percent	N	Percent	N	Percent
Species * Left Pterion	190	96.9%	6	3.1%	196	100.0%

Chi-Square Tests

	Value	df	Asymptotic Significance (2-sided)
Pearson Chi-Square	178.426^a	20	.000
Likelihood Ratio	156.845	20	.000
Linear-by-Linear Association	14.334	1	.000
N of Valid Cases	190		

a. 24 cells (72.7%) have expected count less than 5. The minimum expected count is .03.

Case Processing Summary

	Cases					
	Valid		Missing		Total	
	N	Percent	N	Percent	N	Percent
Species * Right Pterion	183	93.4%	13	6.6%	196	100.0%

Chi-Square Tests

	Value	df	Asymptotic Significance (2-sided)
Pearson Chi-Square	173.733^a	20	.000
Likelihood Ratio	150.982	20	.000
Linear-by-Linear Association	15.927	1	.000
N of Valid Cases	183		

a. 24 cells (72.7%) have expected count less than 5. The minimum expected count is .04.

Species * Left Pterion Crosstabulation

			Left Pterion			
			Spheno-Parietal	Fronto-Temporal	Spheno-Parietal-Epipteric	Total
Species	latrans	Count	29	0	1	30
		Expected Count	24.2	4.9	.9	30.0
		% of Total	15.3%	0.0%	0.5%	15.8%
	vulpes	Count	27	1	0	28
		Expected Count	22.5	4.6	.9	28.0
		% of Total	14.2%	0.5%	0.0%	14.7%
	americanus	Count	28	0	2	30
		Expected Count	24.2	4.9	.9	30.0
		% of Total	14.7%	0.0%	1.1%	15.8%
	concolor	Count	17	0	0	17
		Expected Count	13.7	2.8	.5	17.0
		% of Total	8.9%	0.0%	0.0%	8.9%
	rufus	Count	27	0	3	30
		Expected Count	24.2	4.9	.9	30.0
		% of Total	14.2%	0.0%	1.6%	15.8%
	hamadryas	Count	0	7	0	7
		Expected Count	5.6	1.1	.2	7.0
		% of Total	0.0%	3.7%	0.0%	3.7%
	sciureus	Count	8	0	0	8
		Expected Count	6.4	1.3	.3	8.0
		% of Total	4.2%	0.0%	0.0%	4.2%
	hemionus	Count	13	1	0	14
		Expected Count	11.3	2.3	.4	14.0
		% of Total	6.8%	0.5%	0.0%	7.4%
	elaphus	Count	3	1	0	4
		Expected Count	3.2	.7	.1	4.0
		% of Total	1.6%	0.5%	0.0%	2.1%
	americanus	Count	1	0	0	1
		Expected Count	.8	.2	.0	1.0
		% of Total	0.5%	0.0%	0.0%	0.5%
	americanus	Count	0	21	0	21
		Expected Count	16.9	3.4	.7	21.0
		% of Total	0.0%	11.1%	0.0%	11.1%
Total		Count	153	31	6	190
		Expected Count	153.0	31.0	6.0	190.0
		% of Total	80.5%	16.3%	3.2%	100.0%

Species * Right Pterion Crosstabulation

			Right Pterion			
			Spheno-Parietal	Fronto-Temporal	Spheno-Parietal Epipteric	Total
Species	latrans	Count	27	0	1	28
		Expected Count	22.8	4.6	.6	28.0
		% of Total	14.8%	0.0%	0.5%	15.3%
	vulpes	Count	28	1	0	29
		Expected Count	23.6	4.8	.6	29.0
		% of Total	15.3%	0.5%	0.0%	15.8%
	americanus	Count	27	0	2	29
		Expected Count	23.6	4.8	.6	29.0
		% of Total	14.8%	0.0%	1.1%	15.8%
	concolor	Count	15	0	0	15
		Expected Count	12.2	2.5	.3	15.0
		% of Total	8.2%	0.0%	0.0%	8.2%
	rufus	Count	28	1	1	30
		Expected Count	24.4	4.9	.7	30.0
		% of Total	15.3%	0.5%	0.5%	16.4%
	hamadryas	Count	0	7	0	7
		Expected Count	5.7	1.1	.2	7.0
		% of Total	0.0%	3.8%	0.0%	3.8%
	sciureus	Count	7	0	0	7
		Expected Count	5.7	1.1	.2	7.0
		% of Total	3.8%	0.0%	0.0%	3.8%
	hemionus	Count	11	0	0	11
		Expected Count	9.0	1.8	.2	11.0
		% of Total	6.0%	0.0%	0.0%	6.0%
	elaphus	Count	4	0	0	4
		Expected Count	3.3	.7	.1	4.0
		% of Total	2.2%	0.0%	0.0%	2.2%
	americanus	Count	2	0	0	2
		Expected Count	1.6	.3	.0	2.0
		% of Total	1.1%	0.0%	0.0%	1.1%
	americanus	Count	0	21	0	21
		Expected Count	17.1	3.4	.5	21.0
		% of Total	0.0%	11.5%	0.0%	11.5%
Total		Count	149	30	4	183
		Expected Count	149.0	30.0	4.0	183.0
		% of Total	81.4%	16.4%	2.2%	100.0%

Chi-Squares Family Level

Case Processing Summary

	Cases					
	Valid		Missing		Total	
	N	Percent	N	Percent	N	Percent
Family * Left Pterion	190	96.9%	6	3.1%	196	100.0%

Chi-Square Tests

	Value	df	Asymptotic Significance (2-sided)
Pearson Chi-Square	171.910[a]	12	.000
Likelihood Ratio	148.233	12	.000
Linear-by-Linear Association	12.819	1	.000
N of Valid Cases	190		

a. 13 cells (61.9%) have expected count less than 5. The minimum expected count is .03.

