

DIETARY CONSISTENCY AND SUTURAL MORPHOLOGY: THE COMPLEXITY
OF THE MID-PALATAL SUTURE IN *Procolobus badius* AND *Colobus polykomos*

By

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The mechanical environment is one of many influential factors affecting craniofacial growth and development. Although the mechanism is unclear, consensus exists that loads elicit a morphogenetic response from bone in general, including the maxillary bone in the craniofacial region. Mastication is one of the major sources of loading for the facial and cranial regions. The morphology of cranial and facial sutures is thought to be affected by the loading environment to which it is exposed. If this is true, then dietary consistency, which requires changes in the mechanics of mastication, should also affect the morphology of sutures.

The hypothesis under construction is that the higher the loads the suture is exposed to, the more complexity the suture should exhibit. In order to test this hypothesis, the mid-palatal suture of two sympatric species of colobus monkeys was examined. One species (*Colobus polykomos*) has a particularly hard seed present in its diet that *Procolobus badius* does not have. If the above hypothesis is true, then *Colobus*

polykomos would be expected to have a more complex mid-palatal suture due to its requirement of producing larger masticatory forces than *Procolobus badius*. Fractal analysis was used to measure the complexity of the sutures. Once the fractal dimensions were obtained, a 2-way ANOVA was performed, separating the species as well as the sexes. There were no significant differences in the complexities of the mid-palatal sutures of the two species. The data collected do not support the hypothesis that masticatory changes associated with diet directly influence sutural complexity.

CHAPTER 1 MECHANICS IN BONE GROWTH

Craniofacial growth and development is influenced by many different factors, including the mechanical environment (Herring 1993). The maxillary bone, in particular the palate, is more than likely exposed to different types of loads throughout the earliest stages of growth. For example, human infants suckle and as they grow older, are weaned and then engage in mastication. These different activities likely result in different types and magnitudes of stress, which elicit a morphogenetic response from the bone (Herring 1993, Martin et al. 1998). When mastication begins, the consistency of the diet has been shown experimentally to affect craniofacial growth and development (Beecher et al. 1983, Kiliaridis et al. 1985, Yamamoto 1996, Ciochon et al. 1997).

In addition to affecting overall bone growth and development, masticatory loads may also influence the morphology of cranial sutures. Several researchers have postulated that sutural morphology can reflect the load history of the structure in question (Herring 1972, Herring and Teng 2000, Wagemans et al. 1988). Provided this is the case, then the morphology of the sutures located in the palate should reflect its load history. If development is mechanically mediated, sutural morphology could provide insight into possible etiologies for abnormal craniofacial developments such as cleft lip and palate, a common birth defect requiring surgical intervention.

Wolff's Law

The idea that bone adapts to its mechanical environment is not new. Julius Wolff has been credited with formulating this idea in the late 1800s, but the idea has been traced

as far back as Galileo in the 1600s (Martin et al. 1998). Wolff's law states that the architecture of living bone continuously adapts to changes in the mechanical environment to which bone is subjected. Although Wolff's law is generally accepted as true, the biological aspects of the law that he formulated have proven to be false (Dibbets 1992). Three main biases exist in his arguments: his theory on interstitial bone growth, the role of heredity in bone growth, and his concept of function (Dibbets 1992).

Wolff was convinced that bone growth underwent the same mechanisms as soft tissue growth, which is to say that bone growth consisted solely of cell division and the accumulation of intracellular material. He adamantly denied the process of remodeling because he did not believe that bone actually resorbed. Dibbets (1992) points out that the reason Wolff held so firmly to this concept of interstitial bone growth was because, in his view, the trabecular architecture preexisted in the compacta (cortical bone) and was not the result of a dynamic process.

The idea that trabecular bone architecture was inherited was based on the fact that Wolff had observed the distinct trabecular patterns in fetuses, which could not have been exposed to loads yet (Dibbets 1992). However, the fetus is exposed to mechanical forces *in utero*. Forces are intermittently imposed on the fetus by skeletal tissue stresses that are caused by muscular contractions from the increasingly strong and active developing muscular system (Carter and Beaupre 2001).

Wolff's concept of function is the third bias because the definition he provided differs greatly from how function is usually defined today. If researchers were asked to define the term function today, they would probably define it as changing structure, i.e. a dynamic process requiring action (Wainwright 1988). Wolff defined function as a static

requirement that needed to be met (Dibbets 1992). Unfortunately, the term function is often not explicitly defined by researchers, which causes ambiguity as to exactly which definition of function is being applied.

If Wolff defined function completely differently than it is defined by most today, where did the modern day definition develop? The answer is from one of Wolff's contemporaries, Wilhelm Roux. Roux saw function as a dynamic interaction as opposed to a static constraint and recognized that information for the developing bone was partially provided by loading and unloading (Dibbets 1992). He referred to the physicochemical processes that aid development as "Entwicklungsmechanik" or "developmental mechanics" (Carter et al. 1998).

The forces that affect skeletogenesis can be studied at different scales of analysis, including the molecular, cellular, tissue, and organ levels (Carter and Beaupre 2001). In the time period in which Wolff and Roux worked, the analyses generally took place on the tissue level due to lack of technology. As technological advances are made, more studies are conducted at the molecular and cellular levels (Carter et al. 1998). Molecular level studies have begun to study the role of integrins, which are cell surface receptors involved in cell adhesion to other cells and the extracellular matrix, and the cytoskeleton, while cellular studies have shown that hydrostatic pressure and shear loading of cells have a direct influence on gene expression and cell biosynthesis (Carter et al. 1998). The tissue level, however, is still the scale at which most analyses occur, including the one conducted here. One reason for this is because the technology needed to conduct tissue level analyses is generally more accessible than the technology needed for cellular and molecular studies. Analyses can also be conducted at the organ level, but they provide

little insight into the underlying mechanisms of how bone responds to different mechanical conditions (Carter and Beaupre 2001). Only when the organs are broken down into smaller units, e.g., tissues, can we begin to evaluate and understand the physical conditions of connective tissue cells (Carter and Beaupre 2001).

Concepts of Stress and Strain

Two very important concepts that are useful when studying mechanical forces at the tissue level are stress and strain. When discussing stress and strain in biological materials, it is important to keep in mind that they are defined as if the tissue under study, in this case bone, was a homogenous material (Carter et al. 1998). In this “continuum model” representation, the fact that bone consists of molecules, discrete atoms, and crystals interacting with one another is ignored (Carter and Beaupre 2001). This means that the material properties represent average properties over some volume that is large in comparison to the microstructural features of the tissue (Carter and Beaupre 2001).

Stress is a measure of normalized intensity of a force and is the load per unit area, while strain is a measure of normalized load deformation. Strain, in simplest terms, is defined as the fractional change in dimension of a loaded body (Martin et al. 1998). Both stress and strain are tensor quantities, so they have a magnitude and direction. The stress state can also be represented with scalar quantities referred to as invariants. Scalar quantities have a magnitude, but no direction. The two most common stress invariants are referred to as hydrostatic stress and octahedral shear stress. Hydrostatic stress can either be positive (hydrostatic tension) or negative (hydrostatic compression or pressure) and is calculated as the average value of the three principal stresses. On the other hand, octahedral stress can only be a positive number and will only change the shape and not the volume of the material in question (Carter and Beaupre 2001). These two stress

invariants affect cartilage growth and ossification differently. Octahedral shear stress causes an acceleration of cartilage growth and ossification, while hydrostatic compressive stress slows it down (Carter and Beaupre 2001).

Primary and Secondary Cartilages

Primary and secondary cartilages are both important to skull growth. These two cartilages are distinguished based on the timing of their formation. Primary cartilage precedes the development of the replacement bones that form the primary skeleton. Secondary cartilage is different because it does not form on dermal bones until after intramembranous ossification has begun (Hall 1984). Unlike most of the bones in the human skeleton, dermal bones are not preformed in cartilage, but arise directly from connective tissue membranes. When studying the influence of mechanics on craniofacial growth, the secondary cartilage is important because it does not develop in the absence of mechanical stimulation (Herring 1993). Secondary cartilage only differentiates from progenitor cells in response to mechanical stimulation (Hall 1984). This cartilage is found in association with many cranial bones, sutures, and the upper and lower alveolar processes in mammals. These locations are sites of either articulations or muscle attachments, which provides support for the idea that mechanical stimulation is necessary for the differentiation of secondary cartilages (Herring 1993).

The mandibular condyle is the only major growth site of secondary cartilage anywhere in the mammalian skeleton (Herring 1993); therefore most of the studies on jaws have been on the condyle (Simon 1977, Copray 1985, Throckmorton and Dechow 1994). However, the condyle is not the only secondary cartilage that is sensitive to mechanical changes in the environment. Hinton (1988) studied the response of the cartilage that is present in the mid-palatal suture to changes in masticatory function. He

divided rats into separate groups based on dietary consistency and/or incisor amputation, then performed biochemical and histological analyses. Dietary consistency and/or incisor amputation did alter the morphology and the metabolism of the mid-palatal suture to varying degrees. The group of rats that were fed a soft diet and had their incisors amputated were affected the most, with their sutures becoming largely fibrous. The effect of dietary consistency on bone growth will be discussed in more detail later.

Bone Modeling and Remodeling

There is consensus that the mechanical environment affects bone growth, but how is another story. Several factors are involved when discussing the mechanical environment, such as the frequency of the loading and the types of loads applied. Bone growth and modeling are not the only processes that the loading conditions affect. Bone remodeling is also heavily influenced by mechanical conditions. Bone modeling and remodeling both refer to the actions of osteoblasts and osteoclasts in reshaping and replacing portions of the skeleton (Martin et al. 1998). However, these two processes are different from one another in several ways.

Martin et al. (1998) provide a list of differences that exist between the processes of modeling and remodeling. Although both modeling and remodeling involve osteoblasts and osteoclasts, in modeling these two cell types work independently while in remodeling their actions are coupled, i.e. sequential. Another difference between these two processes is that modeling affects the size and/or shape of the bone, while remodeling typically does not affect either size or shape. Modeling and remodeling are both most active before skeletal maturity is reached; however, the rate of modeling versus remodeling is much more reduced after skeletal maturity is reached. Unlike modeling, remodeling occurs throughout life. Finally when modeling occurs at a particular site the

process is continuous and prolonged while remodeling is episodic and has a definite beginning and ending.

