METAMERIC VARIATION IN THE EXPRESSION OF THE INTERCONULUS IN *PAPIO* AND *MACACA*

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By

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San Francisco, California

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CERTIFICATION OF APPROVAL

I certify that I have read *Metameric Variation in the Expression of the Interconulus in Papio and Macaca* by Tesla Allyse Monson, and that in my opinion this work meets the criteria for approving a thesis submitted in partial fulfillment of the requirements for the degree: Master of Art in Anthropology: Evolution and Human Variation at San Francisco State University

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ABSTRACT

The interconulus is a trait that expresses between the protocone and the hypocone of the maxillary molars in populations of *Papio* and *Macaca*. The interconulus is a nonmetric dental trait that ranges in expression from a lingual groove to a pronounced cingulum. Hlusko's (2002) study found that the interconulus in a population of *Papio hamadryas* from the Southwest National Primate Research Center has increasing expression from M1 to M3, an example of ordered metameric variation. This study examined the molars of *Papio* (n=42) and *Macaca* (n=136) individuals from three museum skeletal collections for variation in the expression of the interconulus. Because the interconulus is a nonmetric trait, a standard of five discrete categories of expression (score 1-5; Hlusko 2002) was used to quantify the trait. The *Papio* individuals did not demonstrate statistically significant ordered metameric variation in the expression of the interconulus. However, the *Macaca* sample did have significant ordered metameric variation with mean expression scores of M1=1.12, M2=1.47 and M3=1.75. Assessment of mean expression scores at the species and subspecies level suggests that patterns of metameric variation may differ across populations. Metameric variation is found in numerous parts of the metazoan body plan, from body segments, to sets of appendages, to the vertebral column. This project aims to characterize the metameric variation seen in the Old World Monkey dentition, ultimately contributing to a more general understanding of the role that metameric variation has played and continues to play in primate evolution.

I certify that the Abstract is a correct representation of the content of this thesis.

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Chair, Thesis Committee Date

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INTRODUCTION

Teeth are highly durable and constitute a significant portion of fossil remains (e.g. Butler 1939). Dental anthropology, the study of teeth in the primate fossil record, makes extensive use of variation in dental morphology for species differentiation, population distance studies, life-statistics and behavioral analysis (e.g. Hanihara 1967; Ossenberg 1969; Pilbrow 2003). The subtle morphology of teeth differs across species, but all primates follow the ancestral mammalian pattern with dentition expressing as four discrete classes: incisor, canine, premolar and molar (Swindler 1976). The molars are the focus of this study.

Background

Variation in dental morphology is classified as metric or nonmetric. Metric dental traits like tooth length, width or cusp area, express on a continuous quantitative scale and can often be easily measured. Nonmetric dental traits present as extra cusps, puckers, styles and wrinkles in dental morphology, the expression of which is frequently broken down into discrete categories for quantitative comparison (Berry and Berry 1967; Scott and Turner II 1997). Many metric and non-metric dental traits have been shown to have high heritability estimates (Baume and Crawford 1978; Cheverud and Buikstra 1982;

Corruccini and Shimada 2002). Because dental traits are often heritable and have a strong genetic basis, they can be used as evidence in species and population distance studies of humans and nonhuman primates (e.g. Guatelli-Steinberg and Irish 2005; Harris 2007; Johanson 1974).

In addition to variation in dental morphology across populations and species, variation in dental morphology exists within the dental arcade of a single individual (Grine 2005; Hlusko 2002b). Minor variation among duplicate units, like the molars, is referred to as 'metameric variation' (Butler 1939; Osborn 1978). Metameric variation has been described during the evaluation of dental traits (Garn, Lewis and Vicinus 1963). When morphological variations can be correlated with tooth position within the dental arcade, they can be described as expressing with ordered metameric variation. Many metric and nonmetric dental traits in primates have been shown to express with ordered metameric variation (e.g. Scott and Lockwood 2004). Of these, molar maxillary dental traits most frequently increase in expression advancing distally in the dental arcade, with the third molar having greatest expression (Braga et al. 2010; Grine et al. 2005; Smith et al. 2006).

Purpose of this Study

This thesis aims to analyze the expression of the interconulus, a nonmetric dental trait, in baboons and macaques. The interconulus expresses lingually on the maxillary molars of some Old World Monkeys, and descriptive studies have demonstrated that the third molar is most likely to exhibit presence of the trait (Batujeff 1896; Saheki 1966; Swindler 1976). The interconulus has been shown to express with ordered metameric variation in baboons, with greatest expression of the trait occurring on the third molar (Hlusko 2002a). Overall, there is limited data on the pattern of interconulus expression in baboons (Hlusko 2002a) and almost no data on the pattern of interconulus expression in macaques (Saheki 1966). This study will assess interconulus expression in a museum sample of baboons and macaques. Variation in expression across species and subspecies populations will also be considered.

Hypothesis. This thesis hypothesizes that the interconulus will express with ordered metameric variation in the maxillary dental arcade of the baboon and macaque samples. Based on previous assessments of metameric variation in the maxilla (Hlusko 2002a; Olejniczak, Martin and Ulhaas 2004), this thesis predicts that the expression of the interconulus will vary with increasing expression from M1 to M3. Due to the heritability of the interconulus (Hlusko and Mahaney 2003), this thesis also hypothesizes that expression of the trait will differ significantly across populations.

Methods. The interconulus will be analyzed using a 5-category expression model developed by Hlusko (2002a), and based on the qualitative dental trait criteria formalized by the Arizona State University Dental Standard (Scott and Turner II 1997). This study will assess data on interconulus expression in 42 baboons and 136 macaques from the

Museum of Vertebrate Zoology (MVZ), the American Museum of Natural History (AMNH) and the National Museum of Natural History (NMNH). Analysis will be performed correlating sex with interconulus expression and correlating interconulus expression with tooth position using exact test statistics. General frequency statistics will be run to compare interconulus expression across species and subspecies populations of the baboon and macaque samples.

Limitations. While use of discrete category analysis is currently recognized as the best way to assess trait expression (e.g. Koh et al. 2010), there are limitations to the qualitative assignment of trait expression to discrete categories. The imposition of discrete categories on nonmetric traits results in the loss of data (Nichol 1989; Scott and Turner II 1997). Qualitative application of categories is based on subjective researcher interpretation, and human error and discrepancy in the technique is inevitable. Small sample sizes and the application of a baboon trait model to a macaque sample will also limit this study. Additionally, the interconulus trait has only been shown to express in a few species of *Cercopithecidae*, and therefore analysis of interconulus expression in *Cercopithecidae* cannot be directly compared to metameric variation in the dentition of other primates. Identifying variation in patterns of interconulus expression can only be theorized to have developmental significance until heritability of the pattern is determined.

Significance of this Study

Metameric variation has been specifically noted in dental studies examining both metric and nonmetric traits, including the interconulus (Harris 2007; Hlusko 2002a; Braga et al. 2010; Skinner et al. 2010). Ordered metameric variation in the dentition is currently considered a likely origin for new cusp morphologies in the evolutionary record (e.g. Salazar-Ciudad and Jernvall 2002). Metameric variation as a developmental system allows for the accumulation and expression of minor variation in species, populations and individuals, and is found in numerous parts of the metazoan body plan, from body segments, to sets of appendages, to the vertebral column (Stock 2001; Townsend et. al 2009; Wagner 1996). Even genotypic elements, such as nucleotides and amino acids, have been described as expressing with metameric variation (Donoghue 2002; Weiss 1990). This project aims to characterize the metameric variation seen in Old World Monkey dentition, ultimately contributing to a more general understanding of the role that metameric variation has played and continues to play in primate evolution.