Family * Left Pterion Crosstabulation

			Left Pterion			Total
			Spheno-Parietal	Fronto-Temporal	Spheno-Parietal-Epipteric	
Family	Canidae	Count	84	1	3	88
		Expected Count	70.9	14.4	2.8	88.0
		% within Family	95.5%	1.1%	3.4%	100.0%
		% within Left Pterion	54.9%	3.2%	50.0%	46.3%
		% of Total	44.2%	0.5%	1.6%	46.3%
	Felidae	Count	44	0	3	47
		Expected Count	37.8	7.7	1.5	47.0
		% within Family	93.6%	0.0%	6.4%	100.0%
		% within Left Pterion	28.8%	0.0%	50.0%	24.7%
		% of Total	23.2%	0.0%	1.6%	24.7%
	Cercopithecidae	Count	0	7	0	7
		Expected Count	5.6	1.1	.2	7.0
		% within Family	0.0%	100.0%	0.0%	100.0%
		% within Left Pterion	0.0%	22.6%	0.0%	3.7%
		% of Total	0.0%	3.7%	0.0%	3.7%
	Cebidae	Count	8	0	0	8
		Expected Count	6.4	1.3	.3	8.0
		% within Family	100.0%	0.0%	0.0%	100.0%
		% within Left Pterion	5.2%	0.0%	0.0%	4.2%
		% of Total	4.2%	0.0%	0.0%	4.2%
	Cervidae	Count	16	2	0	18
		Expected Count	14.5	2.9	.6	18.0
		% within Family	88.9%	11.1%	0.0%	100.0%
		% within Left Pterion	10.5%	6.5%	0.0%	9.5%
		% of Total	8.4%	1.1%	0.0%	9.5%
	Bovidae	Count	1	0	0	1
		Expected Count	.8	.2	.0	1.0
		% within Family	100.0%	0.0%	0.0%	100.0%
		% within Left Pterion	0.7%	0.0%	0.0%	0.5%
		% of Total	0.5%	0.0%	0.0%	0.5%
	Leporidae	Count	0	21	0	21
		Expected Count	16.9	3.4	.7	21.0
		% within Family	0.0%	100.0%	0.0%	100.0%
		% within Left Pterion	0.0%	67.7%	0.0%	11.1%
		% of Total	0.0%	11.1%	0.0%	11.1%
Total		Count	153	31	6	190
		Expected Count	153.0	31.0	6.0	190.0
		% within Family	80.5%	16.3%	3.2%	100.0%
		% within Left Pterion	100.0%	100.0%	100.0%	100.0%
		% of Total	80.5%	16.3%	3.2%	100.0%

Case Processing Summary

	Cases					
	Valid		Missing		Total	
	N	Percent	N	Percent	N	Percent
Family * Right Pterion	183	93.4%	13	6.6%	196	100.0%

Chi-Square Tests

	Value	df	Asymptotic Significance (2-sided)
Pearson Chi-Square	169.779[a]	12	.000
Likelihood Ratio	144.343	12	.000
Linear-by-Linear Association	16.488	1	.000
N of Valid Cases	183		

a. 13 cells (61.9%) have expected count less than 5. The minimum expected count is .04.

Family * Right Pterion Crosstabulation

			Right Pterion			
			Spheno-Parietal	Fronto-Temporal	Spheno-Parietal Epipteric	Total
Family	Canidae	Count	82	1	3	86
		Expected Count	70.0	14.1	1.9	86.0
		% within Family	95.3%	1.2%	3.5%	100.0%
		% within Right Pterion	55.0%	3.3%	75.0%	47.0%
		% of Total	44.8%	0.5%	1.6%	47.0%
	Felidae	Count	43	1	1	45
		Expected Count	36.6	7.4	1.0	45.0
		% within Family	95.6%	2.2%	2.2%	100.0%
		% within Right Pterion	28.9%	3.3%	25.0%	24.6%
		% of Total	23.5%	0.5%	0.5%	24.6%
	Cercopithecidae	Count	0	7	0	7
		Expected Count	5.7	1.1	.2	7.0
		% within Family	0.0%	100.0%	0.0%	100.0%
		% within Right Pterion	0.0%	23.3%	0.0%	3.8%
		% of Total	0.0%	3.8%	0.0%	3.8%
	Cebidae	Count	7	0	0	7
		Expected Count	5.7	1.1	.2	7.0
		% within Family	100.0%	0.0%	0.0%	100.0%
		% within Right Pterion	4.7%	0.0%	0.0%	3.8%
		% of Total	3.8%	0.0%	0.0%	3.8%
	Cervidae	Count	15	0	0	15
		Expected Count	12.2	2.5	.3	15.0
		% within Family	100.0%	0.0%	0.0%	100.0%
		% within Right Pterion	10.1%	0.0%	0.0%	8.2%
		% of Total	8.2%	0.0%	0.0%	8.2%
	Bovidae	Count	2	0	0	2
		Expected Count	1.6	.3	.0	2.0
		% within Family	100.0%	0.0%	0.0%	100.0%
		% within Right Pterion	1.3%	0.0%	0.0%	1.1%
		% of Total	1.1%	0.0%	0.0%	1.1%
	Leporidae	Count	0	21	0	21
		Expected Count	17.1	3.4	.5	21.0
		% within Family	0.0%	100.0%	0.0%	100.0%
		% within Right Pterion	0.0%	70.0%	0.0%	11.5%
		% of Total	0.0%	11.5%	0.0%	11.5%
Total		Count	149	30	4	183
		Expected Count	149.0	30.0	4.0	183.0
		% within Family	81.4%	16.4%	2.2%	100.0%
		% within Right Pterion	100.0%	100.0%	100.0%	100.0%
		% of Total	81.4%	16.4%	2.2%	100.0%