Although both modeling and remodeling are affected by mechanical conditions, most of the experimental studies have only involved the process of remodeling (Lanyon et al. 1982, O'Connor et al. 1982, Carter 1984, Lanyon 1984, Lanyon and Rubin 1984, Meade et al. 1984, Burr et al. 1985, Rubin and Lanyon 1985). The reason for this is that mature experimental animals are used to try to eliminate as many unknown variables as possible. So many factors influence bone growth that controlling all these variables, some of which are still unknown, is difficult, if not impossible. For this reason, most of the experimental research focuses on the process of remodeling since modeling is practically nonexistent once the skeleton has reached full maturity.

Three important variables that are known to influence remodeling include strain magnitude, strain rate, and strain distribution (Lanyon 1984). Lanyon et al. (1982) conducted an experiment using mature sheep that involved excising a portion of a sheep's ulna and then exposing the sheep to peak principle walking strains. They found that the bone adapted to produce strains that were lower than before the osteotomy, which is not consistent with the view that bone reacts to control strain magnitude. Instead, they concluded that adaptive remodeling of periosteal bone is influenced by alterations in strain distribution rather than peak strains alone. Rubin and Lanyon (1985) conducted a similar study using turkeys and came to a comparable conclusion that bone remodeling is sensitive to both strain distribution as well as strain magnitude.

Strain rate is also an influential variable in bone remodeling. In order to evaluate how strain rate affects remodeling, O'Connor et al. (1982) chronically inserted implants

into the radius and ulna of mature sheep. These implants were subjected to both bending and compressive loads while varying the peak strains and strain rates. Their conclusion was that in order for remodeling to occur there needs to be sufficiently high strains and appropriate strain rates. This leads to the question of whether or not the frequency of the loads, i.e. static and dynamic loads, affect bone remodeling.

Lanyon and Rubin (1984) conducted experiments on avian ulna in order to address the question of whether or not both static and dynamic loads affect bone remodeling. Remodeling activity was assessed under three different conditions, disuse alone, disuse with a superimposed continuous compressive load, and disuse interrupted by a short daily period of intermittent loading. From this experiment, Lanyon and Rubin (1984) concluded that remodeling occurs under both dynamic and static loads when the bone is exposed to strains within the functional strain range, but the remodeling is more effective under dynamic loading conditions. Meade et al. (1984) conducted a similar experiment by exposing the femora of adult dogs to continuously applied loads and noted that there was an outward movement of the periosteal surface in response to the continuously applied loads, but little or no effect was seen on the endosteal surface of the bone.

In addition to the changes in strain distribution, strain magnitude, and strain rate, bone also initiates remodeling as a response to fatigue microdamage (Burr et al. 1985). Burr et al. (1985) tested the validity of the theory that osteonal remodeling is triggered by microdamage by conducting several different experiments on adult dogs. The data that was collected support the idea that fatigue microdamage is a significant factor in the initiation of remodeling.

No doubt exists that the mechanical environment is influential to bone remodeling. Factors other than mechanical environment, however, can also affect bone remodeling. For example, bioelectrical currents generated by blood flow and cell membranes may also affect bone remodeling, so the situation is not straightforward (Rubinacci and Tessari 1983).

According to Herring (1993), characterization of the real loading regime of skeletal elements is needed in order to determine the functional influences of bone growth. Although computer models and strain gage technology have been helpful in trying to determine stress distributions, both have limitations. The major limitation of the computer models is that all local effects must be ignored or modeled precisely, which is currently impractical. Strain gages help overcome this problem, but they are limited to a very restricted area of the structure being studied. Even though there are technological difficulties when trying to determine the loading regime of skeletal elements, successful experiments have been conducted that yielded useful information.

Lanyon (1973, 1974) performed experiments on the calcaneus of sheep using rosette strain gages and was able to demonstrate that the trabecular orientation corresponded with the principal compressive and tensile strain directions. This experiment was able to confirm what Wolff had postulated earlier about principal stress directions coinciding with trabecular orientation (Martin et al. 1998). Once this was confirmed, attention turned to the question of what type of load is responsible for apposition and resorption. Herring (1993) argues that resorption corresponds to the orientation of compressive strain, while periosteal bone growth corresponds generally with the orientation of tensile strain. Of course, as mentioned earlier, it is not only the

type of force applied, but also the frequency and magnitude that determines whether or not bone is deposited or resorbed.

The skull may experience loading from several sources including forces from the inertia and weight of the skull itself, joint reaction forces, forces from the muscles, and trauma (Russell and Thomason 1993). If these forces act directly on the structure, then shearing stresses will result. Other types of forces that the skull may experience include bending and torsion. Preuschoft (1989) stated that the bite forces inside the upper jaw evoke shearing forces, torsional moments, and bending moments; unfortunately he does not specify the sources or nature of these different loading conditions. Different regions of the facial skeleton seem to experience variable amounts of stress during biting and mastication, so every facial bone may not be specifically designed for countering mechanical loads from mastication (Hylander et al. 1991, Hylander and Johnson 1997).

The mandible is one area of the face where extensive research has been conducted to determine the forces experienced during mastication (Hylander 1975, Hylander 1979). Hylander (1975) explored the issue of whether or not the mandible functions like a lever during mastication and concluded that the mandible does function like a lever and behaves more or less like a curved beam. Hylander (1979) also explored the functional significance of the primate mandibular form and concluded that the symphyseal region does appear to be an adaptive response to masticatory loads, particularly unilateral molar bite force. Unfortunately the upper and lower jaws do not function in the same manner. Due to the structural nature of the maxilla, modeling the lower jaw experimentally has been difficult, if not impossible, to date. Although the conclusion can be made that the maxilla does experience bending and twisting like the mandible due to the presence of the

hard palate, there is no experimental evidence present that does state what type of stresses the maxilla experiences during mastication (Daegling and Hylander 1997). Nevertheless, the forces generated by mastication are still of particular interest when examining the palate.

Effect of Dietary Consistency on Bone Growth

Several studies have been conducted over the years that support the idea that dietary consistency affects craniofacial bone growth and development. Many of these studies were initiated in an attempt to determine why Western societies had such high rates of malocclusion compared to non-industrial societies (Beecher et al. 1983, Ciochon et al. 1997). The theory that forceful chewing was necessary for proper growth became one avenue of exploration. Beecher et al. (1983) examined this hypothesis by raising two groups of squirrel monkeys; one group was given a naturally tough diet while the other was given a diet of artificially softened foods. Significant differences were noted between the two groups and they concluded that there is a minimum threshold of stress needed for proper craniofacial development to occur.

The animals given the soft diet in the study of Beecher et al. (1983) exhibited maxillary arch narrowing and increased palatal height. These two characteristics occurring simultaneously suggests that maxillary arch collapse (maxillary arch narrowing), the most common occlusal problem in American youths, probably occurs because of differences in the growth of the mid-palatal suture and the fact that teeth from the maxillary alveolar process are not correctly aligned with the mandibular teeth. Other cranial sutures were also affected by dietary consistency. Distinct differences in calcification were seen in the lambdoid and sagittal sutures through the use of radiographs. The soft diet animals had a much broader radiolucent area at the sutures

than the hard diet animals, which means that the sutures in the soft diet area are more patently opened and less calcified.

Squirrel monkeys are not the only experimental animals that have supported the idea that craniofacial growth and development is affected by the consistency of diet. Experiments have also been conducted using rats (Beecher and Corruccini 1981, Bouvier and Hylander 1984, Kiliaridis et al. 1985, Yamamoto 1996) and minipigs (Ciochon et al. 1997). Differences were found in the mandibles of Yucatan minipigs that were raised on diets of varying consistencies (Ciochon et al. 1997). In addition to examining the bones, Ciochon et al. (1997) also examined the weight of the muscles involved in mastication. They found that the weights for the superficial masseter, deep masseter, and temporalis muscles were all significantly higher in the hard diet group. The frontal profiles of the cranium also differed between the two groups; the hard diet group displayed a steep profile while the soft diet group displayed an overall more horizontally oriented profile. Morphological differences in the shape of the mandible between the two groups were also noted. Unfortunately, the maxilla was not the main focus of this study so very little information concerning this structure was presented. However, Ciochon et al. (1997) did note that the palate was relatively longer in the soft diet group. They also took measurements of the maxillary arch breadth and unlike the results reported by Beecher et al. (1983) in the squirrel monkeys, there was no difference found between the groups of the Yucatan minipigs.

Rats have served as another common experimental animal for pursuing the effects of dietary consistency on craniofacial growth and development. Beecher and Corruccini (1981) conducted a study using rats that consisted of two groups, a soft diet group and a

hard diet group. They reported that the rats fed a soft diet had a significantly narrower maxillary arch breadth compared to the hard diet group. The animals in the soft diet group weighed approximately 13% less than the animals in the hard diet group at the end of the experiment; however, the weight difference was not found to be significant.

Bouvier and Hylander (1984) disagree with Beecher and Corruccini (1981) about the weight differences not being significant. Bouvier and Hylander (1984) conducted a similar experiment and found that the maxillary arch length was significantly different between the animals raised on different diets, but once corrections were made for the weight differences, the maxillary arch differences became nonsignificant.

Kiliaridis et al. (1985) used cephalometric longitudinal analysis for growing rats using a normal diet group and a group fed a soft diet. Differences were noted in the growth patterns of both the neurocranium and the viscerocranium between the two groups. The viscerocranium of the soft diet group showed a more orthocranial position, which refers to the skull being of medium height relative to length, with the most noticeable changes occurring in the nasal area. Changes were also noted in the incisors of the upper jaw as well as the mandible. The incisors of the upper jaw showed a greater proclination in relation to occlusal and palatal planes in the soft diet group, while the gonial angle of the mandible showed a decreased appositional rate.