LITERATURE REVIEW

The durability of teeth in the fossil record has led to an increasing focus on dentition in biology and anthropology. The diversity of dental features, both metric and nonmetric, has resulted in studies ranging from individual life stories, including diet, age and sex, to evolutionary histories. However, many of the traits specific to our more distant primate relatives have not been studied in detail. This study assesses the expression of the interconulus in a sample of *Papio* and *Macaca*. Baboons and macaques belong to the tribe Papionini of the subfamily Cercopithecinae, one of two subfamilies in the family Cercopithecidae; Cercopithecidae encapsulates all Old World Monkeys. Cercopithecinae have a wide range of distribution from North Africa through Japan, and are comprised of both arboreal and terrestrial species. Baboons and macaques are omnivorous primates with a primarily vegetarian diet, living in large population groups (e.g. Delson 1975; Swindler 1976).

Baboons and macaques are thought to have diverged from one another eight to 10 million years ago, and are closely related (e.g. Caccone and Powell 1989). Both species have been shown to demonstrate expression of the interconulus, the dental trait assessed in this study (Eck 1977; Hlusko 2002a; Saheki 1966). Baboons and macaques are also used extensively in biomedical research due to their close genetic relationship with humans. Morphological, behavioral and genetic qualities make baboons and macaques comparable to humans in a scientifically significant way, and research drawn from baboon and macaque models can frequently be applied to humans as well as other Old World Monkey genera (e.g. Hayes, Freedman and Oxnard 1990; Jolly 1993).

Tooth Development

Primates follow the ancestral mammalian pattern of heterodonty, with dentition expressing in four discrete classes: incisor, canine, premolar and molar. This is significantly different from most fish, reptiles, and amphibians whose dentition consists of a singular shape with teeth constantly being replaced throughout the lifetime (e.g. Butler 1956). The variation that occurs within the mammalian heterodonty is the basis for much of the phylogenetic and evolutionary analysis of fossil dentition. The numbers and morphology of teeth within each tooth class vary by species (e.g. Line 2001). Non-essential dental traits (traits not necessary for survival), such as the interconulus, often express with a level of variation that differs at the taxonomic level and are crucial for analysis of closely related mammalian species. Understanding the genetic mechanisms that result in minor variations in form can shed light on the accumulation of changes in the evolutionary history of mammalian dentition (e.g. Weiss, Stock and Zhao 1998; Rizk et al. 2009).

Tooth development is comprised of several stages. These are most commonly divided into the bud stage, development of the cap, development of the bell, and maturation. Hard tissues are formed during the maturation stage with the development of the enamel crown (e.g. Catón and Tucker 2009; Gleiser and Hunt 1955). There have been studies on the development of teeth going back well over 100 years. Understanding the more precise model of development throughout the early stages of an individual's life has been largely a product of advancing technologies. Swindler and Meekins (1991) used mixed-longitudinal lateral head radiographs to track the dental development of 20 unrelated *Papio cynocephalus* who were born and raised at the Regional Primate Research Field Station in Washington State. The baboons were measured and x-rayed under anesthesia approximately every 3 months after birth for a period of 3 years. After the 3 years, the baboons were x-rayed twice a year for a period of an additional 4 years. Swindler and Meekins recorded the time of first observation of four specific stages of tooth development including initial calcification, crown completion, root formation and apical closure. They found that in baboons, the first permanent molar begins calcification before birth, common in most primates, and completes development before the other teeth at approximately 2.4 years of age.

Overall, Swindler and Meekins demonstrated that Old World Monkeys and humans pass through similar stages of tooth development. Although their study used mandibular teeth, maxillary and mandibular teeth are considered to have comparable rates of development (e.g. Demirjian, Goldstein and Tanner 1973). These developmental stages can be directly related to chronologic age in species, thereby providing a valuable estimation of age in unknown individuals. Some differences in the sequence of tooth formation can be identified between primate species, but this study notes that baboons, macaques and humans all go through similar stages of tooth development.

Cusp Development. The cusp pattern in primates is thought to have evolved from a more ancient trigonid pattern. Old world monkeys like baboons and macaques have a bundont molar pattern with the molars of the maxilla expressing four cusps: the metacone, paracone, protocone and hypocone (Simpson 1936). The protocone and hypocone are the lingual cusps, and the paracone and metacone are oriented on the bucchal side of the mouth. The protocone and paracone are mesial cusps, presenting closest to the front of the mouth (e.g. Swindler 1976). Cusp development takes place with the final calcification of the crown. Since cusps are essential eating tools that form the boundary between teeth and the rest of the mouth, cusp topography can reveal crucial information about their owner. Genetic traits appearing as accessory cusps, cingular remnants and calcified lumps on the teeth can also provide information about the individual, the population and the species (Butler 1956; Corruccini 1974; Johanson 1974; Martinon-Torres et al. 2007). The interconulus is expressed as an accessory cusp between the protocone and hypocone of the maxillary molars (Saheki 1966).

The teeth express as metameres, or as a series of common form, both within the dental arcade and as cusps on the individual teeth. In this way, cusps can be described as units, a stipulation supported by the fact they develop in an order similar to their phylogenetic relatedness (e.g. Hershkovitz 1971; Kraus 1959). In order to develop a more exact model of molar cusp formation and it's variation within the mouth, Smith et al. (2007) studied cusp development in several collections of wildborn chimpanzees. They prepared histological cross-sections for 272 cusps, on 135 molars from 175 individuals, with the individuals ranging in developmental age from unerupted first molars to adults with heavy wear on the third molars. By measuring and calculating the distribution of lines of long-term enamel deposition, or Retzius lines, the study was able to calculate a daily enamel secretion for the sample. They found that daily secretion rate varies based on the part of the cusp, as well as across cusp and molar types. Overall, the study reports that daily enamel secretion is greater in the outer cuspal enamel than inner cuspal enamel. They also note that cusp initiation and completion times vary across cusps, although the mandibular cuspal development seems to be more consistent. The variation in developmental times between cusps, teeth and across the jaws shown in this study suggests that these factors should be considered when analyzing small teeth samples of primates, both extinct and extant.

In general, outer cusp morphology is considered to be a reflection of the underlying enamel core. Recent studies have shown that dental traits like the interconulus are often expressed in the outer enamel surface (OES) as a reflection of the underlying enamel-dentine junction (EDJ). The structure of these traits is therefore dependent on the formation and expression of both the EDJ and the OES (Olejniczak et al. 2007). The EDJ has been used extensively in studies pertaining to cusp morphology and development, and most research concludes that the OES is largely a reflection of the shape of the EDJ with the enamel cap representing only a small amount of variation in the OES morphology. (e.g. Kraus 1952; Korenhof 1960; Skinner 2008).

Kraus (1952) demonstrated that the OES follows the morphology of the EDJ closely by measuring 42 unerupted mandibular first molars that were extracted from the mandibles of skeletons excavated from Arizona sites dating to approximately 1200 C.E. The teeth were measured, and casts were made, before the OES was removed using a warm-HCl bath. The dentine topography was measured and compared to the enamel topography. While Kraus noted a general correspondence of dental traits between the enamel and dentine surfaces, he was unable to provide a standardized metrical model for differences in size. Overall, Kraus concluded that the EDJ provides a base template for the development of non-essential dental traits, with developmental and environmental factors resulting in OES morphological variation, an observation that has been confirmed by other studies (e.g. Olejniczak, Martin and Ulhaas 2004).

To investigate whether or not EDJ measurements can be used to reliably differentiate taxonomic groups, Olejniczak, Martin and Ulhaas (2004) analyzed cross-sections of maxillary molars. Using molars from three extant anthropoid superfamilies, including *Ceboidae, Cercopithecoidea* and *Hominoidae*, as well as a few samples from fossil cattarhine taxa, a total of 107 sectioned, maxillary molars were assessed. Nine linear distances were measured using landmarks in the EDJ. They conclude that dentine shape can significantly distinguish taxa. However, there does not appear to be a predictive relationship between the EDJ and the OES.