Chi-Squares Order

Case Processing Summary

	Cases					
	Valid		Missing		Total	
	N	Percent	N	Percent	N	Percent
Order * Left Pterion	190	96.9%	6	3.1%	196	100.0%

Chi-Square Tests

	Value	df	Asymptotic Significance (2-sided)
Pearson Chi-Square	143.411[a]	6	.000
Likelihood Ratio	125.829	6	.000
Linear-by-Linear Association	13.290	1	.000
N of Valid Cases	190		

a. 7 cells (58.3%) have expected count less than 5. The minimum expected count is .47.

Order * Left Pterion Crosstabulation

			Left Pterion			Total
			Spheno-Parietal	Fronto-Temporal	Spheno-Parietal-Epipteric	
Order	Carnivora	Count	128	1	6	135
		Expected Count	108.7	22.0	4.3	135.0
		% within Order	94.8%	0.7%	4.4%	100.0%
		% within Left Pterion	83.7%	3.2%	100.0%	71.1%
		% of Total	67.4%	0.5%	3.2%	71.1%
	Primates	Count	8	7	0	15
		Expected Count	12.1	2.4	.5	15.0
		% within Order	53.3%	46.7%	0.0%	100.0%
		% within Left Pterion	5.2%	22.6%	0.0%	7.9%
		% of Total	4.2%	3.7%	0.0%	7.9%
	Artiodactyla	Count	17	2	0	19
		Expected Count	15.3	3.1	.6	19.0
		% within Order	89.5%	10.5%	0.0%	100.0%
		% within Left Pterion	11.1%	6.5%	0.0%	10.0%
		% of Total	8.9%	1.1%	0.0%	10.0%
	Lagomorpha	Count	0	21	0	21
		Expected Count	16.9	3.4	.7	21.0
		% within Order	0.0%	100.0%	0.0%	100.0%
		% within Left Pterion	0.0%	67.7%	0.0%	11.1%
		% of Total	0.0%	11.1%	0.0%	11.1%
Total		Count	153	31	6	190
		Expected Count	153.0	31.0	6.0	190.0
		% within Order	80.5%	16.3%	3.2%	100.0%
		% within Left Pterion	100.0%	100.0%	100.0%	100.0%
		% of Total	80.5%	16.3%	3.2%	100.0%

Case Processing Summary

	Cases					
	Valid		Missing		Total	
	N	Percent	N	Percent	N	Percent
Order * Right Pterion	183	93.4%	13	6.6%	196	100.0%

Chi-Square Tests

	Value	df	Asymptotic Significance (2-sided)
Pearson Chi-Square	143.894[a]	6	.000
Likelihood Ratio	124.565	6	.000
Linear-by-Linear Association	19.211	1	.000
N of Valid Cases	183		

a. 7 cells (58.3%) have expected count less than 5. The minimum expected count is .31.

Order * Right Pterion Crosstabulation

			Right Pterion			
			Spheno-Parietal	Fronto-Temporal	Spheno-Parietal Epipteric	Total
Order	Carnivora	Count	125	2	4	131
		Expected Count	106.7	21.5	2.9	131.0
		% within Order	95.4%	1.5%	3.1%	100.0%
		% within Right Pterion	83.9%	6.7%	100.0%	71.6%
		% of Total	68.3%	1.1%	2.2%	71.6%
	Primates	Count	7	7	0	14
		Expected Count	11.4	2.3	.3	14.0
		% within Order	50.0%	50.0%	0.0%	100.0%
		% within Right Pterion	4.7%	23.3%	0.0%	7.7%
		% of Total	3.8%	3.8%	0.0%	7.7%
	Artiodactyla	Count	17	0	0	17
		Expected Count	13.8	2.8	.4	17.0
		% within Order	100.0%	0.0%	0.0%	100.0%
		% within Right Pterion	11.4%	0.0%	0.0%	9.3%
		% of Total	9.3%	0.0%	0.0%	9.3%
	Lagomorpha	Count	0	21	0	21
		Expected Count	17.1	3.4	.5	21.0
		% within Order	0.0%	100.0%	0.0%	100.0%
		% within Right Pterion	0.0%	70.0%	0.0%	11.5%
		% of Total	0.0%	11.5%	0.0%	11.5%
Total		Count	149	30	4	183
		Expected Count	149.0	30.0	4.0	183.0
		% within Order	81.4%	16.4%	2.2%	100.0%
		% within Right Pterion	100.0%	100.0%	100.0%	100.0%
		% of Total	81.4%	16.4%	2.2%	100.0%

Chi-Squares Suture Complexity

Case Processing Summary

	Cases					
	Valid		Missing		Total	
	N	Percent	N	Percent	N	Percent
Species * Left Pterion	190	96.9%	6	3.1%	196	100.0%

Chi-Square Tests

	Value	df	Asymptotic Significance (2-sided)
Pearson Chi-Square	178.426[a]	20	.000
Likelihood Ratio	156.845	20	.000
Linear-by-Linear Association	14.334	1	.000
N of Valid Cases	190		

a. 24 cells (72.7%) have expected count less than 5. The minimum expected count is .03.