As can be seen by comparing the studies of Beecher and Corruccini (1981) and Bouvier and Hylander (1984), no consensus exists on the effect dietary consistency has on the growth of the palate. Yamamoto (1996) examined how food consistency effects the growth of the palatal region of the maxillary complex through the use of bone histomorphometry to try to aid in the resolution of this issue. Specifically, the goal was

to investigate how the consistency of the diet affected the pattern of bone apposition at the growth site of the palatal region. As with the previous studies, the rats were divided into two groups; one was fed a hard (solid) diet while the other was fed a soft (liquid) diet. There were significant differences found between the two groups.

Yamamoto's (1996) results agreed with those of Kiliaridis et al. (1985) in that the vertical growth of the palate differed between the two groups and there was a more anteriorly directed growth rotation of the palate in the soft diet group. Other studies that examine the underlying mechanism for this difference have noted a marked decrease in the bone appositional rate in the areas of muscle insertion in the anterior part of the viscerocranium (Engstrom et al. 1986); however, the area under consideration in Yamamoto's (1996) study is not an area of muscle insertion. This implies that the changes in the palatal region of the maxilla cannot be caused directly by activities such as muscle action; however, muscle action can have large effects due to mechanical activities such as bending and twisting. Yamamoto (1996) proposes that although the mechanical forces generated by mastication probably have an indirect affect on the growth, another factor to consider is that the growth of other structures such as the neurocranium also affects the growth of the viscerocranium under different occlusal loading conditions.

As mentioned previously with the study of Ciochon et al. (1997), the growth of the mandible has also been explored in relation to dietary consistency. One line of reasoning is if an animal has a diet that consists of hard items then their mandible would be more massive in terms of bone than a similar sized animal with a softer diet. Just like the differences reported in the maxillary arch breadth between the different studies cited above, differences exist on this issue concerning the mandible. A study conducted by

Daegling and McGraw (2001) does not support the line of reasoning expressed above. They examined the mandibles from two different species of colobus monkeys that are similar in size and sympatric, but one of the species (*Colobus polykomos*) has a diet containing food items of harder consistency. One would expect that *Colobus polykomos* would have a more robust mandible than the other species (*Procolobus badius*), but this is not the case. In fact, mandibular morphology does not reflect the differences in diet.

The studies mentioned so far have been concerned with mastication, but this is not the only process that mammals use for oral food intake. Infant mammals engage in a unique form of feeding referred to as suckling. Although the mechanism of suckling has been explored (German et al. 1992) as well as the transition from suckling to drinking at weaning (Thexton et al. 1998), there have been no studies conducted on the types of loads this mechanism produces and whether or not these loads also affect craniofacial growth and development.

CHAPTER 2 GROWTH OF THE PALATE

Embryological Growth and Development

Facial development begins around the third week of gestation with the development of five facial swellings, or primordia, in the frontonasal and visceral arch regions. These five primordia consist of the frontonasal prominence, which forms the forehead and nose, two maxillary prominences, which form the lateral stomodeum, or primitive mouth, and two mandibular prominences, which form the caudal stomodeum (Bender 2000, Scheuer and Black 2000). Within each of these prominences, neural crest cells differentiate into fibrous connective tissue, all the dental tissues except enamel, skeletal and connective tissue of the face, cartilage, and bone. By the end of the fourth week, the lower aspect of the frontonasal prominences develop bilateral oval thickenings of the surface ectoderm known as nasal placodes, which will produce the medial and lateral nasal prominences (Kirschner and LaRossa 2000, Moore and Persaud 2003). The intermaxillary segment of the maxilla forms when the medial nasal prominences merge. This segment gives rise to the philtrum of the upper lip, the premaxillary part of the maxilla, and the primary palate (Moore and Persaud 2003). The maxillary prominences enlarge during the fifth week and connect with the lateral nasal prominences to establish continuity between the nose and the cheek while the maxillary prominences fuse with the medial nasal prominences to complete the lip.

Palatogenesis begins at the end of the fifth week and continues until the twelfth week. The median palatine process develops from the intermaxillary segment during the

sixth week (Moore and Persaud 2003). This process forms the primary palate, which gives rise to the premaxillary part of the maxilla. In the adult hard palate, the premaxilla represents only a small portion of the hard palate anterior to the incisive foramen forming the part of the maxillary alveolus that bears the incisors.

During the sixth week, the secondary palate develops from the paired lateral palatine processes also known as the palatal shelves. The lateral palatine processes are two mesenchymal projections that extend from the internal aspects of the maxillary prominences (Moore and Persaud 2003). Initially both palatal shelves are oriented vertically on either side of the developing tongue. As the tongue descends, the palatal shelves gradually move to a horizontal position where they will meet and fuse at the midline. An intrinsic shelf elevating force is believed to be responsible for the movement of the palatal shelves. This force is generated by the hydration of hyaluronic acid in the mesenchymal cells within the palatal processes (Moore and Persaud 2003). Hyaluronic acid acts as a water barrier and provides “tissue turgor” that moves the palatal shelves (Brinkley and Morris-Wiman 1984). The movement of the palatal shelves begins in the seventh week, but fusion is not completed until the twelfth week. Fusion of the palatal shelves results in the formation of the uvula, soft palate, and hard palate posterior to the incisive foramen (Kirschner and LaRossa 2000).

For nonhuman primates such as baboons and macaques, palatogenesis occurs approximately at the same stage as humans (Hendrickx and Peterson 1997). The underlying mechanisms for palatal closure are also thought to be the same between these primate species and humans (Bollert and Hendrickx 1971, King and Schneiderman 1993). Since the timing and the underlying mechanisms of palatal closure are similar in

baboons, macaques, and humans, then catarrhine primates may be appropriate animals to use in order to explore orofacial teratogenesis in humans (Bollert and Hendrickx 1971).

Postnatal Growth and Development

Growth refers to a structure, in this case bone, changing in magnitude (Enlow and Hans 1996). Contrary to prior belief, there are no centralized and self-contained growth centers; instead all portions of the bone play a role in the growth of the structure (Enlow and Hans 1996). As opposed to growth centers, the functional matrix is the determinant of the skeletal growth processes. The functional matrix is all the tissues and spaces that work together to fulfill a particular function (Moss 1969). This concept provides an explanation of what happens during craniofacial growth, but not how the cellular and molecular mechanisms underlying growth work.

Remodeling and displacement are two basic kinds of growth movements involved in facial growth. Remodeling serves five main functions that are outlined by Enlow and Hans (1996): 1) progressively changes the size of the whole bone, 2) sequentially relocates the component regions of the whole bone to allow for overall enlargement, 3) shapes the bone for its functions, 4) fine-tunes the outline of separate bones to each other and their surrounding soft tissues, and 5) carries out structural adaptations to the intrinsic and extrinsic changes in conditions. This remodeling is not synonymous with the type of remodeling discussed earlier. Unlike Martin et al. (1998), Enlow and Hans (1996) do not make a distinction between the processes of modeling and remodeling. Instead, Enlow and Hans (1996) make a distinction between remodeling (as defined above) and displacement. Displacement is the process of the physical movement of the whole bone and occurs when remodeling is simultaneously resorbing and depositing bone.

Palatal remodeling occurs through a process known as the “V” principle. This concept is based on the fact that many cranial and facial bones, including the palate, have a V-shaped configuration (Enlow and Hans 1996). Bone deposition takes place on the inner side of the V while resorption takes place on the outer side of the V (Figure 1, adapted from Enlow and Hans (1996)). In the case of the maxillae, the external side of the anterior part of the maxillary arch is resorbed while bone is deposited on the inside of the arch. This process increases the width of the arch causing the palate to become wider (Enlow and Hans 1996). Growth along the mid-palatal suture also adds to the progressive widening of the palate and maxillary (alveolar) arch (Friede 1998). Widening of the palate continues into adulthood (Scheuer and Black 2000).

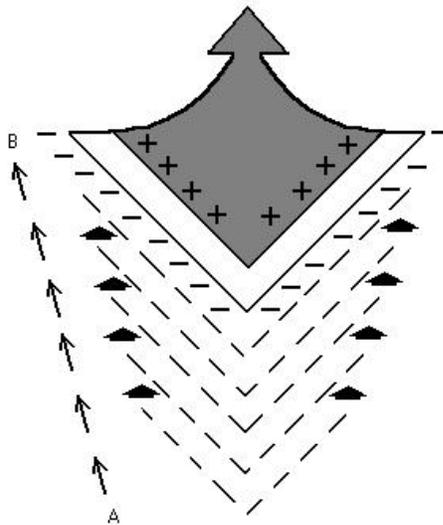


Figure 1. “V” principle of facial growth. As the V moves from position A to position B, the structure increases in overall dimensions. The + marks indicate bone deposition on the inner side of the V, while the – marks indicate bone resorption on the outside surface.

Lengthening of the hard palate occurs partly in the transverse suture and partly by the apposition of bone to the posterior margin (Melsen 1975). The growth in the transverse suture continues until puberty, but the appositional activity continues until

approximately 18 years of age. Disagreement exists concerning the appositional activity on the posterior margin of the palate. According to Sejrnsen et al. (1996), little growth occurs at the posterior border of the hard palate. They reached this conclusion by studying archaeological samples that show a constant distance between the greater palatine foramen and the posterior margin of the palatine bone at various dental stages. Sejrnsen et al. (1996) attribute lengthening of the hard palate almost solely to growth in the transverse suture. Although the amount of apposition that occurs on the posterior margin is controversial, consensus exists on the fact that little to no apposition occurs on the anterior margin. The transverse palatine suture remains in the posterior part of the bony palate from birth to adulthood regardless of the minute amount of activity on the anterior margin, which suggests that highly differentiated growth must occur postnatally in the transverse palatine suture (Silau et al. 1994).

The palatal growth rates of several nonhuman primates, specifically *Macaca nemestrina* and *Papio cynocephalus*, were investigated to see if there were any differences between the two genera (Swindler and Sirianni 1973). Although the absolute size of these primates is different, the growth of the palate occurred at similar rates with both gradually decelerating with age. The deceleration of the growth rate is also characteristic of humans. Another significant finding from this study is that no sexual dimorphism exists in the rate of growth of the palate within either species (Swindler and Sirianni 1973).