Olejniczak, Martin and Ulhaas note the interconulus specifically, suggesting that the lingual trait is a dentine horn that appears in the OES morphology as a result of enamel folding over the underlying morphology of the EDJ. They report that the dentine of *Papio* maxillary molars expresses a dentine cingulum along the lingual edge. This dentine cingulum is not present in the *Cercopithecus* sample analyzed in the study. Olejniczak, Martin and Ulhaas suggest that the interconulus visible in *Papio* individuals may be the result of a folding of the enamel surface over the dentine cingulum. The study proposes that *Papio* maintain the ancestral lingual cingulum common to the primate super-family. In this case, the interconulus represents a derived folding of the OES. The interconulus has not been described in the *Cercopithecus* species, which is consistent with a lack of underlying cingulum in the maxillary, molar dentine (FIG. I). This correlation between the interconulus OES and EDJ in *Papio* specimens suggests that the trait is highly heritable with limited environmental input during enamel formation. This is consistent with studies that have demonstrated the high heritability of dental traits (e.g. Berry 1976; Biggerstaff 1973; Scott and Turner II 1997), as well as the significant heritability quotient specifically assigned to the interconulus trait (Hlusko 2002a; Hlusko and Mahaney 2003).

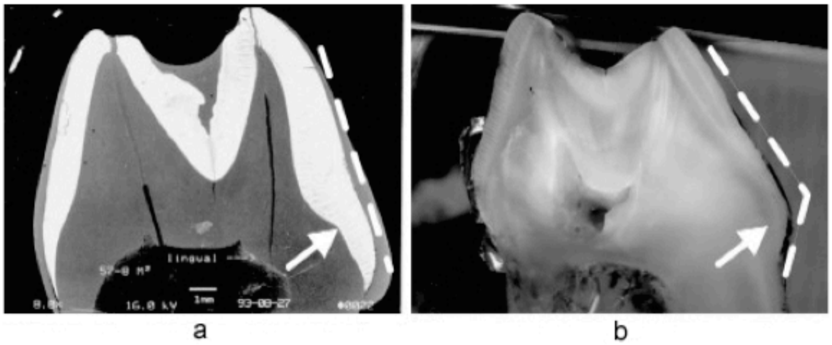

FIG. 1. White arrows point to the “dentine cingulum” expressed in *Papio* and *Cercopithecus*. In the molar of *Papio* (left), the enamel does not follow the same path as the EDJ. From Olejniczak, Martin and Ulhaas (2004).

Tooth Genetics. Over the last several decades, an increasing number of genes and signaling pathways have been associated with mammalian dentition. BMP, FGF, SHH and WNT represent the key pathways for the dentition and are highly conserved throughout development (Amendt 2005, Bei 2009, Chen et al. 2009). Studies have shown that disruption of these pathways, or their inhibitors, can lead to abnormalities in the development of the dentition. Transcription factors have also been shown to be crucial for normal dental development suggesting that a complex system of interconnecting gene factors is responsible for the mammalian dentition (Brook 2009; Pereira et al. 2006; Rizk et al. 2009; FIG. 2).

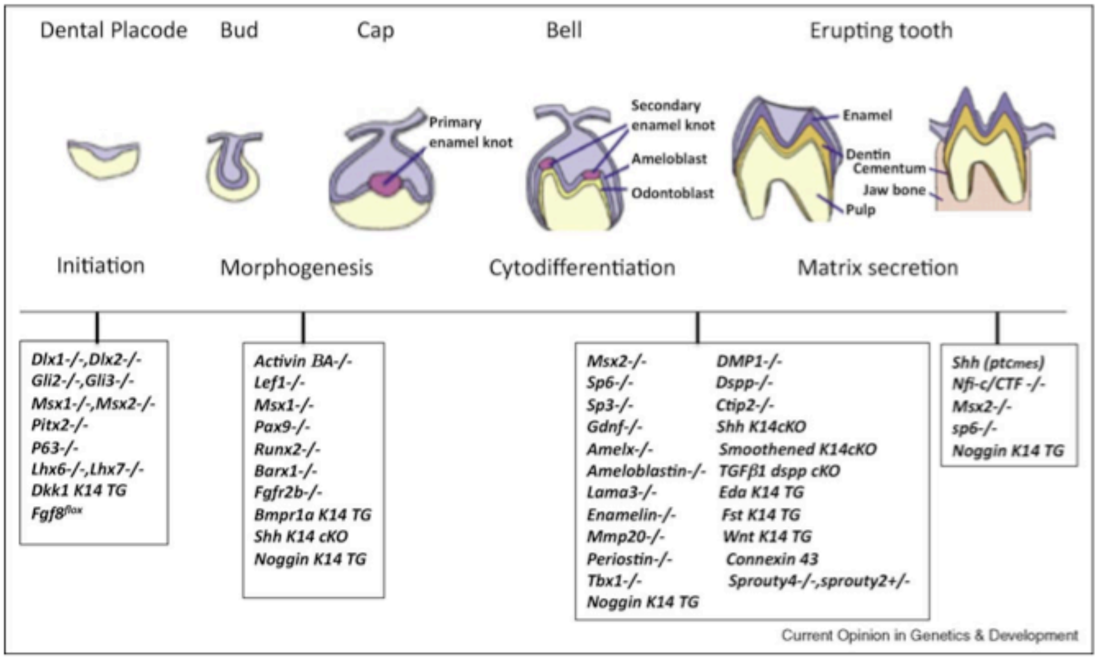

FIG. 2. Known genes associated with dental development in mammals. From Bei (2009).

The primary and secondary enamel knots play a key role in development of dental crowns in mammals. The primary enamel knot forms just before the cap stage, and the secondary knot forms during the bell stage of development. These knots have been associated with several bone morphogenetic proteins (BMPs) and growth factors (e.g. Dassule et al. 2000; Loes et al. 2001). Kassai et al. (2005) examined the effects of interrupting the ectodin pathway, a protein inhibitor of BMPs secreted by the enamel knots. They showed that ectodin deficiency in developing mice results in enlarged enamel knots, excess teeth and altered cusp patterns. The study exposed ectodin-deficient mice molars, in culture, to excess BMP in order to assess whether BMP and ectodin pathways are directly related. While the control group showed no change in development pace, ectodin-deficient molars with excess BMP showed increased growth rates. The study concludes that ectodin serves as a regulating pathway, and ectodin deficiency can result in unchecked growth of mammalian molars. This supports other research showing that BMPs can be directly associated with the expression of cusp development and cingular remnants through the examination of pathway disruption (Bei 2009; Jernvall, Keranen and Thesleff 2000, Thesleff and Sharpe 1997).

Heritability of Dental Traits. Dental traits like cingular remnants vary across species and have a strong genetic basis (Baume and Crawford 1978; Cheverud and Buikstra 1982; Corruccini and Shimada 2002). For this reason, cingular remnants have been used extensively in inferring biological relationships among modern humans, nonhuman primates and fossil hominins (e.g. Guatelli-Steinberg and Irish 2005; Pilbrow 2003; Ullinger et al. 2005; Wood and Abbott 1983). The heritability of dental traits has been the focus of many research projects over the last century. The general consensus is that most dental traits display a high level of heritability and genetic control (e.g. Berry 1976; Townsend and Martin 1992)

Berry's (1976) study provided evidence that dental traits can be used to differentiate species populations, including humans. Examining 31 traits on dental casts of six European populations, Berry calculated distance statistics between the variables that correlated with genetic distance between the samples. He also noted that nonmetric traits, such as extra cusps, tended to occur together within the dentition. As Berry argues, the correlation between dental traits in the arcade suggests that thorough description needs to occur before the traits can be used to differentiate anthropological samples.