Species * Left Pterion Crosstabulation

			Left Pterion			
			Spheno-Parietal	Fronto-Temporal	Spheno-Parietal-Epipteric	Total
Species	latrans	Count	29	0	1	30
		Expected Count	24.2	4.9	.9	30.0
		% of Total	15.3%	0.0%	0.5%	15.8%
	vulpes	Count	27	1	0	28
		Expected Count	22.5	4.6	.9	28.0
		% of Total	14.2%	0.5%	0.0%	14.7%
	americanus	Count	28	0	2	30
		Expected Count	24.2	4.9	.9	30.0
		% of Total	14.7%	0.0%	1.1%	15.8%
	concolor	Count	17	0	0	17
		Expected Count	13.7	2.8	.5	17.0
		% of Total	8.9%	0.0%	0.0%	8.9%
	rufus	Count	27	0	3	30
		Expected Count	24.2	4.9	.9	30.0
		% of Total	14.2%	0.0%	1.6%	15.8%
	hamadryas	Count	0	7	0	7
		Expected Count	5.6	1.1	.2	7.0
		% of Total	0.0%	3.7%	0.0%	3.7%
	sciureus	Count	8	0	0	8
		Expected Count	6.4	1.3	.3	8.0
		% of Total	4.2%	0.0%	0.0%	4.2%
	hemionus	Count	13	1	0	14
		Expected Count	11.3	2.3	.4	14.0
		% of Total	6.8%	0.5%	0.0%	7.4%
	elaphus	Count	3	1	0	4
		Expected Count	3.2	.7	.1	4.0
		% of Total	1.6%	0.5%	0.0%	2.1%
	americanus	Count	1	0	0	1
		Expected Count	.8	.2	.0	1.0
		% of Total	0.5%	0.0%	0.0%	0.5%
	americanus	Count	0	21	0	21
		Expected Count	16.9	3.4	.7	21.0
		% of Total	0.0%	11.1%	0.0%	11.1%
Total		Count	153	31	6	190
		Expected Count	153.0	31.0	6.0	190.0
		% of Total	80.5%	16.3%	3.2%	100.0%

Case Processing Summary

	Cases					
	Valid		Missing		Total	
	N	Percent	N	Percent	N	Percent
Species * Right Pterion	183	93.4%	13	6.6%	196	100.0%

Chi-Square Tests

	Value	df	Asymptotic Significance (2-sided)
Pearson Chi-Square	173.733[a]	20	.000
Likelihood Ratio	150.982	20	.000
Linear-by-Linear Association	15.927	1	.000
N of Valid Cases	183		

a. 24 cells (72.7%) have expected count less than 5. The minimum expected count is .04.

Species * Right Pterion Crosstabulation

			Right Pterion			
			Spheno-Parietal	Fronto-Temporal	Spheno-Parietal Epipteric	Total
Species	latrans	Count	27	0	1	28
		Expected Count	22.8	4.6	.6	28.0
		% of Total	14.8%	0.0%	0.5%	15.3%
	vulpes	Count	28	1	0	29
		Expected Count	23.6	4.8	.6	29.0
		% of Total	15.3%	0.5%	0.0%	15.8%
	americanus	Count	27	0	2	29
		Expected Count	23.6	4.8	.6	29.0
		% of Total	14.8%	0.0%	1.1%	15.8%
	concolor	Count	15	0	0	15
		Expected Count	12.2	2.5	.3	15.0
		% of Total	8.2%	0.0%	0.0%	8.2%
	rufus	Count	28	1	1	30
		Expected Count	24.4	4.9	.7	30.0
		% of Total	15.3%	0.5%	0.5%	16.4%
	hamadryas	Count	0	7	0	7
		Expected Count	5.7	1.1	.2	7.0
		% of Total	0.0%	3.8%	0.0%	3.8%
	sciureus	Count	7	0	0	7
		Expected Count	5.7	1.1	.2	7.0
		% of Total	3.8%	0.0%	0.0%	3.8%
	hemionus	Count	11	0	0	11
		Expected Count	9.0	1.8	.2	11.0
		% of Total	6.0%	0.0%	0.0%	6.0%
	elaphus	Count	4	0	0	4
		Expected Count	3.3	.7	.1	4.0
		% of Total	2.2%	0.0%	0.0%	2.2%
	americanus	Count	2	0	0	2
		Expected Count	1.6	.3	.0	2.0
		% of Total	1.1%	0.0%	0.0%	1.1%
	americanus	Count	0	21	0	21
		Expected Count	17.1	3.4	.5	21.0
		% of Total	0.0%	11.5%	0.0%	11.5%
Total		Count	149	30	4	183
		Expected Count	149.0	30.0	4.0	183.0
		% of Total	81.4%	16.4%	2.2%	100.0%