As previously noted, both the mid-palatal and transverse palatine sutures play a role in the growth of the palate. In the embryonic stage, the incisive suture separates the premaxilla and the maxilla, but this suture fuses before birth; although a slight visible

suture line may appear on the lingual surface of the palate and persist into adulthood (Mann et al. 1987). The mid-palatal and transverse palatine sutures fuse erratically, but they remain open well into adulthood. The morphology of these two sutures changes throughout the different stages of palatal growth. The transverse suture begins broad and slightly sinuous at birth and later develops into a typical squamous suture (Melsen 1975). The mid-palatal suture progresses through three stages; in the first stage the suture is short, broad, and Y-shaped, with the vomerine bone in the groove of the Y between the two maxilla halves; in the second stage the suture is more sinuous; and in the third stage the suture is heavily interdigitated (Melsen 1975). The change in sutural morphology may be attributed to changes in the mechanical environment. Sutural biology, function, and morphology will be explored further as well as how sutures are affected by loads.

CHAPTER 3 SUTURES

Functions of Sutures

Sutures are any articulation between dermal bones of the skull (Herring 2000). These articulations are usually fibrous but sometimes contain cartilage or fibrocartilage. Evolutionarily, the earliest sutures developed in the armored jawless fish and consisted simply of the skin that remained between the dermal plates. The properties that are typically associated with sutures, mobility, growth, and the potential for synostosis (closure), were already present in these armored jawless fish (Herring 2000). Mammals show no evolutionary progression of sutures; in fact, they have lost some of the sutural diversity. All taxonomic groups that have sutures show a complete range of sutural morphology, from loose connective tissue to elaborate interdigitations joined by a well-defined ligament (Herring 2000).

Three main biological functions are associated with sutures: to unite bones while still allowing slight movement, to act as growth areas, and to absorb mechanical stress (Persson 1995, Cohen Jr. 2000). Two types of movements typically take place at the sutures. At birth is when the first type of movement occurs, which entails the displacement of the calvaria bones as the human head is compressed through the birth canal (Persson 1995). This causes a molding of the head that resolves during the first week of life through cranial re-expansion and widening of the sutural areas (Cohen Jr. 2000). The other type of movement at the sutures is caused by the displacement of bones relative to one another as the skull grows (Persson 1995).

As previously mentioned, the amount of growth that occurs at the sutures is debated, but there is no doubt that sutures do play a role in craniofacial growth. Sarnat (2003) conducted experiments on macaque monkeys that involved surgically producing clefts of the palate on one side only. The severity in the clefts varied from a narrow slit to almost the entire half of the palate excised. No significant differences were noted in the growth and development of the hard palate or maxillary arch between the operated and unoperated sides or between the experimental (operated) and control (not operated) macaques. Sarnat (2003) postulated two possible conclusions; either the transverse palatine and mid-palatal sutures do not make a primary contribution to growth or other areas of growth compensated for the altered condition. From this particular experiment there is no way to decide which conclusion is correct, but other researchers have postulated that the palatal sutures only secondarily contribute to growth (Melsen 1975). Not only does the same suture grow differentially at various times, but the rate and the amount of growth varies for different sutures at different times (Persson 1970, Sarnat 2003). The problem with intervention studies is that they create a situation that will never be found in nature, so the results cannot be applied to animals in nature.

Persson (1970) conducted a study on the postnatal growth of facial sutures in the rat that revealed different growth patterns in individual sutures as well as in the bony margins of the same suture. Four different growth patterns were observed. The first pattern was appositional growth against both sutural margins, which was observed in the premaxillary part of the mid-palatal suture. Another type of pattern observed was appositional growth against only one sutural margin while the other remained inactive. This pattern was found in the main part of the naso-premaxillary suture. The palato-

maxillary suture showed appositional growth against one sutural margin, while the other margin showed resorption. This contradicts Sarnat (2003) who states that sutural growth is only through apposition with no resorption involved. The final growth pattern observed by Persson (1970) is perichondral growth in the maxillary part of the mid-palatal suture. This suture is an example of cartilage being present in the articulation as opposed to just collagenous fibers (Herring 2000).

Mechanical environment also affects sutural growth and development. Mao (2002) concluded that sutural growth is accelerated when exposed to tension and compression. Another potential stimulus for sutural growth is the oscillatory component of cyclic force. Kopher and Mao (2003) demonstrated that small doses of oscillatory mechanical stimuli can affect sutural growth by either accelerating osteogenesis of the suture or initiating net sutural bone resorption. This information can potentially affect therapeutic goals in craniofacial disorders.

The third biological function of sutures is that they act either as a shock absorber for mechanical stress or to transmit force across the sutures (Herring 1972, Persson 1995). The majority of mechanical stress in the suture areas is associated with mastication (Persson 1995). Sutural morphology has been postulated to reflect the loading environment under which the suture is subjected (Herring 1972, Wagemans et al. 1988, Herring and Teng 2000). Whether or not this is true will be explored in the following sections.

Sutural Biology and Morphology

Pritchard et al. (1956) outlined the development of cranial and facial sutures based on six different species: humans, sheep, pigs, cats, rabbits and rats. At all stages of development, sutures exhibit five intervening layers as well as two uniting layers between

the adjoining bones. The five intervening layers consist of a pair of cambial layers, a pair of periosteal fibrous capsular layers, and a middle looser layer of cellular mesenchymal tissue. The cambial layers are the sites of active osteogenesis producing woven bone, but the capsular layers must also expand in order to keep pace with the growing bone. The two uniting layers occur when the fibrous capsules are joined by means of two fibrous laminae, an external and an internal. The extremities of the fibrous capsules retain their separate identities due to the intervening layer of loose mesenchymal tissue.

The facial and cranial sutures have the same structure, but they arise somewhat differently. Before the sutures are formed in the face, the cambial and capsular layers are already present with the middle and uniting layers being derived from the mesenchyme between the approaching bone territories. The bones in the cranial vault approach each other within an already differentiated fibrous membrane referred to as the ectomeninx. The capsular layers do not form in the cranium until the cambial layers have almost met and the middle and uniting layers are derived from the delamination of the ectomeninx between the bones (Pritchard et al. 1956).

The histological structure of sutures, however, is not agreed upon. Pirelli et al. (1999) conducted a study using biopsy samples of the mid-palatal suture obtained from patients ranging in age from 10 years old to 30 years old. They reported that the capsular and cambial layers reported by Pritchard et al. (1956) were not detected in any of their samples nor were the cells typically associated with these layers, osteoblasts and osteoclasts. The absence of osteoblasts and osteoclasts suggest that the bone was in a resting period at the time of the sample. Unlike the woven bone detected by Pritchard et al. (1956), Pirelli et al. (1999) stated that all the sutures were formed by lamellar and

bundle bone. Bundle bone is the term used to describe bone in the suture that closely resembles the alveolar bone lining the periodontal ligament with a high turnover rate (Pirelli et al. 1999). Although the functional significance of the lamellar bone in the sutures is unclear, Pirelli et al. (1999) stated that the lamellar bone may possibly progressively replace the bundle bone when the suture is no longer active in growth and remodeling. If this is the case, the lamellar bone may represent the structural basis of the physiological process of synostosis (Pirelli et al. 1999). The discrepancies in the sutural structures between Pritchard et al. (1956) and Pirelli et al. (1999) may be attributed to the differences in the ages of the samples examined.

The functional significance of the presence of cartilage in some of the postnatal sutures is heavily debated. The cartilage is only present for a limited time and usually only appears in the midline sutures, i.e. the sagittal and mid-palatal sutures. The function of this cartilage seems to be linked to changes in the mechanical environment (Wagemans et al. 1988). Sutures are normally under tension, but during growth the sutures may be exposed to particularly strong pressure and shearing stresses (Pritchard et al. 1956). The secondary cartilage that is present in these sutures is mainly found in rapidly growing areas (Perssons 1995). Pritchard et al. (1956) recommends that the effect of masticatory forces should be considered in relation to the development of sutures.

The morphology of sutures is not only different between sutures, but the morphology of a single suture can vary throughout its life. Melsen (1975) identified three morphological stages in the development of the mid-palatal suture: Y-shaped, slightly sinuous at birth, and interdigitated at puberty. Del Santo Jr. et al. (1998)

conducted a study of the morphological aspects of the mid-palatal suture in the human fetus that partially confirmed the changes in morphology described by Melsen (1975). The first group of fetuses (16-23 weeks) in this study showed a mid-palatal suture that was rectilinear in nature with a wide zone of intense cellular proliferation. The second (24-31 weeks) and third groups (32-39 weeks) displayed a sinuous form with a narrower cellular proliferation zone.

The complex morphology of sutures is thought to reflect their functional environment (Rafferty and Herring 1999). Oudhof (1982) found that although sutural tissue has hereditary characteristics that determine the specific differentiation, certain environmental influences are necessary for the manifestation and development of qualities associated with sutures. For example, in the transplantation experiments conducted by Oudhof (1982), when a portion of a suture was relocated to an area of little or unspecified growth, the suture gradually lost its specific structure. On the other hand, when a suture was transplanted to an area of active growth, the suture adapts to its surroundings. This was witnessed when a portion of the sagittal suture of a rat was transplanted into a coronal suture. The sagittal suture adapted by developing a more intensive formation of fibers and more and longer lingulae (Oudhof 1982). The influence of the mechanical environment on sutures will be the next topic covered.

Sutures and Loads

Suture morphology is extremely complex and several researchers have postulated that the mechanical environment is one factor that influences their morphology (Linge 1970, Herring 1972, Oudhof 1982, Wagemans et al. 1988, Herring and Teng 2000, Mao 2002). Herring (1972) examined sutural morphology in suoids to explore the use of cranial sutures as indicators for the amount and direction of stress in the skull. She

assessed sutural morphology in two ways: first she examined disarticulated sutural surfaces for six specimens, second she examined dried articulated suoid skulls and subjectively categorized them as straight, slightly interdigitated, interdigitated, and very interdigitated. Another way to classify sutures is as either beveled or butt-ended.