Dental traits have been used in an effort to differentiate even closely related human populations. Corruccini and Shimada (2002) examined 23 nonmetric dental characteristics in 29 individuals at an internment site in Huaca Loro, Peru. Using multivariate analyses, Corruccini and Shimada were able to demonstrate a non-random grouping of dental characteristics that correlated with separate burial areas at the site. According to Corruccini and Shimada, these dental analyses support the theory of a highly planned and segregated elite cemetery.

In an effort to measure the amount of environmental input affecting the development of nonmetric traits, Townsend and Martin (1992) assessed the expression of the Carabelli's trait on 122 pairs of monozygous (MZ) and 102 pairs of dizygous (DZ) twins ranging from ages 10 to 46. Both the frequency of occurrence and degree of expression of the Carabelli's trait were examined in the sample. An eight-grade scale was applied to the expression of the Carabelli's trait in the twins. Using a statistical model of fit designed for the genetics of the teeth, Townsend and Martin report a heritability of 90% for the Carabelli's Cusp. Due to studies like these, the heritability of many dental traits has been broadly accepted (e.g. Harris 2007; Nichol 1989; Scott and Turner 1997).

Primate Expression of Dental Traits. Primates have been shown to express a variety of dental traits, both metric and nometric. There is substantial evidence to suggest that many dental traits have high heritability. Baume and Lapin (1983) assessed the impact of inbreeding on tooth size and shape using a sample of baboons. They compared an inbred group of 91 baboons and an outbred group of 420 baboons using casts taken at the Institute of Experimental Pathology and Therapy in the former USSR. The length and breadth of each tooth, as well as the presence frequency of eight nonmetric traits, was recorded. Baume and Lapin demonstrated that inbreeding has an apparent effect on tooth size in baboon populations, but has no apparent effect on tooth shape as defined by nonmetric dental traits. The tooth area of inbred individuals was significantly larger than the tooth area in outbred individuals. However, no corresponding difference in frequency of trait presence in the baboon samples was reported. According to Baume and Lapin, there might be some evolutionary function associated with tooth morphology and nonmetric trait presence that can account for conservation of the traits despite inbreeding.

Analysis of the diverse range of these dental traits suggests that unique patterns of trait expression can be associated with inter- and intra-populational variation (e.g. Ossenberg 1969; Scott and Turner II 1997). Pilbrow (2006) demonstrated that it is possible to make species and subspecies differentiations using statistical analysis of incisor trait frequency by assessing the morphology of lingual incisor traits on a sample of 229 gorillas, 142 orangutans and 314 gibbons. He noted unique incisor morphologies that differed in expression and frequency across primate taxa, However, the range of dental traits in primate species, and the variation in expression, requires that these morphologies be thoroughly documented before being used to assess extant or fossil relationships.

Like most morphologies, dental traits in primates are likely to be affected by both developmental and environmental factors. Even highly heritable traits can express variably as a result of phenotypic interactions. Teaford (1983) showed that a trait like the lingual notch has a range of expression, some of which can be attributed to wear and differences in diet. Teaford examined a molar trait in macaques and langurs, focusing on the lingual notch between the metaconid and the entoconid of the mandibular M2. Taking three angular and two lingual measurements from n=56 *Macaca* and *Presbytis*, Teaford found differences in the angle and length of the lingual notch in the three species examined. Occlusal traits such as cusp height and angle have significant function and more likely to be related to diet patterns. This function also suggests that they are likely to be highly heritable (e.g. Berry 1976).

Nonmetric Traits

Nonmetric traits differ from metric traits in that they have a finite range of expression that can frequently be broken down into distinct categories for analysis. Nonmetric traits are either present or absent, and presence of the trait results in a range of expression types (Berry and Berry 1967; Scott and Turner II 1997). In the case of teeth, addtitive genetic effects must exceed the trait threshold liability for the trait to express.

Below that level of liability, the trait is absent, and above it, the trait expresses (Grüneberg 1952).

Recognized at the turn of the century (e.g. Batujeff 1895), the study of nonmetric traits gained momentum in the 1950's and 60's with research expanding into genetic studies of expression. Most notably, Grüneberg (1952) developed the theory of quasi-continuous traits based on genetic crossbreeding studies of mice. Grüneberg noted skeletal variations that were both heriable and impacted by environmental factors. The phrase 'quasi-continuous' reflects the process of development for these traits, including: an underlying continuity created by of a suite of acting genes and the discontinuity created by differences in developmental environments resulting in varying phenotypes.

Nonmetric traits often express as threshold traits, with greater expression resulting in additional cusplets, wrinkles or folds. This threshold variation lends itself to the discrete categorical patterning of many nonmetric traits, allowing for the conversion of the trait into a quantitatively assessable, quasi-continuous element (e.g. Scott and Turner II 1997). Imposing discrete categories on a nonmetric element almost always results in the loss of data. However, the use of discrete categories is currently considered to be the most successful method for analysis of nonmetric traits (e.g. Townsend et al. 2009; Koh et al. 2010). Because variation is often continuous within the finite range of expression, the term quasi-continuous has been broadly accepted when describing nonmetric traits. Factors like developmental physiology and chemical environment play a role in the quasi-continuous expression of nonmetric traits, and input may differ within the dental arcade (Berry and Berry 1967; Grüneberg 1952; Harris and Bailet 1980; Scott and Turner II 1988).

Many nonmetric traits have been to found to have high heritability and a strong genetic basis (e.g. Berry and Berry 1967; Coppa et al. 1998). Nonmetric trait analysis has frequently been applied in population distance studies. Over the last century there has been some disagreement about the use of metric traits over nonmetric traits in morphological analyses because nonmetric traits often prove difficult to measure. However, the sheer number of nonmetric traits in the mammalian dentition suggests that they provide useful information and should be assessed. Cheverud and Buikstra (1982) compared the heritability of skeletal metric traits and nonmetric traits in a population of rhesus macaques by analyzing 134 offspring-parent pairs, of both sexes and a variety of ages, and scoring the pairs for 56 metric traits and 14 nonmetric traits. In their findings, Cheverud and Buikstra (1982) suggest that nonmetric traits in the skeleton are significantly more heritable than metric traits, a theory that has also been proposed in other studies (Coppa et al. 1998; Richtsmeier, Cheverud and Buikstra 1984). The heritability of nonmetric traits lends weight to the use of the interconulus in expression studies.

Nonmetric Dental Traits With a greater understanding of the heritability of dental traits, nonmetric traits have begun to play a more significant role in population distance studies and species differentiation (Berry and Berry 1967; Griffin 1993; Ossenberg 1969; Suwa, White and Howell 1996). Current theory suggests that nonmetric traits are determined by multiple suites of genes acting together to create the dental phenotype (e.g. Nieminen et al. 1998; Rizk et al. 2009). However, there is some suggestion that the additive genetic component may vary between teeth within a dental class. Analyzing the expression of the metaconule cusp in 1,217 Melanesians, Harris and Bailet (1980) demonstrated an additive genetic component of 65% for the maxillary first molar, but only 15% for the second molar. Other studies have also provided support for the theory that nonmetric trait expression varies within an individual dental class. It seems likely that heritability, and the amount of environmental input associated with the expression of nonmetric traits, varies by tooth in the dental arcade (Harris and Bailet 1980; Hlusko and Mahaney 2008).

Coppa et al. (1998) assessed biological similarities and differences among 13 populations in central-southern Italy by analyzing a total of 8,836 teeth, belonging to 1,114 individuals from both sides of the Apennine mountain range. All teeth were bioarchaeological samples dating from the first millennium B.C.E. Scoring 59 nonmetric dental traits, the researchers performed a principle components analysis to assess the relationship between the populations based on both metric and nonmetric traits. Despite the presence of the mountain range, dental trait distribution in the populations seemed to cluster more based on time than geography, suggesting that the mountains were not a significant boundary. Archaeological evidence is in concordance with the dental trait distribution that suggests contact across the Apennine Mountain range. In this study, nonmetric data provided finer detail in sorting populations than metric variation, a factor the researchers attribute to the large number of nonmetric traits available for analysis in the dentition, and the high heritability of those traits. Using their findings, the study asserts that dental nonmetric data can be more useful for distinguishing populations than metric data.