Species Level Stepwise Regression

Coefficientsa,b

Species	Model		Unstandardized Coefficients		Standardized Coefficients	t	Sig.
			B	Std. Error	Beta		
latrans	1	(Constant)	11.114	3.598		3.089	.005
		lnSpcsRPtoAJ	-1.785	.729	-.463	-2.449	.023
	2	(Constant)	-.250	3.425		-.073	.942
		lnSpcsRPtoAJ	-3.048	.572	-.790	-5.332	.000
		lnSpcsLPtoPP	4.263	.871	.725	4.893	.000
	3	(Constant)	-3.584	3.436		-1.043	.309
		lnSpcsRPtoAJ	-10.426	3.237	-2.703	-3.221	.004
		lnSpcsLPtoPP	4.954	.848	.843	5.844	.000
		lnSpcsLPtoAJ	7.464	3.232	1.883	2.310	.032
americanus	1	(Constant)	-13.399	3.583		-3.740	.001
		lnSpcsLPtoPP	3.499	.785	.681	4.459	.000
	2	(Constant)	-11.350	3.289		-3.451	.002
		lnSpcsLPtoPP	4.175	.745	.813	5.601	.000
		lnSpcsPOC	-1.191	.453	-.382	-2.631	.015
rufus	1	(Constant)	-39.463	8.958		-4.405	.000
		lnSpcsRPtoPP	10.219	2.270	.655	4.502	.000
	2	(Constant)	-44.508	8.397		-5.301	.000
		lnSpcsRPtoPP	14.089	2.563	.903	5.497	.000
		lnSpcsMO	-3.091	1.209	-.420	-2.555	.017
	3	(Constant)	-52.970	8.742		-6.059	.000
		lnSpcsPOC	2.309	1.054	.272	2.191	.038
		lnSpcsRPtoPP	13.996	2.395	.897	5.845	.000
		lnSpcsMO	-2.938	1.132	-.399	-2.595	.016

a. Dependent Variable: lnCombinedSutLength

Excluded Variables[a,j]

							Collinearity Statistics
Species	Model		Beta In	t	Sig.	Partial Correlation	Tolerance
latrans	1	lnSpcsTL	.631[b]	1.787	.088	.363	.261
		lnSpcsTH	.233[b]	1.169	.256	.247	.885
		lnSpcsPOC	-.239[b]	-1.209	.240	-.255	.897
		lnSpcsMA	.490[b]	2.383	.027	.461	.695
		lnSpcsMO	.452[b]	1.380	.182	.288	.319
		lnSpcsLPtoPP	.725[b]	4.893	.000	.730	.796
		lnSpcsRPtoPP	.604[b]	3.728	.001	.631	.859
		lnSpcsLPtoAJ	.202[b]	.165	.871	.036	.025
	2	lnSpcsTL	-.226[c]	-.684	.502	-.151	.164
		lnSpcsTH	.014[c]	.095	.925	.021	.795
		lnSpcsPOC	.094[c]	.592	.561	.131	.708
		lnSpcsMA	.160[c]	.885	.387	.194	.541
		lnSpcsMO	.123[c]	.493	.627	.110	.291
		lnSpcsRPtoPP	.180[c]	.822	.421	.181	.372
		lnSpcsLPtoAJ	1.883[c]	2.310	.032	.459	.022
	3	lnSpcsTL	-.496[d]	-1.645	.116	-.353	.147
		lnSpcsTH	.054[d]	.390	.701	.089	.782
		lnSpcsPOC	.140[d]	.971	.344	.217	.696
		lnSpcsMA	-.016[d]	-.085	.933	-.020	.428
		lnSpcsMO	.014[d]	.059	.954	.014	.278
		lnSpcsRPtoPP	-.069[d]	-.295	.771	-.068	.276
americanus	1	lnSpcsTL	-.418[e]	-2.324	.030	-.444	.605
		lnSpcsTH	.164[e]	1.070	.296	.222	.981
		lnSpcsPOC	-.382[e]	-2.631	.015	-.489	.881
		lnSpcsMA	-.035[e]	-.207	.838	-.044	.841
		lnSpcsMO	-.112[e]	-.642	.528	-.136	.782
		lnSpcsRPtoPP	-.245[e]	-.639	.529	-.135	.163
		lnSpcsLPtoAJ	-.368[e]	-2.341	.029	-.447	.788
		lnSpcsRPtoAJ	-.420[e]	-2.621	.016	-.488	.725
	2	lnSpcsTL	-.227[f]	-1.059	.301	-.225	.401
		lnSpcsTH	.095[f]	.668	.512	.144	.940
		lnSpcsMA	-.027[f]	-.175	.862	-.038	.841
		lnSpcsMO	.166[f]	.892	.383	.191	.537
		lnSpcsRPtoPP	-.077[f]	-.220	.828	-.048	.157
		lnSpcsLPtoAJ	-.260[f]	-1.651	.114	-.339	.694
		lnSpcsRPtoAJ	-.300[f]	-1.807	.085	-.367	.611
rufus	1	lnSpcsTL	-.134[g]	-.728	.473	-.141	.640
		lnSpcsTH	.022[g]	.147	.885	.029	1.000
		lnSpcsPOC	.292[g]	2.132	.043	.386	.999
		lnSpcsMA	-.075[g]	-.406	.688	-.079	.638
		lnSpcsMO	-.420[g]	-2.555	.017	-.448	.651
		lnSpcsLPtoPP	-.378[g]	-1.662	.108	-.310	.384
		lnSpcsLPtoAJ	-.287[g]	-1.583	.125	-.297	.608
		lnSpcsRPtoAJ	-.320[g]	-1.796	.084	-.332	.617
	2	lnSpcsTL	.190[h]	.913	.370	.180	.408
		lnSpcsTH	-.042[h]	-.304	.763	-.061	.966
		lnSpcsPOC	.272[h]	2.191	.038	.401	.996
		lnSpcsMA	.048[h]	.273	.787	.055	.587
		lnSpcsLPtoPP	-.186[h]	-.789	.438	-.156	.320
		lnSpcsLPtoAJ	-.025[h]	-.114	.910	-.023	.369
		lnSpcsRPtoAJ	-.110[h]	-.530	.601	-.105	.418
	3	lnSpcsTL	.099[i]	.489	.629	.099	.387