One tentative conclusion that Herring (1972) drew from this research was that the beveling of sutures may allow adjustive movements or stress reductions during forceful operations, like rooting in pigs. Another conclusion was that interdigitations are instrumental in the transmission of force from one bone to another and to resist shear loads. Generally speaking, the interdigitations of the sutures will be either perpendicular or parallel to the main force applied and these interdigitations serve to increase the surface area for collagen fibers to attach (Herring 1972, Jaslow 1990, Rafferty and Herring 1999). Jaslow (1990) examined the mechanical properties of sutures and concluded that increased interdigitations do improve the bending strength when sutures are loaded slowly when compared to cranial bone alone.

Jaslow (1990) was also able to provide support for the hypothesis that sutures act as shock absorbers in the skull. This is based on the discovery that cranial bone with a suture present was able to absorb more energy, regardless of the sutural morphology, than the pure cranial bone. The sutural morphology also influences the amount of energy absorbed. Energy absorption increased as the complexity of sutural interdigitation increased. Interdigitation also seems to be correlated with the degree of compressive strain. The more compressive strain a suture is exposed to, the higher the degree of interdigitation (Rafferty and Herring 1999). Adjacent sutures also seem to experience large magnitude strains of opposite polarity during normal mastication, at least in pigs

(Rafferty and Herring 1999). This result is intuitive because when one side of a structure is experiencing tension, the other side is experiencing compression.

The cranium is a difficult bone to model because of its unusual morphology. The palate in general provides special difficulties because the structure is curved which makes techniques such as strain gages difficult to use. Since the loading environment influences craniofacial growth and development, determining the loading environment of bones such as the maxilla is important.

CHAPTER 4 ECOLOGY AND DIET OF COLOBUS MONKEYS

Background Information

Historically, researchers have classified colobus monkeys as specialists, based on the amount of leaves in their diets. The origin of this belief seems to stem from an early paper by Booth (1956) that refers to colobus monkeys as ‘purely leaf-eating.’ Casual observations and the study of the contents of the stomach formed the basis of this assumption. Anatomical features such as the large complex stomach and high-crowned molars and premolars also support the notion that colobus monkeys are largely leaf-eaters (Campbell and Loy 2000). Recent evidence, however, suggests that this initial view of colobines is not accurate, at least not for all species and/or groups (Maisels et al. 1994). Leaves do make up a large portion of most, if not all, colobus monkey diets, but seeds, fruits, and flowers also contribute significantly to their diets. The original belief that colobines were specialists was based on studies conducted on groups of colobines in east Africa (Dasilva 1994). Research at sites such as Tiwai Island in western Africa has shown that seasonal variability exists in their diets, including seeds, fruits, and both young and mature leaves (Dasilva 1994, Davies et al. 1999).

Feeding techniques do not vary much between different species of colobines. The type of food eaten affects the technique used, but regardless of the food type, there is very little manual manipulation involved (Clutton-Brock 1975). Colobus monkeys have reduced thumbs, which may explain the little amount of manipulation. This appendage does not provide them with the grip of other primates who have larger thumbs that allow

more precise gripping. Clutton-Brock (1975) did observe some manipulation, though, such as stripping the pinnules off of the leaf stem by gripping the stem in their teeth and dragging the stem through their clenched fists. He states that he never saw them use their hands to strip or break open fruit; if the covering was removed from a fruit they opted to use their teeth instead (Clutton-Brock 1975).

One difference between red colobus (*Procolobus badius*) and king colobus (*Colobus polykomos*) is their preference for location of feeding. The former usually acquires a large portion of their food from some of the largest trees in the upper canopy of their habitat, while the latter choose to forage lower in the canopy (Oates 1994). In areas where both of these colobine groups co-occur, the red colobus monkeys choose a more diverse diet than the king colobus. Another difference is the amount of seeds that are consumed. All colobus species ingest seeds, but only in the black and white forms do seeds sometimes dominate the diet (Oates 1994). Some researchers argue that African colobines eat a large portion of seeds whenever the quality of the tree foliage is poor via poor soils (Maisels et al. 1994). Evidence supports this statement for some areas such as Zaire (Maisels et al. 1994), but this explanation does not explain the difference in seed exploitation between sympatric species of colobus monkeys.

Study Sample

The colobus monkeys used in this study are *Procolobus badius* (n=39) and *Colobus polykomos* (n=13) from the Tai Forest of Cote d'Ivoire. They are sympatric throughout most of their range and are similar in body size and diets except the king colobus exploits a particularly hard seed from the African oil bean (*Pentaclethra macrophylla*, Mimosaceae) at a much larger frequency than the red colobus monkeys.

This African oil bean tree is usually 21 m in height with a girth of about 60 cm. The pods are 40-50 cm long and usually 5-10 cm wide. Inside the pods are 6-10 flat glossy brown seeds that are up to 7 cm long. *Colobus polykomos* focuses on seeds from this plant and others like it whereas *Procolobus badius* focuses on leaf eating (Davies *et al* 1999). The reason for this difference probably stems from their individual preference in foraging, i.e. upper versus lower canopy.

When the king colobus preys on these hard seeds, they expend a great amount of effort gnawing them until they break through the encasing (Davies *et al.* 1999). As mentioned earlier, Daegling and McGraw (2001) predicted that the species exploiting the hard seeds should have a more robust mandibular corpus than the species that does not exploit this food item. This prediction is based on the reasoning that the king colobus would have to apply larger loads, therefore stressing the mandible more, to gnaw through the tough encasements. The results of the study, however, showed that the variation in mandibular morphology in these two sympatric colobines does not correspond to the predictions based on the dietary differences (Daegling and McGraw 2001).

The underlying reasoning behind the current project is that the palates of these two species of colobus monkeys are exposed to different loading environments. The extensive gnawing of *Colobus polykomos* on the hard seeds may cause a significantly larger amount of force on the palate. If this is the case, the complexity of the palatal sutures of these two species may reflect this difference in loading environment. In order to test this hypothesis, fractal analysis was completed on the mid-palatal sutures of *Colobus polykomos* and *Procolobus badius*.

CHAPTER 5 FRACTAL ANALYSIS

One of the most difficult tasks facing morphologists is that of quantifying and measuring size and shape. Traditionally, parameters such as length and volume were used to try to quantitatively describe and compare morphological characteristics. In Euclidean geometry linear measures are considered one dimension, smooth surfaces are two dimensions, and volumes and weights are three dimensions. Objects that occur in nature, however, seldom have edges that are straight or surfaces that are smooth (Long 1985). Some objects in nature possess certain qualities that can be described by a non-Euclidean fractional dimension, which lies between the values of one and two (Mandelbrot 1977). These objects are known as fractals. Fractals are geometric objects that are self-similar in nature. Self-similarity means that the fractal object is composed of smaller units that possess the same shape as the whole object. Fractals have complex edges or surfaces that increase linearly as the resolution of the units used to measure them increase (Hartwig 1991). Fractal analysis is a technique used to interpret the geometric complexities of fractals.

Several researchers believe some cranial sutures are fractal objects (Long 1985, Hartwig 1991, Long and Long 1992, Gibert and Palmqvist 1995, Montiero and Lessa 2000, Yu et al. 2003). Long (1985) explored the idea of whether or not complex sutures exhibit fractal properties such as self-similarity and a dimension between one and two. To address this question, Long (1985) examined the sutures on the shells of extinct ammonites and cranial sutures of white-tailed deer. The sutures in both of these

organisms are incredibly complex and did exhibit fractal properties. Other cranial sutures that have been examined using fractal analysis are the sagittal suture in humans (Hartwig 1991, Yu et al. 2003), the sagittal and lambdoidal sutures in humans (Long and Long 1992, Gibert and Palmqvist 1995), and cranial sutures in the genus *Caiman* (Montiero and Lessa 2000). In each of these studies, the structures under examination exhibited the characteristics of fractals.

In this study, fractal analysis was conducted with the use of a software program known as Benoit 1.3 (St. Petersburg, FL). This program allows the user to choose from several different methods on how the fractal analysis is conducted. The different methods provided in this program are tailored to accommodate different types of data sets. Based on this data set, three methods seemed equally applicable. Each of these is discussed in further detail.

Box Dimension and Information Dimension Methods

The box dimension method of fractal analysis is one of the most widely used methods due to the relatively simple mathematics involved (Falconer 1990). In Benoit 1.3, the box dimension is defined as the exponent D_b in the relationship:

$$N(d) \approx \frac{1}{d^{D_b}}$$

where $N(d)$ is the number of boxes of linear size d necessary to cover a data set of points distributed in a two-dimensional plane. A number of boxes are used to cover the data set points that are evenly distributed on a plane. This may indicate that point density may influence the results, i.e. the number of data points collected will affect the outcome of the fractal dimension. This method is often referred to as the grid dimension because the boxes used are usually part of a grid system.

To accomplish this method, a series of different box sizes d are laid over the object and the program works by tallying the number of boxes filled during each box size overlay. One of the problems with this method is that the boxes are weighted the same whether the entire box is full or just a tiny portion. The information dimension method addresses this problem by assigning weights to the boxes so boxes containing more points are counted more than the boxes with fewer points (Benoit 1.3). Unfortunately this makes the mathematics involved much more complicated.

Ruler Dimension

Mandelbrot (1977) examined the coastline of Britain and determined that this object was fractal. How was the fractal dimension of this jagged, self-similar line calculated? The method he used is now referred to as the ruler, or yardstick, method.

The ruler method D_r is defined as:

$$N(d) \approx d^{-D_r}$$

where $N(d)$ represents the number of steps taken to walk a divider (or ruler) that is length d . According to Benoit 1.3, the formal equivalence between this method and the box dimension can be shown mathematically. Algebraically, this claim is logical, since the box dimension is simply the reciprocal of the ruler dimension.

CHAPTER 6
MATERIALS AND METHODS

The skulls of 39 *Procolobus badius* and 13 *Colobus polykomos* were examined from a collection housed at Ohio State University. Eight measurements were also taken from each skull: palate height, internal palate breadth, external palate breadth, palate length, palate depth, upper facial height, facial width, and skull length. With the exception of palate depth and palate height, the measurements are defined in Bass (1995). Table 1 provides a brief definition of the six measurements taken from Bass (1995). Palate depth was measured using an instrument colloquially referred to as a carpenter's tool or a contouring tool. The contour was traced from the edge of the alveolar ridge of the second molar to the level of the mid-palatal suture. The height of the contoured tracings was then measured resulting in the depth of the palate. Palate height was measured with sliding calipers by placing one edge of the caliper on the mid-palatal suture and one edge on the alveolar ridge at the level of the second molar.