Dental traits can also be used to distinguish extinct and extant species (e.g. Johanson 1974; Uchida 1996), fossil hominoids (e.g. Pilbrow 2006), and fossil hominins (Bailey and Lynch 2005; Guatelli- Steinberg and Irish 2005; Martinon-Torres et al. 2007). Studies have shown that certain species display unique patterns of discrete dental traits. Bailey's (2002) examination of 6 Neanderthal P4s and 125 modern human P4s demonstrated that Neanderthals exhibit a unique pattern of dental trait expression, with modern humans displaying simplified expression patterns when compared to Neanderthals. Due to the significant differences in trait expression, Bailey (2002) suggests that Neanderthals may have been evolving their own dental pattern. The ability to associate teeth with a species based on the pattern of dental trait expression would be uniquely helpful in analyzing fossil morphology, as well as play a role in understanding the genetic basis for dental patterning and cusp formation.

While many dental studies have focused on humans (Corruccini 1974; Hanihara, Ishida and Dodo 2003; Ullinger et al. 2005), nonhuman primates have come to play an increasingly important role in understanding variation in vertebrate dentition (e.g. Butler

1939; Grine et al. 2005) Recognizing non-human primates as a useful model for understanding human evolution and variation, many morphological assessments have been performed on the dentition of monkeys and apes (e.g. Swindler 1976). Most research on nonmetric traits in nonhuman primate dentition has been focused on the distribution of trait presence (e.g. Cheverud and Buikstra 1982; Saheki 1966). However, as Griffin (1993) notes, the range of expression in quasi-continuous traits must be evaluated as a condition of presence/absence studies if intra-populational studies are to be conducted. It was not until more recently that researchers have begun to examine the range of nonmetric trait expression within an individual dental arcade (e.g. Hlusko 2002a).

Metameric Variation in the Dentition

This project aims to build on Hlusko's (2002a) study that found ordered metameric variation in the expression of the interconulus in a population of baboons. The metameric variation demonstrated by Hlusko recapitulates a trend that has been observed with several traits in the dentition (Harris 2007; Braga et al. 2010; Skinner et al. 2010). Tooth size, enamel thickness and expression of dental traits like the Carabelli's cusp have been the focus of many of these metameric studies (e.g. Smith et al. 2006).

Noting that modern humans exhibit metameric variation in the form of increasing enamel thickness from M1 to M3, Grine et al. (2005) assessed the relative enamel thickness in a sample of baboons. Baboons were chosen because they are known to display ordered metameric variation in molar tooth size, with the third molars being the largest. The study examined 59 permanent molars from 59 baboon individuals and found that the relative area of the enamel cap increased from M1 to M3 in the maxilla, but decreased in the mandible. No variation in enamel thickness was observed. The study reports that the lack of increasing enamel thickness in the baboon samples suggests that enamel thickness and molar size may be negatively correlated. They hypothesize that the distally decreasing molar size in humans can be correlated with an increase in enamel thickness, resulting in a more uniform overall molar size. Correlations in metameric variation expression lend support to the general hypothesis that dental traits are formed as the result of coordinating but distinct suites of genes (Nieminen et al. 1998; Rizk et al. 2009).

Metameric expression has been assessed for both metric and nonmetric dental traits (e.g. Harris 2007; Hlusko 2002b; Kraus 1959; Townsend and Martin 1992). The Carabelli's cusp in humans has been the target of significant research into dental metameric variation. Kondo and Townsend (2006) examined 308 standardized occlusal photographs from a population of Australians, all of European descent. They quantitatively assessed the cusp area of each molar cusp and examined the amount of variability present within the population. Overall, Kondo and Townsend report that the cusps that develop earlier had less variability in area. They conclude that the presence of Carabelli's cusp can be correlated with molar size area, with larger molars more likely to express the Carabelli's cusp. Among those molars expressing the Carabelli's cusp, larger area is associated with greater expression. The correlations between trait presence and molar area, as well as trait expression and molar area, have also been suggested in other scientific studies (Garn, Lewis and Vicinus 1963; Harris 2007; Scott and Lockwood 2004).

The EDJ of various primate species has been noted to express metameric morphological variability (e.g. Hlusko 2002b). Using micro-computed tomography and other virtual tools, Braga et al. (2010) analyzed morphological and metric features at the EDJ and the OES for a 2.5 million year old fossil hominin, two chimpanzee specimens and three extant humans. They noted a distinct pattern of metameric variation present in the mandible morphology of all of the examined specimens, with M2 showing greater morphological variability than M1. Despite small sample sizes, the study argues that metameric variation within the dentition of an individual, especially a modern human, is so great that it must be thoroughly assessed before comparisons between hominin taxa can be made.

Metameric Variation as a Developmental Mechanism. A growing focus on non-human dental traits has led to increasing interest in ordered metameric variation in the dentition. Current theories suggest that metameric variation is caused by a combination of field effect and cascade models, resulting in the greatest variation at the edge of the field (e.g. Townsend et al. 2009). In the case of the interconulus, the field of question refers to the molar tooth class. Metameric variation results from repeated activation of developmental pathways, with M3, the final molar to develop, exhibiting greatest variation (e.g. Skinner and Gunz 2010).

Morphogenetic fields have been studied over the last century as a response to increasing recognition of the patterned series of skeletal and dental elements in mammalian morphology. The idea of "ordered form" (Townsend 2009) has resulted in many theories on the genetic basis for development of patterned series. Focus on mammalian teeth as classes with distinct genetics has created great interest in the development of these complex, yet repetitive forms. Bateson (1894) was one of the first researchers to explore the extent of numerical variation in mammalian dentition. For Bateson, assessment of meristic series in the skeleton and dentition is invaluable for understanding developmental mechanisms and the process of species differentiation. His compilation of data demonstrates that the most variable teeth within any dental class are most often those that form the latest, and are therefore at the edge of the field of development for that class. Bateson demonstrated that the later forming teeth are most often subject to the greatest amount of morphological variation, an observation that has been acknowledged in many studies of mammals, including humans (e.g. Butler 1939, 1956; Townsend et al. 2009).

Butler (1939) expounded on the idea of patterned series in the dentition, arguing that repetition in developmental mechanisms gives rise to similar structures, with variation in morphology occurring as a result of position within the arcade. He also noted a range in the complexity of the morphology of mammalian molars, suggesting that certain elements have an expression tendency that correlates with position in the dental arcade. Butler refers to teeth as repeated organs, expressing across a "continuous morphogenetic field" (Butler 1939). These serial fields can shift along the arcade throughout evolutionary history, resulting in minor changes that can lead to the differentiation of dentition across phylogenies. The clone theory played a significant role in the understanding of repeated series in the dentition throughout the 20th century (Dahlberg 1951; Jernvall and Jung 2000; Weiss 1990, 1993).

Osborn (1978) applied an updated understanding of development to Butler's (1939) theory on fields of expression. According to Osborn, each tooth class is the result of the differentiation of clonal cells. Field gradients have traditionally been assumed to be solely the effect of variation in the developmental environment (e.g. Crick 1970). However, Osborn suggests that the variation in developmental environment ripples out from the stem progenitor, or clonal origin. Osborne's review generated substantial interest in the role of duplicated genes and homeobox elements in ondontogenesis (e.g. Weiss 1990, 1993; Townsend et al. 2009).