	lnSpcsTH	-.164[i]	-1.225	.233	-.243	.838
	lnSpcsMA	.076[i]	.465	.646	.094	.584
	lnSpcsLPtoPP	-.261[i]	-1.189	.246	-.236	.313
	lnSpcsLPtoAJ	-.078[i]	-.374	.711	-.076	.364
	lnSpcsRPtoAJ	-.172[i]	-.885	.385	-.178	.410

a. Dependent Variable: lnCombinedSutLength
b. Predictors in the Model: (Constant), lnSpcsRPtoAJ
c. Predictors in the Model: (Constant), lnSpcsRPtoAJ, lnSpcsLPtoPP
d. Predictors in the Model: (Constant), lnSpcsRPtoAJ, lnSpcsLPtoPP, lnSpcsLPtoAJ
e. Predictors in the Model: (Constant), lnSpcsLPtoPP
f. Predictors in the Model: (Constant), lnSpcsLPtoPP, lnSpcsPOC
g. Predictors in the Model: (Constant), lnSpcsRPtoPP
h. Predictors in the Model: (Constant), lnSpcsRPtoPP, lnSpcsMO
i. Predictors in the Model: (Constant), lnSpcsRPtoPP, lnSpcsMO, lnSpcsPOC
j. There are no valid cases in one or more split files. Statistics cannot be computed.

Residuals Statistics[a,b]

Species		Minimum	Maximum	Mean	Std. Deviation	N
latrans	Predicted Value	2.0434	2.6733	2.3053	.17564	27
	Residual	-.24829	.27421	.01832	.12665	27
	Std. Predicted Value	-1.398	1.987	.009	.944	27
	Std. Residual	-1.948	2.151	.144	.993	27
americanus	Predicted Value	2.0985	2.9026	2.5906	.20684	29
	Residual	-.51433	.28552	-.04238	.20251	29
	Std. Predicted Value	-2.225	1.519	.066	.963	29
	Std. Residual	-2.762	1.533	-.228	1.087	29
rufus	Predicted Value	-.4799	1.9258	.8656	.60381	29
	Residual	-1.20070	.66877	.00000	.47571	29
	Std. Predicted Value	-2.228	1.756	.000	1.000	29
	Std. Residual	-2.385	1.328	.000	.945	29

a. Dependent Variable: lnCombinedSutLength
b. There are no valid cases in one or more split files. Statistics cannot be computed.

Family Level Stepwise Regression:

Coefficientsa,b

			Unstandardized Coefficients		Standardized Coefficients		
Family	Model		B	Std. Error	Beta	t	Sig.
Canidae	1	(Constant)	-.581	.500		-1.162	.250
		lnSpcsLPtoPP	.696	.116	.631	5.984	.000
	2	(Constant)	-1.327	.435		-3.049	.004
		lnSpcsLPtoPP	3.641	.575	3.305	6.334	.000
		lnSpcsTL	-2.559	.492	-2.711	-5.196	.000
	3	(Constant)	-3.484	.836		-4.167	.000
		lnSpcsLPtoPP	4.312	.583	3.914	7.394	.000
		lnSpcsTL	-2.092	.486	-2.217	-4.301	.000
		lnSpcsPOC	-.750	.254	-1.125	-2.953	.005
Felidae	1	(Constant)	-8.481	3.236		-2.621	.013
		lnSpcsRPtoPP	2.353	.806	.443	2.920	.006
	2	(Constant)	-20.939	4.678		-4.476	.000
		lnSpcsRPtoPP	10.940	2.655	2.058	4.120	.000
		lnSpcsRPtoAJ	-5.260	1.568	-1.676	-3.356	.002
	3	(Constant)	-28.622	5.789		-4.944	.000
		lnSpcsPOC	2.229	1.070	.277	2.084	.045
		lnSpcsRPtoPP	11.330	2.541	2.131	4.460	.000
		lnSpcsRPtoAJ	-5.724	1.512	-1.824	-3.785	.001

a. Dependent Variable: lnCombinedSutLength

b. There are no valid cases in one or more split files. Statistics cannot be computed.