Table 1. Definitions of measurements collected.

Measurement	Definition (Cranio-metric Points*)
Facial width	zygion to zygion
External palate breadth	ectomolare to ectomolare
Internal palate breadth	endomolare to endomolare
Palate length	prosthion to alveolon
Skull length	alveolare to opisthocranion
Upper facial height	nasion to alveolare

*Cranio-metric points defined in Bass (1995)

In addition to the measurements taken, the palate of each specimen was photographed using a Minolta 35mm camera with a macro lens attached. Each specimen was oriented with the palate parallel to the lens of the camera. The film was developed

and the negatives were made into 35 mm slides. These slides were then scanned into the computer and saved as bitmap images. Each image was imported into SigmaScan where the mid-palatal suture of each specimen was digitized. The x-y coordinates were imported into SigmaPlot and subsequently graphed using a single spline curve. The spline curve option was chosen over the single straight line option because this represented a more accurate depiction of the sutures. The reason this has to be done is to override the automated scaling function of SigmaPlot. The scale of the graphs were changed so equal units were represented on the x and y axes. The image was then inverted from black on white to white on black. This was done because Benoit 1.3 software recognizes white points as data points and the black points as the background.

The images were converted to bitmap files and imported into Benoit 1.3 for the fractal analysis. After exploring the different methods available through the software, the two methods chosen were the information dimension and ruler dimension. The information dimension was chosen over the box dimension because the boxes are weighted and therefore provide a more accurate fractal dimension than the box dimension. There was not, however, an obvious advantage of either the information dimension or ruler dimension over the other, so both were used to calculate the fractal dimensions of the colobine mid-palatal sutures. Other researchers have chosen one of the methods over the other but the reasoning behind their choice is often not made clear, although the researchers who chose the ruler dimension often state that they use this method because Mandelbrot (1977) used this method when examining the coastline of Britain.

Once the fractal dimensions were obtained, several statistical procedures were conducted. A 2-way ANOVA was run separating the sexes and species which resulted in four groups. Regressions were also conducted between the fractal dimensions and each size/shape variable to try to determine if there was a predictable relationship between any of these variables. The regressions were conducted with only the species separated not the sexes. Both of these procedures were evaluated for significance based on a P-value < 0.05. The fractal dimension data for the four groups was also bootstrapped to obtain a more reliable mean since the sample sizes were small. Bootstrapping makes no assumptions about the distributional properties of the data.

CHAPTER 7 RESULTS

Including both fractal dimensions, ten variables were examined. Basic statistics were computed for each variable independently (Tables 2 and 3). The parametric medians for each group are graphically represented for both fractal dimensions in Figures 2 and 3. Since the samples sizes for these groups are small, the data was bootstrapped for 1000 iterations to try to obtain more reliable means and standard errors, since no assumption is made regarding the distribution of the data. As shown in Tables 4 and 5, there was little difference between the parametric mean and the bootstrapped mean.

The ruler and information fractal dimensions for each species were regressed against each of the measured size/shape variables. Out of the 32 regressions performed, only three resulted in significant P-values, i.e. P-values less than .05. However, the coefficient of determination (r-squared) was very weak for these three regressions, ranging from 12.1% to 37.2% (Table 6).

Tables 7 and 8 report the ruler and information fractal dimensions calculated for both species. One interesting (and seemingly impossible) aspect of two of these fractal dimensions is that they are below 1.0. Note in Table 3, *Procolobus badius* specimen number 2107 (Figure 4) has a ruler fractal dimension of 0.99209 and *P. badius* specimen number 9433 (Figure 5) has a ruler fractal dimension of 0.98466. However, their information fractal dimensions are both above

Table 2. Basic statistics for variables associated with *Colobus polykomos*

Variable	N	Mean	Median	StDev	SE Mean	Minimum	Maximum	Q1	Q3
Ruler Fractal Dimension	13	1.1880	1.1903	0.0599	0.0166	1.0795	1.2836	1.1416	1.2341
Information Fractal Dimension	13	1.0994	1.1018	0.0404	0.0112	1.0268	1.1659	1.0781	1.1247
Palate Height	13	12.550	12.500	1.268	0.352	10.400	14.800	11.495	13.680
Internal Palate Breadth	13	18.472	19.400	2.513	0.697	12.100	20.700	17.120	20.045
External Palate Breadth	13	36.278	36.800	1.906	0.529	32.200	38.800	35.310	37.450
Palate Length	13	44.138	44.600	2.992	0.830	36.600	48.200	42.800	45.990
Palate Depth	13	6.808	7.000	1.032	0.286	5.000	8.000	6.000	8.000
Upper Facial Height	13	40.124	40.200	3.350	0.929	34.200	46.410	38.700	42.000
Facial Width	13	75.91	74.00	5.53	1.53	67.90	83.60	71.75	81.25
Skull Length	13	108.96	108.00	4.01	1.11	103.00	115.70	106.05	112.65

Table 3. Basic statistics for variables associated with *Procolobus badius*

Variable	N	Mean	Median	StDev	SE Mean	Minimum	Maximum	Q1	Q3
Ruler Fractal Dimension	39	1.1355	1.1093	0.0983	0.0157	0.9847	1.3455	1.0615	1.2121
Information Fractal Dimension	39	1.1085	1.1058	0.0276	0.0044	1.0643	1.1676	1.0883	1.1310
Palate Height	39	10.086	9.970	1.181	0.189	6.830	12.130	9.470	10.870
Internal Palate Breadth	39	16.347	16.460	1.554	0.249	12.180	18.740	15.380	17.370
External Palate Breadth	39	32.081	32.030	1.441	0.231	29.280	35.040	30.910	33.000
Palate Length	38	39.170	39.085	2.035	0.330	35.340	43.570	37.615	41.030
Palate Depth	39	6.122	6.000	1.305	0.209	3.000	8.500	5.000	7.000
Upper Facial Height	39	40.784	41.150	2.743	0.439	34.010	44.990	38.900	42.910
Facial Width	37	77.686	78.510	5.002	0.822	68.110	86.750	73.725	81.975
Skull Length	36	101.46	101.90	3.56	0.59	93.54	109.27	99.69	103.71

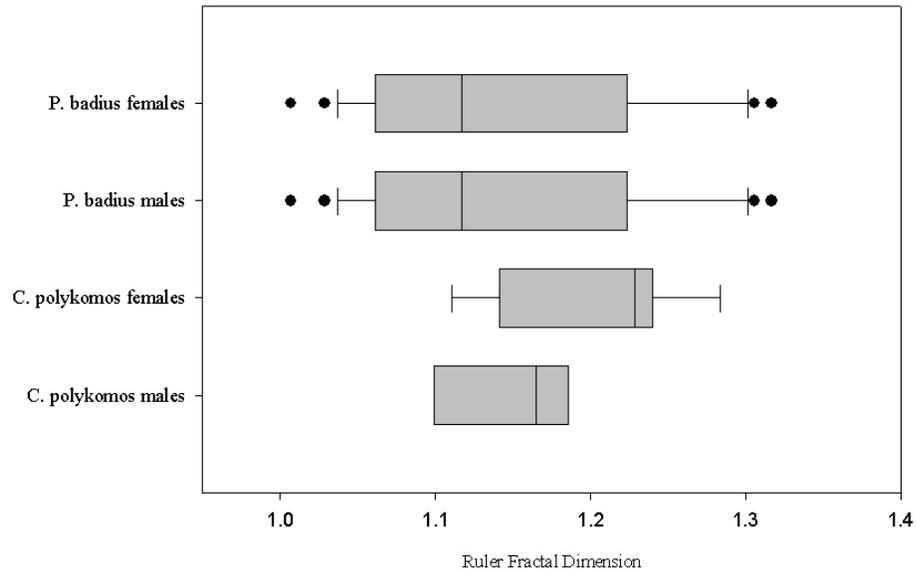


Figure 2. Box plot of median values for the ruler fractal dimensions.

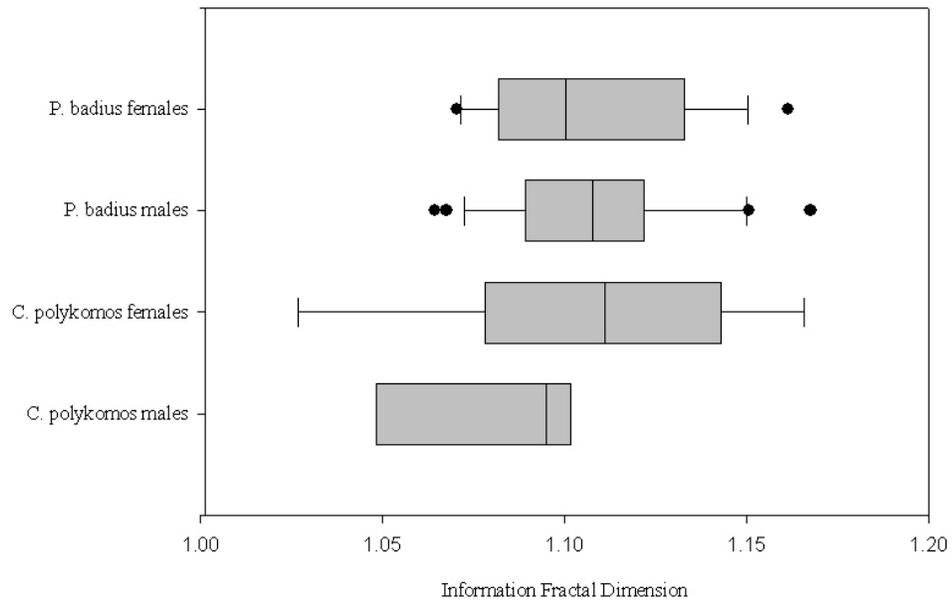


Figure 3. Box plot of median values for the information fractal dimensions.