The cusps of the teeth form as part of a developmental cascade with enamel knots controlling the initiation and formation of the tooth crown. A tooth with multiple cusps responds to signals from multiple enamel knots, each one associated with a specific cusp. The primary enamel knot initiates the formation of subsequent knots, resulting in a cascade of development. The first cusps formed are the most evolutionary stable and the least variable in morphology (e.g. Jernvall 1995). Using data from a sample of carnivores, Polly (1998) showed that cusp variability is associated with timing of cusp formation in the developmental cascade. Polly suggests that this variability is a response to the changing biochemical environment of the developmental cascade. According to Polly, this developmental cascade allows for modifiable patterns of cusp morphology. Metameric variation in the dentition, created from a developmental cascade of enamel knots, represents the flexibility of dental change as an evolutionary response.

The cascade patterning model of dental development and differentiation is currently considered a valid model for understanding variation in primate dentition. To determine whether variation in Cusp 6 (C6) expression is consistent with a cascade patterning model of cusp development, Skinner and Gunz (2010) analyzed shape variation in the lower molars of 55 chimpanzees and bonobos. They found that both later developing cusps and larger molars have a higher frequency of C6. Both of these observations are consistent with previous studies of metameric variation and the expression of dental traits (e.g. Harris 2007, Kondo and Townsend 2006).

Current theory on dental classes, and the metameric variation that expresses within each class, suggests that developmental effects cascade out from a clonal origin and create ordered metameric variation for some dental traits. The greatest variation in expression occurs at the edge of the field, or on the third molar, and is frequently associated with non-essential traits, traits not necessary for survival (e.g. Salazar-Ciudad and Jernvall 2002; Tummers and Thesleff 2009). Small changes in the biochemical environment and presence activating substrates can initiate a chain of effects resulting in morphological change in the teeth (Grine et al. 2005; Koh et al. 2010). As the enamel buds form, reactivation of the developmental pathway causes a chemical environment to cascade along the molar row, resulting in ordered metameric variation in the expression of dental traits (e.g. Jernvall and Salazar-Ciudad 2007).

The interconulus is a dental trait that has been shown to express with ordered metameric variation in the dental arcade (Hlusko 2002a). This thesis assumes that the interconulus phenotype is the result of the cascade model of development. Based on that assumption, this study expects to find ordered metameric variation in the expression of the interconulus. Tooth size and development ranking order tend to increase distally along the tooth row in baboons and macaques. It can be hypothesized that interconulus expression will also increase distally along the molar tooth class.

The Interconulus

The interconulus is a dental trait that expresses lingually on the maxillary molars. The expression of the interconulus ranges from a pit groove to a pronounced cingulum between the protocone and hypocone (Fig. 3). Cingular remnants, or accessory cusps like the interconulus, are traits commonly found in the dentition of primate species (e.g. Scott and Turner II 1997). These cuspules are likely derived from the reduction of more ancestral mammalian morphology (e.g. Delson and Andrews 1975; James 1960). The interconulus is an example of a cingular remnant that expresses as a nonmetric trait in the dentition of some primate species.

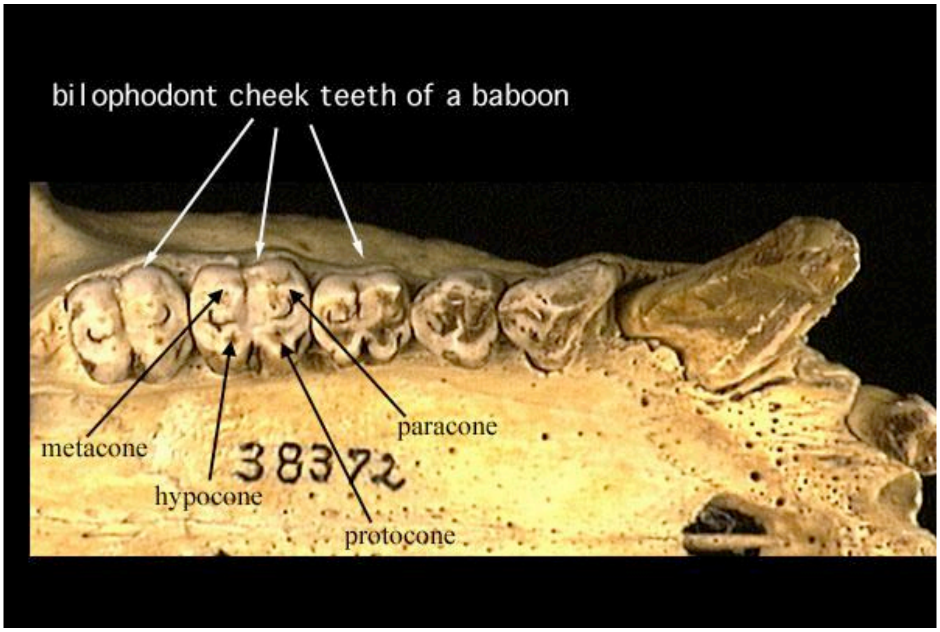

Fig. 3. Maxillary molar morphology of a baboon. Note the interconulus trait present between the hypocone and protocone. From the University of Michigan Museum of Zoology website.

The interconulus was noted in descriptive analysis as early as the 19th century (Batujeff 1896), and has gone by many different names including lingual cingulum, tuberculum cingulum, median lingual accessory groove cusp, and groove cusp. Current research suggests that the interconulus is a remnant trait derived from the ancestral form of a pronounced lingual shelf that characterizes primitive mammalian morphology (e.g. Hlusko 2002; Saheki 1966). The shelf has been reduced in many of the higher primates including *Papio* and *Macaca*. The interconulus is likely a derivative cuspule expressing in some members of *Cercopithicodae*. The ancestral lingual shelf is still expressed in many extant primates including *Anthropoidae* (e.g. Swindler 1976).

With the strong genetic component reported for most dental traits, expression of the interconulus is likely associated with one of the gene pathways that codes for development of the EDJ and OES. This is consistent with studies that have shown the underlying reflection of the interconulus in the EDJ (Olejniczak, Martin and Ulhaas 2004). While the interruption of major genetic pathways can result in significant alterations in tooth development, it has been suggested that disruption in non-essential pathways can lead to minor modifications in tooth morphology. These minor modifications can accumulate without altering function of the tooth, and are potentially at the root of dental differentiation (e.g. Salazar-Ciudad and Jernvall 2002; Tummers and Thesleff 2009). The interconulus is a non-essential trait hypothesized to be formed as a product of non-essential gene pathways, or as a byproduct of variation in essential gene pathways (Hlusko and Mahaney 2003, 2007).

Expression of the Interconulus in Primate Species. The interconulus has only been described in species *Macaca* and *Papio* of the Cercopithecidae family (de Terra 1905; Hlusko 2002a; Hlusko and Mahaney 2003; Swindler 1976), although there has been some suggestion that other *Papionini*, such as *Theropithecus* and *Mandrillus* may also express the interconulus trait (Batujeff 1895; Eck 1977). The earliest studies only describe the presence of the interconulus while cataloguing variable cusp types in mammals. (Batujeff (1895) noted the interconulus as a lingual groove cusp while describing Carabelli's cusp in humans and non-human primates. De Terra (1905) also pointed out this groove cusp, citing Batujeff's drawing of a mandrill molar. It was not until Saheki (1966) that a more descriptive analysis of the interconulus trait was performed. Saheki assessed the frequency of interconulus presence in a sample of *Macaca iris, Macaca fuscata yakui* and *Macaca fuscata fuscata*. The presence of the interconulus trait in his sample showed an ordered metameric distribution of trait presence with the M3's exhibiting presence of the trait most frequently (Table 1).

Table 1. Frequency of interconulus expression in three species of macaque. From Saheki (1966).

SPECIES		M1	M2	M3
M. iris	N	204	206	145
	n	11	37	32
	%	5.4	18.0	22.1
M.f. yakui	N	52	46	26
	n	2	3	5
	%	3.9	6.5	19.2
M.f. fuscata	N	31	31	21
	n	5	4	10
	%	16.1	45.2	47.6

Using a sample of *M. mulatta, M. fascicularis, M. nemestrina,* and *M. niger*, Swindler (1976) also assessed the frequency of interconulus presence. He found that the highest incidence of the interconulus occurred in *M. nemestrina* (38%). While several studies have focused on a descriptive count of how many individuals within a species express the interconulus (Saheki, 1966; Swindler 1976), there are only a few studies that have investigated the degree of interconulus expression within the dental arcade (Hlusko 2002a).