Excluded Variables[a,h]

Family	Model		Beta In	t	Sig.	Partial Correlation	Collinearity Statistics Tolerance
Canidae	1	lnSpcsTL	-2.711[b]	-5.196	.000	-.581	.028
		lnSpcsTH	.045[b]	.413	.682	.057	.972
		lnSpcsPOC	-1.657[b]	-3.988	.000	-.480	.051
		lnSpcsMA	-.102[b]	-.495	.623	-.068	.266
		lnSpcsMO	-.434[b]	-1.525	.133	-.205	.134
		lnSpcsRPtoPP	-1.656[b]	-1.293	.202	-.175	.007
		lnSpcsLPtoAJ	-.842[b]	-3.249	.002	-.407	.141
		lnSpcsRPtoAJ	-.827[b]	-3.215	.002	-.404	.144
	2	lnSpcsTH	.040[c]	.453	.652	.063	.972
		lnSpcsPOC	-1.125[c]	-2.953	.005	-.379	.045
		lnSpcsMA	.189[c]	1.071	.289	.147	.240
		lnSpcsMO	.600[c]	2.001	.051	.267	.079
		lnSpcsRPtoPP	.473[c]	.411	.683	.057	.006
		lnSpcsLPtoAJ	.141[c]	.398	.692	.055	.061
		lnSpcsRPtoAJ	.025[c]	.077	.939	.011	.072
	3	lnSpcsTH	.021[d]	.250	.804	.035	.966
		lnSpcsMA	-.039[d]	-.210	.834	-.029	.191
		lnSpcsMO	.457[d]	1.581	.120	.216	.076
		lnSpcsRPtoPP	1.314[d]	1.200	.236	.166	.005
		lnSpcsLPtoAJ	-.278[d]	-.779	.439	-.109	.052
		lnSpcsRPtoAJ	-.392[d]	-1.195	.237	-.165	.061
Felidae	1	lnSpcsTL	-1.075[e]	-2.146	.039	-.345	.083
		lnSpcsTH	-.287[e]	-1.163	.253	-.196	.375
		lnSpcsPOC	.203[e]	1.308	.200	.219	.937
		lnSpcsMA	-.337[e]	-.760	.453	-.129	.118

		lnSpcsMO	-1.109[e]	-2.778	.009	-.430	.121
		lnSpcsLPtoAJ	-1.479[e]	-2.882	.007	-.443	.072
		lnSpcsRPtoAJ	-1.676[e]	-3.356	.002	-.499	.071
		lnSpcsLPtoPP	-1.770[e]	-2.839	.008	-.438	.049
	2	lnSpcsTL	.232[f]	.324	.748	.056	.036
		lnSpcsTH	-.139[f]	-.620	.539	-.107	.358
		lnSpcsPOC	.277[f]	2.084	.045	.341	.917
		lnSpcsMA	.355[f]	.803	.428	.138	.092
		lnSpcsMO	-.593[f]	-1.325	.194	-.225	.087
		lnSpcsLPtoAJ	2.481[f]	1.190	.243	.203	.004
		lnSpcsLPtoPP	-.856[f]	-1.130	.267	-.193	.031
	3	lnSpcsTL	.148[g]	.216	.831	.038	.035
		lnSpcsTH	-.353[g]	-1.575	.125	-.268	.309
		lnSpcsMA	.585[g]	1.377	.178	.236	.087
		lnSpcsMO	-.513[g]	-1.191	.242	-.206	.086
		lnSpcsLPtoAJ	3.026[g]	1.531	.136	.261	.004
		lnSpcsLPtoPP	-.853[g]	-1.183	.245	-.205	.031

a. Dependent Variable: lnCombinedSutLength

b. Predictors in the Model: (Constant), lnSpcsLPtoPP

c. Predictors in the Model: (Constant), lnSpcsLPtoPP, lnSpcsTL

d. Predictors in the Model: (Constant), lnSpcsLPtoPP, lnSpcsTL, lnSpcsPOC

e. Predictors in the Model: (Constant), lnSpcsRPtoPP

f. Predictors in the Model: (Constant), lnSpcsRPtoPP, lnSpcsRPtoAJ

g. Predictors in the Model: (Constant), lnSpcsRPtoPP, lnSpcsRPtoAJ, lnSpcsPOC

Residuals Statisticsa,b

Family		Minimum	Maximum	Mean	Std. Deviation	N
Canidae	Predicted Value	1.9208	2.8804	2.4032	.23416	64
	Residual	-.38038	.34692	-.00157	.17176	64
	Std. Predicted Value	-2.063	2.022	-.009	.997	64
	Std. Residual	-2.188	1.996	-.009	.988	64
Felidae	Predicted Value	-.3173	1.9942	1.0095	.50254	41
	Residual	-1.49739	.82330	-.03014	.51767	41
	Std. Predicted Value	-2.583	2.085	.096	1.015	41
	Std. Residual	-2.706	1.488	-.054	.935	41

a. Dependent Variable: lnCombinedSutLength

b. There are no valid cases in one or more split files. Statistics cannot be computed.