Table 4. Bootstrapped versus parametric means for ruler fractal dimension

Species	Sex	N	Bootstrap Mean for 1000 samples	Bootstrap Standard Error	Parametric Mean	Parametric Standard Error
<i>Colobus polykomos</i>	Male	4	1.1365	0.0200	1.1500	0.0244
<i>Colobus polykomos</i>	Female	9	1.1953	0.0172	1.2049	0.0195
<i>Procolobus badius</i>	Male	23	1.1295	0.0178	1.1380	0.0194
<i>Procolobus badius</i>	Female	16	1.1230	0.0230	1.1362	0.0274

Table 5. Bootstrapped versus parametric means for information fractal dimension

Species	Sex	N	Bootstrap Mean for 1000 Samples	Bootstrap Standard Error	Parametric Mean	Parametric Standard Error
<i>Colobus polykomos</i>	Male	4	1.0748	0.0145	1.0817	0.0163
<i>Colobus polykomos</i>	Female	9	1.1000	0.0118	1.1072	0.0143
<i>Procolobus badius</i>	Male	23	1.1078	0.0056	1.1107	0.0062
<i>Procolobus badius</i>	Female	16	1.1030	0.0061	1.1070	0.0071

Table 6. Significant regressions

Species	Variables Regressed	N	Slope	Y-intercept	r	r-squared (%)
<i>Procolobus badius</i>	Ruler vs Palate Height	39	0.0289	0.844	.35	12.1
<i>Procolobus badius</i>	Ruler vs Palate Depth	39	0.0289	0.959	.38	14.7
<i>Colobus Polykomos</i>	Information vs Facial Width	13	0.3100	0.624	.61	37.2

According to Benoit 1.3 software, the ruler and information fractal dimensions are equivalent. If this is true, then a simple regression of these two dimensions should show a linear relationship. As Figure 6 shows, this is not the case. In fact, there is no discernible pattern whatsoever in this graph and the r-squared value is 0.0402. Another indication that these methods for determining fractal dimensions are not equivalent is that

Table 7. Fractal dimensions of *Colobus polykomos*

Specimen Designation	Sex	Ruler Fractal Dimension	Information Fractal Dimension
2100	Male	1.07953	1.03320
2216	Male	1.19034	1.09408
2311	Male	1.15727	1.10373
9418	Male	1.17273	1.09593
2102	Female	1.28359	1.08546
2103	Female	1.24256	1.02679
2119	Female	1.22849	1.10182
2123	Female	1.23009	1.13283
2124	Female	1.11034	1.11666
2238	Female	1.14829	1.15345
2245	Female	1.13496	1.16592
2314	Female	1.22786	1.07076
9426	Female	1.23806	1.11099

the specimens exhibiting the highest and lowest fractal dimension values differ between these two methods. The highest ruler fractal dimension is 1.34546 (*Procolobus badius* 227, Figure 7) while the highest information fractal dimension is 1.16761 (*Procolobus badius* 942, Figure 8). The lowest ruler fractal dimension is 0.98466 (*Procolobus badius* 9433, Figure 5) while the lowest information fractal dimension is 1.02679 (*Colobus polykomos* 2103, Figure 9).

Regardless of which fractal dimension is used, a pure model II 2-way ANOVA showed that no significant differences exist in the fractal dimensions between species or sexes. There is also no interaction effect between species and sex. A pure model II was chosen because there were no fixed treatment effects but rather only random effects (Sokal and Rohlf 1981).

Table 8. Fractal dimensions of *Procolobus badius*

Specimen Designation	Sex	Ruler Fractal Dimension	Information Fractal Dimension
2027	Male	1.04962	1.08833
2028	Male	1.29563	1.10579
2118	Male	1.06146	1.14878
2125	Male	1.12647	1.11583
2126	Male	1.30574	1.11583
2013	Male	1.15642	1.11931
2022	Male	1.07645	1.08920
2104	Male	1.13798	1.09966
2105	Male	1.07308	1.09533
2110	Male	1.24166	1.11158
2113	Male	1.23780	1.15081
222	Male	1.13614	1.14766
2231	Male	1.00705	1.10777
224	Male	1.11669	1.11242
2243	Male	1.22389	1.06426
2255	Male	1.07371	1.08930
232	Male	1.10572	1.08667
233	Male	1.06071	1.08017
235	Male	1.07599	1.09189
239	Male	1.14051	1.12176
9413	Male	1.05565	1.11252
942	Male	1.02873	1.16761
945	Male	1.31662	1.06753
2005	Female	1.05978	1.09521
2032	Female	1.09483	1.10217
223	Female	1.30888	1.13372
227	Female	1.34546	1.07348
2014	Female	1.11507	1.16151
2107	Female	0.99209	1.13472
2112	Female	1.09099	1.09856
2215	Female	1.10713	1.11771
2219	Female	1.14706	1.14561
2220	Female	1.10925	1.11490
2240	Female	1.29973	1.07179
2313	Female	1.20520	1.07042
236	Female	1.21207	1.08017
9422	Female	1.07231	1.13104
9433	Female	0.98466	1.08724
972	Female	1.03491	1.09268



Figure 4. Mid-palatal suture of *Procolobus badius* specimen 2107 with a ruler fractal dimension of 0.99209 and information fractal dimension of 1.13472. The suture is oriented with the anterior portion at the top of the page.



Figure 5. Mid-palatal suture of *Procolobus badius* 9433 with a ruler fractal dimension 0.98466 and information fractal dimension of 1.08724. The suture is oriented with the anterior portion at the top of the page.

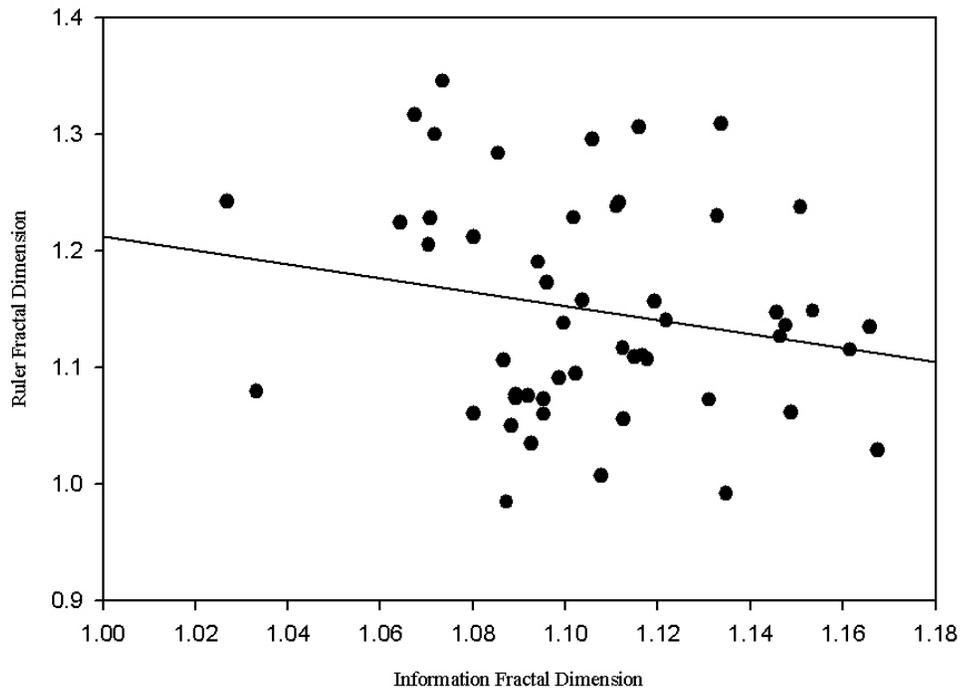


Figure 6. Regression of ruler fractal dimension vs information fractal dimension.



Figure 7. Mid-palatal suture of *Procolobus badius* specimen 227 with a ruler fractal dimension of 1.34546 and information fractal dimension of 1.07348. The suture is oriented with the anterior portion at the top of the page.



Figure 8. Mid-palatal suture of *Procolobus badius* specimen 942 with a ruler fractal dimension of 1.02873 and information fractal dimension of 1.16761. The suture is oriented with the anterior portion at the top of the page.



Figure 9. Mid-palatal suture of *Colobus polykomos* specimen 2103 with a ruler fractal dimension of 1.24256 and information fractal dimension of 1.02679. The suture is oriented with the anterior portion at the top of the page.

CHAPTER 8 DISCUSSION

The results of the 2-way ANOVA indicate that the hypothesis proposed for this study, i.e. these two species would differ in mid-palatal suture complexity, is not supported. The colobine monkeys used in this study only have one major difference in their diets. *Colobus polykomos* must gnaw through a tough pod in order to gain access to a particular type of seed they eat. One possible explanation for why no significant differences were found is that the seeds do not make up a large enough portion of their diets to have an effect on the sutural complexity. In other words, seed-eating is dominant in both of these colobine monkeys, but the actual proportion of *Pentaclethra macrophylla* seeds to the *Colobus polykomos* diets has never been identified (Davies et al. 1999). The difference in masticatory loads between these two species may not be large enough to elicit a morphological response from the mid-palatal suture.

The distribution of stress throughout the palate during mastication may also be a contributing factor to the non-significant results reported here. Although numerous studies exist that explore the loading environment during mastication in certain parts of the face and cranium, few studies mention any stress the palate may receive during this activity. Due to the morphological structure of the palate, mechanical modeling is difficult. Although the palate probably experiences different types of stress such as shearing forces, torsional moments, and bending moments (Preuschoft 1989), it is possible that the stress level is not significant enough to elicit a response from the bone. In order to figure out what the strains are, the maxilla needs to be explored

experimentally. As mentioned earlier, the issue becomes how to model the maxilla. One possible reason the maxilla may experience small loads is the presence of the hard palate. Unlike the mandible, the maxilla has the hard palate which may serve to eliminate or greatly reduce twisting and bending (Daegling and Hylander 1997).