Metameric Variation in the Expression of the Interconulus. Metameric variation has been described in the expression of many dental traits (e.g. Braga et al. 2010; Hlusko 2002b; Smith et al. 2008). However, Hlusko's (2002a) study was the first to formally characterize metameric variation in the expression of the interconulus. Hlusko (2002a) qualitatively scored expression of the interconulus in 329 baboons from dental casts made at the Southwest Foundation for Biomedical Research in Texas. Hlusko noted that approximately 40% of the sample exhibited expression of the interconulus, with degree of expression increasing distally. Based on descriptive statistics, Hlusko concluded that interconulus expression increased from M1 to M3 in the pedigreed sample (Table 2). She used the expression patterns identified in the study to develop a formal typology for the characterization of interconulus expression in baboons. The Hlusko model for scoring the interconulus was used in this thesis to score the baboon and macaque samples.

Table 2. Mean interconulus expression scores in a sample of *Papio*. From Hlusko (2002a). L indicates 'left,' R indicates 'right.'

Molar Position	N	Mean Score	Std. Deviation
LM1	318	1.59	0.71
LM2	320	1.64	0.90
LM3	305	2.09	1.24
RM1	304	1.50	0.61
RM2	310	1.58	0.82
RM3	293	1.98	1.18

In a later study, Hlusko and Mahaney (2003) analyzed the expression of the interconulus and interconulid, cingular remnants on the maxilla and mandible, in a sample of 479 modern savannah baboons from the Southwest Foundation of Biomedical Research. Using the method of expression assessment previously devised by Hlusko (2002a), their statistics demonstrated a heritability estimate of between 0.33 and 0.73 for the interconulus trait. They also found that sex and age had negligible effects on interconulus expression, although molar length was positively correlated with interconulus expression on second molars.

Due to the genetic relatedness of the baboons in the population, Hlusko and Mahaney were only able to run descriptive statistics on interconulus frequencies. From these descriptive statistics, they found that the interconulus was present in 44% of the population. The mean expression scores for the interconulus (ranging from 1 to 5, with 1 being the lowest score) were M1=1.55, M2=1.6 and M3=2.05. Hlusko and Mahaney report a correlation of approximately 1.0 between interconulus expression scores on the left and right sides of the dental arcade and theorize that the same genes code for the interconulus dental trait across the maxilla. Correlations between trait expression and molar tooth number within the tooth row ranged from 0.73 to 1.0 suggesting that the degree of expression of the trait can be specifically correlated with tooth position. Hlusko and Mahaney hypothesize that ordered metameric variation in the expression of the interconulus across the maxilla is the result of additive and overlapping genetic effects. However, they note that this pleiotropy appears to be confined to a single arch. In their quantitative assessment, the difference between expression of the interconulus and interconulid, a mandibular trait, suggests that inter-arch expression of the traits is the result of overlapping but distinct sets of genes.

How This Thesis Contributes to the Body Of Knowledge

The interconulus, present only in the maxillary molars of some primates, is a nonmetric trait that most likely represents the remnants of the ancestral cusp form (e.g. Hlusko and Mahaney 2003; Saheki 1966). If the interconulus has evolved from the ancestral form, it can be proposed that it is a highly heritable nonmetric trait, a theory that concurs with current research (e.g. Hlusko and Mahaney 2003). Building off of Hlusko's (2002a) study that found ordered metameric variation for the expression of the interconulus in a sample of baboons, this thesis hypothesizes that the interconulus will express with metameric variation, increasing distally across the molars, in this sample of *Papio* and *Macaca.*

The evolutionary modularity associated with tooth class in mammals has been the focus of considerable study over the last century. Research in developmental genetics has shown that patterned morphologies, such as the dental arch, are the result of complex interactions between genomic units (Butler 1939; Hlusko and Mahaney 2007; Stock 2001; Rizk et al. 2009). Patterned series, and metameric variation, are hypothesized to be the result of cascading field effects that may also be responsible for new variation in the arcade. Developmental and biochemical variation can lead to new cusps, shifting tooth classes and altered morphologies (Butler 1939, 1956; Osborn 1978; Jernvall, Keranen and Thesleff 2000). Tooth size, complexity and trait expression have all been correlated with ordered metameric variation in humans (Guatelli-Steinberg and Irish 2005; Harris 2007; Braga et al. 2010).

Metameric variation is a wide-ranging genetic and developmental mechanism associated with the recombination and expansion of phenotypic elements from limited genetic materials. Weiss (1990) argues that metameric variation can be described in genomic structures and biochemical elements, such as amino acids, as well as in anatomical morphologies, across mammalian and non-mammalian species. Understanding the relationship between the interconulus and metameric variation can give evolutionary perspective to the presence of minor variation between species. The genetic mechanisms that result in metameric variation allow for the accumulation of variation, one of the essential elements of evolution and natural selection. Characterizing the extent and variation of interconulus expression may help shed light on the developmental mechanisms associated with tooth differentiation, heterodonty in mammals and the accumulation of variation in the dentition (e.g Hlusko and Harpending 2004). Metameric variation is found in numerous parts of the metazoan body plan, from body segments, to sets of appendages, to the vertebral column. This project aims to typify the metameric variation seen in the Old World Monkey dentition, ultimately contributing to a more general understanding of the role that metameric variation has played and continues to play in primate evolution.

METHODS

The interconulus is a nonmetric dental trait that expresses between the protocone and the hypocone on the lingual side of the maxillary molars of some primates. For this thesis, the expression of the interconulus was assessed in two genera of Old World Monkey. The baboons sampled represent one species comprised of three subspecies. The macaques sampled represent 10 distinct species. Data was sampled from collections of baboon and macaque maxilla at the Museum of Vertebrate Zoology, U.C. Berkeley (MVZ), the National Museum of Natural History (NMNH) and the American Museum of Natural History (AMNH). The data from the MVZ were collected by the author during the Summer of 2010. All data from the NMNH and AMNH were collected during the Summer of 2008 as part of an NSF funded project directed by L. Hlusko at U.C. Berkeley (NSF BCS-0616308).   The data sampled represents diverse individuals ranging in species, geographic origin and collection date. This diversity limits the possibility of genetic relatedness.

Species Sampled

Four subspecies of baboon and 10 species of macaque were included in this study. According to Jolly's (1993) taxonomy, *Papio* is recognized as a single species with several subspecies populations. A maximum of 36 baboons were used in this study; the subspecies sampled include *P. anubis, P. hamadrayas, P. papio,* and *P. ursinus* (Table 3). This study sampled 10 macaque species. The macaque sample was represented by *M. albobarbatus, M. fascicularis, M. maura, M. mordax, M. mulatta, M. nemestrina, M. nigra, M. radiata, M. sylvana,* and *M. villosa* (Table 4).

TABLE 3. Description of *Papio* subspecies represented in this study.

SUBSPECIES	Molar Position	N=	SUBSPECIES	Molar Position	N=
P. anubis	1	12	*P. papio*	1	1
	2	16		2	0
	3	15		3	0
P. hamadrayas	1	11	*P. ursinus*	1	13
	2	12		2	14
	3	11		3	14

TABLE 4. Description of *Macaca* species sampled in this study.