Order Level Stepwise Regression:

Coefficients[a,b]

Order	Model		Unstandardized Coefficients		Standardized Coefficients	t	Sig.
			B	Std. Error	Beta		
Carnivora	1	(Constant)	-5.539	.532		-10.405	.000
		lnSpcsLPtoAJ	1.579	.114	.825	13.910	.000
	2	(Constant)	-4.348	.728		-5.974	.000
		lnSpcsLPtoAJ	1.823	.152	.952	11.978	.000
		lnSpcsMO	-.662	.283	-.186	-2.337	.022
	3	(Constant)	-5.398	.803		-6.719	.000
		lnSpcsLPtoAJ	1.584	.172	.827	9.235	.000
		lnSpcsMO	-1.656	.458	-.465	-3.615	.000
		lnSpcsRPtoPP	1.353	.500	.405	2.706	.008
	4	(Constant)	-8.284	1.185		-6.993	.000
		lnSpcsLPtoAJ	2.356	.292	1.230	8.070	.000
		lnSpcsMO	-.603	.547	-.169	-1.102	.273
		lnSpcsRPtoPP	4.643	1.136	1.389	4.088	.000
		lnSpcsTL	-4.059	1.272	-1.598	-3.190	.002
	5	(Constant)	-8.872	1.059		-8.377	.000
		lnSpcsLPtoAJ	2.526	.248	1.319	10.171	.000
		lnSpcsRPtoPP	4.994	1.092	1.494	4.574	.000
		lnSpcsTL	-4.906	1.016	-1.931	-4.829	.000

a. Dependent Variable: lnCombinedSutLength

b. There are no valid cases in one or more split files. Statistics cannot be computed.

Excluded Variables[a,g]

Order	Model		Beta In	t	Sig.	Partial Correlation	Collinearity Statistics Tolerance
Carnivora	1	lnSpcsTL	-.165[b]	-1.434	.155	-.149	.261
		lnSpcsTH	.021[b]	.312	.756	.033	.799
		lnSpcsPOC	-.036[b]	-.516	.607	-.054	.712
		lnSpcsMA	-.021[b]	-.092	.927	-.010	.068
		lnSpcsMO	-.186[b]	-2.337	.022	-.239	.531
		lnSpcsLPtoPP	-.067[b]	-.708	.481	-.074	.390
		lnSpcsRPtoPP	-.029[b]	-.301	.764	-.032	.392
		lnSpcsRPtoAJ	-3.610[b]	-1.977	.051	-.204	.001
	2	lnSpcsTL	.261[c]	1.147	.254	.121	.064
		lnSpcsTH	.028[c]	.436	.664	.046	.797
		lnSpcsPOC	.119[c]	1.322	.190	.139	.408
		lnSpcsMA	.425[c]	1.575	.119	.165	.045
		lnSpcsLPtoPP	.314[c]	2.020	.046	.209	.134
		lnSpcsRPtoPP	.405[c]	2.706	.008	.276	.140
		lnSpcsRPtoAJ	-2.488[c]	-1.303	.196	-.137	.001
	3	lnSpcsTL	-1.598[d]	-3.190	.002	-.322	.011
		lnSpcsTH	.020[d]	.310	.757	.033	.795
		lnSpcsPOC	-.292[d]	-1.786	.078	-.187	.114
		lnSpcsMA	.370[d]	1.409	.162	.149	.045
		lnSpcsLPtoPP	-1.265[d]	-2.196	.031	-.228	.009
		lnSpcsRPtoAJ	-3.102[d]	-1.680	.097	-.176	.001
	4	lnSpcsTH	.027[e]	.454	.651	.049	.793
		lnSpcsPOC	-.122[e]	-.715	.476	-.076	.099
		lnSpcsMA	.235[e]	.917	.362	.098	.043
		lnSpcsLPtoPP	-.896[e]	-1.568	.121	-.166	.009
		lnSpcsRPtoAJ	-3.003[e]	-1.709	.091	-.180	.001
	5	lnSpcsTH	.029[f]	.490	.625	.052	.794
		lnSpcsPOC	-.021[f]	-.139	.890	-.015	.124
		lnSpcsMA	.103[f]	.433	.666	.046	.051
		lnSpcsMO	-.169[f]	-1.102	.273	-.117	.121
		lnSpcsLPtoPP	-.905[f]	-1.583	.117	-.166	.009
		lnSpcsRPtoAJ	-3.143[f]	-1.796	.076	-.188	.001

a. Dependent Variable: lnCombinedSutLength
b. Predictors in the Model: (Constant), lnSpcsLPtoAJ
c. Predictors in the Model: (Constant), lnSpcsLPtoAJ, lnSpcsMO
d. Predictors in the Model: (Constant), lnSpcsLPtoAJ, lnSpcsMO, lnSpcsRPtoPP
e. Predictors in the Model: (Constant), lnSpcsLPtoAJ, lnSpcsMO, lnSpcsRPtoPP, lnSpcsTL
f. Predictors in the Model: (Constant), lnSpcsLPtoAJ, lnSpcsRPtoPP, lnSpcsTL
g. There are no valid cases in one or more split files. Statistics cannot be computed.

Residuals Statistics[a,b]

Order		Minimum	Maximum	Mean	Std. Deviation	N
Carnivora	Predicted Value	.4928	2.9360	1.8603	.73884	104
	Residual	-1.95809	.68194	-.00932	.42765	104
	Std. Predicted Value	-1.776	1.466	.039	.980	104
	Std. Residual	-4.389	1.528	-.021	.958	104

a. Dependent Variable: lnCombinedSutLength
b. There are no valid cases in one or more split files. Statistics cannot be computed.