Measurements of different size/shape variables were also taken from each specimen in order to determine whether or not a relationship exists between these particular measurements and the fractal dimensions of the mid-palatal sutures. Only three regressions showed significance, but the correlation values were very weak (Table 6). When these measurements were regressed against the ruler fractal dimension, palate height and palate depth in *Procolobus badius* showed significance. Interestingly there were no significant regressions in *Colobus polykomos* for the ruler fractal dimension. However, the opposite is true for the information fractal dimension. No significant results were found for *Procolobus badius*, but the regression of information fractal dimension versus facial width in *Colobus polykomos* showed significance. The fact that the so-called equivalent fractal dimensions yield different significances is further evidence that these are not equivalent measures. More than likely the significant P-values for these three regressions reflect a type I error instead of real significance, although there is no way to truly know if a type I error was committed. The results of the regressions suggest that there is no predictable pattern between either of the fractal dimensions and any of the size/shape variables.

One problem limiting interpretation was small sample sizes. When dealing with biological samples, obtaining sufficiently large sample sizes can be a problem. An attempt to deal with this problem was made by bootstrapping the data. However, as

previously mentioned, the bootstrapped means were very similar to the parametric means calculated from the raw data, which suggests that the variation captured in this study is probably a fairly accurate representation of the populations in question.

Another issue arising in this study may stem from the methodology used. Fractal analysis has become a popular method for quantifying the complexity of intricate cranial sutures. Long (1985) published one of the earliest works on fractals in biology when he examined the sutures present on the shells of ammonites and the cranial sutures of antlered deer. This study was also the first to describe how fractal elaboration is important in the evolutionary process. Long and Long (1992), however, criticize the use of fractal analysis on human cranial sutures because they feel that these particular sutures are not self-similar and therefore are not fractals even though they yield a dimension between 1 and 2. They state that some waveform curves may yield a dimension up to 1.2, but this is not sufficient to classify them as fractals. Using this reasoning, Long and Long would probably say the sutures presented in this paper are not fractals. If this is true, then this could be an explanation for why the two fractal analysis methods used here do not show equivalence.

The problem with the above supposition is that these sutures do fit the definition of a fractal, i.e. they are self-similar and have a dimension between 1 and 2. The main critique of Long and Long (1992) is that the waveforms that possess a dimension above 1 are not self-similar. Studies conducted on human cranial sutures using the box dimension have shown that human cranial sutures are self-similar through the use of logarithmic plots. These graphs show the relationship of the logarithms of the number of squares with length r occupied by the suture against the logarithm of $1/r$. Benoit 1.3 provided the

logarithmic graphs for each suture analyzed in both of the methods and all of them clearly showed a linear relationship. This suggests that these sutures are self-similar and therefore, by definition, are fractal.

Unfortunately this still leaves the problem of trying to provide an explanation for why the ruler and information fractal dimensions are not demonstrating equivalence like they should. One possibility is that due to the complicated mathematics that are introduced into the information dimension in order to weight the boxes, the equivalence that exists between the box and ruler dimension is lost. To test this theory, fractal analysis was conducted again on the same sutures using the box dimension (Tables 9 and 10). A simple regression was conducted and as Figure 9 demonstrates there is still no linear relationship (r -squared 0.0804). This does not support the idea that the more in depth mathematical calculations affected the equivalence. The reason for this may be that the number of points collected could affect the outcome of the fractal dimension.

This implies that these different methods of fractal analysis are not measuring complexity in the same fashion. Uncertainty exists as to which method is more appropriate for analyzing human cranial and facial sutures, but one insight gained is that these methods are not equivalent. This means more testing (e.g.) needs to be completed in order to try to determine which method is more accurate. Besides the type of dataset utilized, another factor that may affect which method is better is how the data is collected. In other words, it may be that both methods are appropriate for analyzing human sutures, but depending on the method used to extract the suture from the specimen and manipulate it so it can be imported into this software, one method may prevail over

the other. Regardless of which method was used, no significant results were discovered from this data.

Table 9. Box dimensions for *Procolobus badius*

Specimen Designation	Sex	Box Dimension
2027	Male	1.15339
2028	Male	1.11262
2118	Male	1.18019
2125	Male	1.14647
2126	Male	1.12777
2013	Male	1.12626
2022	Male	1.14486
2104	Male	1.11175
2105	Male	1.12366
2110	Male	1.09819
2113	Male	1.14137
222	Male	1.16990
2231	Male	1.12637
224	Male	1.12912
2243	Male	1.11433
2255	Male	1.12925
232	Male	1.12130
233	Male	1.11166
235	Male	1.12101
239	Male	1.15034
9413	Male	1.12463
942	Male	1.17601
945	Male	1.10132
2005	Female	1.11475
2032	Female	1.14087
223	Female	1.12508
227	Female	1.11091
2014	Female	1.17835
2107	Female	1.12846
2112	Female	1.11445
2215	Female	1.13767
2219	Female	1.14574
2220	Female	1.13643
2240	Female	1.11797
2313	Female	1.12303
236	Female	1.13915
9422	Female	1.12672
9433	Female	1.12309
972	Female	1.11693

Table 10. Box dimensions for *Colobus polykomos*

Specimen Designation	Sex	Box Dimension
2100	Male	1.12953
2216	Male	1.11993
2311	Male	1.10920
9418	Male	1.10893
2102	Female	1.10568
2103	Female	1.10836
2119	Female	1.13348
2123	Female	1.17746
2124	Female	1.12773
2238	Female	1.15679
2245	Female	1.17051
2314	Female	1.10595
9426	Female	1.13959

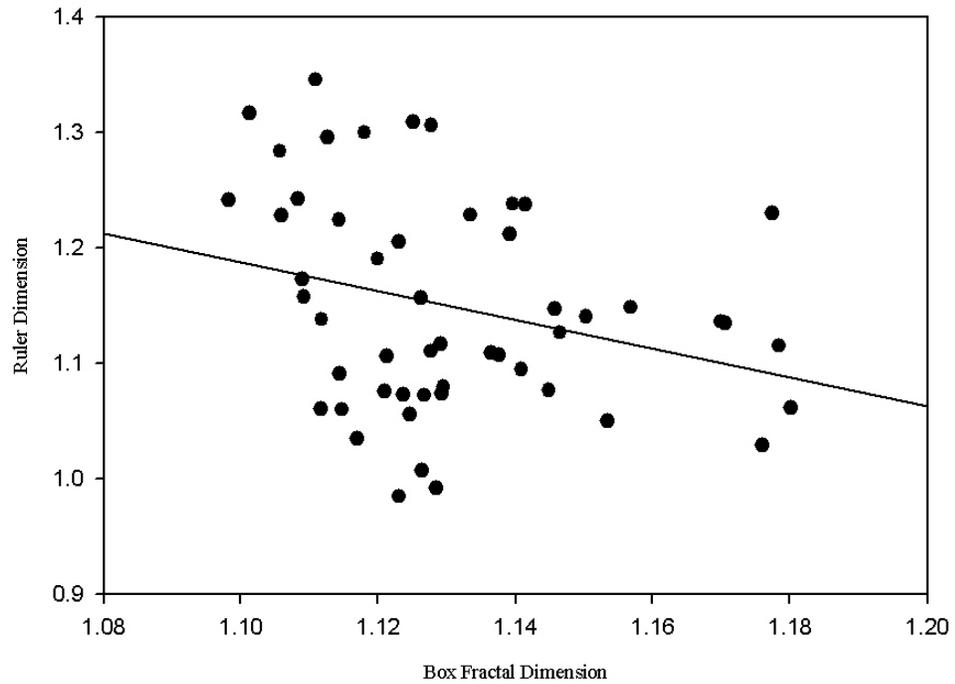


Figure 10. Regression of ruler fractal dimension vs box fractal dimension.

CHAPTER 9 CONCLUSION

One of the proposed functions of cranial sutures is that they play a role in the transmission and absorption of mechanical loads (Herring 1972). If this is true, it stands to reason that the morphology of the sutures may reflect the loading environment to which it is subjected (Rafferty and Herring 1999). Using this reasoning, the hypothesis was made that the more complexity a suture exhibits, the higher amounts of stress it experiences. One problem is how one quantitatively measures sutural complexity. One method that has been applied to this problem over the past two decades is fractal analysis.

The fractal analysis conducted on the mid-palatal sutures of these two species of colobus monkeys did not show a significant difference. Sex also did not have a significant effect on the complexity of the mid-palatal sutures. Although this study does not support the hypothesis that mechanical loading is at least partially responsible for the morphological complexity of sutures, it by no means discredits this idea. The most probable reason behind the lack of support is that the differences in the diet are not great enough to cause significantly more stress in the palate of *Colobus polykomos*. Another aspect that should be examined in the future is the overall structure of the maxilla of these two species. There may possibly be a larger concentration of bone between the point of impact (the teeth) and the mid-palatal suture. If so, this bone may absorb the stress before it reaches the suture. Unfortunately, at this point in time, this is pure speculation.

The suggestion has also been made that most cranial sutures are not intricate enough to be fractals (Long and Long 1992), but as the term is currently defined human

cranial sutures are fractal objects. This leads to the question of which fractal analysis technique is most appropriate for examining human cranial sutures. One conclusion that must be drawn from this study is that the box (information) dimension and the ruler dimension methods are not equivalent. So, which one provides a more accurate depiction of the dimension of these structures? Unfortunately, more intensive investigation is required in order to provide an answer for this question.

The complexity of these particular sutures did not differ significantly between these species, but this does not mean that the loading environment has no effect on sutural growth and morphology. Enough evidence exists to merit further exploration of this topic. Mechanical environments do elicit morphological responses from bone throughout all stages of life whether in modeling or remodeling. An important point to consider is that sutural complexity may not only be influenced by mechanical factors. The sutures serve other functions besides absorption and transmission of loads. These other functions, such as growth, may also affect the complexity of the sutures. Although this is possible, mechanical loading seems to be the most likely factor contributing to the complex morphology of the suture. Many factors play a role in palate growth and development; however, exploring the role of mechanical forces is essential to a comprehensive understanding of this process.

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BIOGRAPHICAL SKETCH

Jennifer Hotzman is one of four children and was born in Meridian, Mississippi. She received her Bachelor of Arts degree in anthropology from the University of Southern Mississippi in 2000. After graduation she continued her education at the University of Florida. While completing her graduate studies, Ms. Hotzman also worked full-time for Regeneration Technologies, a company that manufactures allografts for surgical procedures. After obtaining her Master of Arts degree, she plans on continuing her graduate studies at the University of Florida.