SPECIES	Molar Position	N=	SPECIES	Molar Position	N=	SPECIES	Molar Position	N=
M. albobarbatus	1	1	***M.** mulatta*	1	67	***M.** sylvana*	1	1
	2	1		2	67		2	1
	3	1		3	60		3	1
M. fascicularis	1	27	***M.** nemestrina*	1	3	***M.** villosa*	1	6
	2	21		2	3		2	7
	3	15		3	3		3	7
M. maura	1	1	***M.** nigra*	1	1	*Macaca* ***sp.***	1	4
	2	1		2	1		2	2
	3	1		3	1		3	2
M. mordax	1	24	***M.** radiata*	1	1			
	2	24		2	1			
	3	20		3	1			

Methods

A total of 42 baboons and 136 macaques were included in this study. The expression of the interconulus was assessed using a model developed by Hlusko (2002a). Hlusko's model is based on expression of the interconulus as either present or absent, with presence being characterized on a scale of 1 to 5. A score of 0 indicates that the trait is completely absent. On a scale of 1 to 5, 1 represents the least expression of the interconulus, and 5 represents maximum expression (FIG. 4).

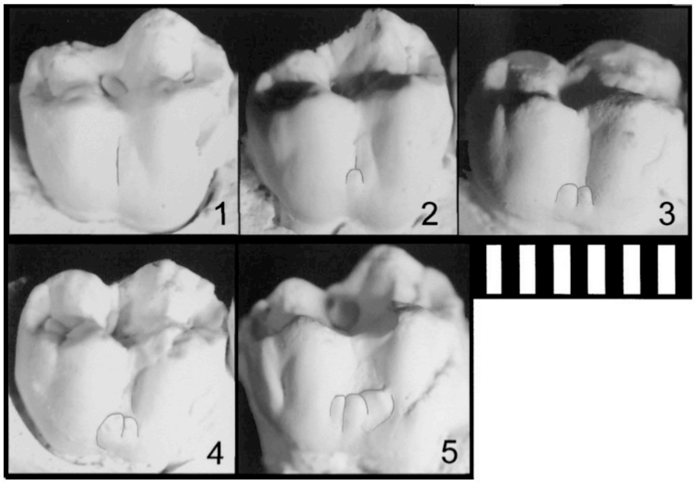

FIG. 4. Interconulus expression types. All the photographs were taken from the lingual side of right maxillary third molars from baboon individuals. The interconulus is highlighted with line drawings to emphasize the characteristics described in the text. Scale is in mm. Photograph taken from Hlusko (2002a).

According to Dr. Hlusko's (2002a) model, the expression scale can be defined as follows:

1 – A cuspule is not present. The area between the protocone and the hypocone is either smooth or characterized by a slight swelling.

2 – A small cuspule is present. The cuspule is separate from both cusps.

3 – A double cuspule is present close to but separate from both cusps.

4 – A large double cuspule is present. This cuspule may project beyond the most lingual points of the molar cusps.

5 – There are multiple cuspule that project lingually and extend towards both cusps.

As a nonmetric trait, imposing a discrete measurement system on expression limits the power of the data. By imposing a discrete system, and converting qualitative expression to quantitative categorization, some data from the nonmetric trait is lost (Scott and Turner II 1997). However, other methods of assessing the interconulus, such as volume, are tedious, time-consuming and not proven to be effective (Nichol 1989). Additionally, the range of expression between scores 1 and 2 is often accompanied by a lingual groove that would be difficult to quantify in volume. The use of discrete categories for assessment of nonmetric traits is a recognized technique that has been performed in many dental studies (e.g. Koh et al. 2010)

All assessments of the interconulus in this study were made by comparison to a high-quality cast created by Hlusko. The dental cast was made from an impression of baboon dentition at the Southwest Foundation for Biomedical Research. During Hlusko's (2002a) research, casts were made of 329 pedigreed baboon individuals while they were anesthetized. The model cast and photos (FIG. 3) represent the most standardized example of interconulus expression as assessed by Hlusko. The genetic heritability of dental traits, and the correlation between the developing EDJ and final cusp morphology, make dental casts a scientifically recognized way of assessing trait expression. Because working with ancient and living specimens can be difficult, dental casts have been used in many scientific studies (e.g. Berry and Berry, 1967; Scott and Turner II 1997).

No model for macaque expression of the interconulus currently exists. The model baboon cast was used to diagnose expression for both the baboons and the macaques. This study found more variability in macaque interconulus expression than described by the Hlusko scoring system. Macaque expression of the interconulus showed a great range of expression between the scores 1 and 2 of the Hlusko model. This variation was not as significant in the baboon samples and suggests that a macaque-specific model would be helpful in assessing the trait. Hopefully species-specific models will be developed as steps are made to understand interspecies distribution of traits like the interconulus,

The interconulus was assessed by comparing expression of the specimens to Hlusko's (2002a) model cast. The MVZ baboon and macaque samples were analyzed over a one-week period of research. Every baboon specimen was examined once, in the order of catalogue. After examining the baboon specimens, every macaque was examined once, in the order of catalogue. For this analysis, the maxilla of each specimen was removed from the box and physically examined. Each specimen was directly compared to the high-quality cast from Hlusko's (2002a) interconulus model. Data was recorded and the individual was returned to the case.

After a complete analysis of every baboon and macaque individual in the MVZ collection, a second analysis of interconulus expression for each individual was completed, in the same order as the first trial. The first and second trials were conducted over a period of four days, with approximately four hours of analysis being conducted each day, in a single block of time. After the first two trials, mismatching interconulus expression scores were noted in the data, and teeth exhibiting mismatched scores were analyzed a third time. In order to maintain whole numbers for expression scores, the mode of the three scores was used in the data analysis.

Statistical Analysis

Studies have shown that the left and right sides of the dental arcade exhibit a high degree of symmetry (Baume and Crawford 1980; Townsend et al. 1990). In this study, statistical analysis was performed on the data recorded from the left molars. In the cases where there was no data present for a left molar, but the data was present for the corresponding right molar, data from the right molar was used instead. This scenario presented itself n=8 times in the baboon sample and n=0 times in the macaque sample.

Scores were analyzed using the SPSS statistics program (v.16 and v.17). The frequency of each expression category (1-5) for each molar within both genera of primate was analyzed. Frequency analysis demonstrated that the data does not exhibit a normal distribution. Due to the lack of normal distribution, non-parametric statistics were used to assess variation in expression within the dental arcades of the two genera.

As part of a subsample study, specimens without an assigned sex were dismissed from the data. Unidentified species were also eliminated from the study. Finally, since the interconulus is a threshold trait, absence of the trait does not relate to ordered metameric variation in expression of the trait. Specimens were analyzed separately by tooth position. Specimens with an expression score of zero (trait absence or damaged tooth) had that tooth eliminated from the sample. After eliminating individuals, data was available from n=41 baboons and n=27 macaques in the MVZ collection. This small subsample was analyzed separately by sex. Previous studies have shown that nonmetric dental traits do not tend to differ in expression between the sexes, but exceptions have been noted (Garn, Kerewsky and Lewis 1966; Hanihara 2008; Townsend et al. 1990). The subsample analysis of sex was performed to affirm that male and female specimens could be pooled to increase strength of the statistics.

The Kruskal-Wallis (K-W) exact test was used to analyze expression of the interconulus by sex and by position for both baboons and macaques. The K-W exact test was chosen because it is a non-parametric test that allows comparison of variables with more than two categories and a small sample size (Field 2000). The independent samples K-W exact test was used to compare expression of the interconulus between male and female baboons as well as between male and female macaques. The terminology "XM1, XM2 and XM3" was used in this study, where 'X' abbreviates for 'maxillary,' 'M' abbreviates 'molar,' and the number represents tooth position. 'XM1' stands for maxillary molar 1 (Table 5).

Table 5. Description of interconulus expression, by sex, for *Papio and Macaca*.

		***Papio* frequencies**			***Macaca* frequencies**		
SEX		XM1	XM2	XM3	XM1	XM2	XM3
F	N=	12	16	17	9	7	5
	Mean	1.29	1.35	1.35	1.22	1.71	1.80
M	N=	20	25	22	18	13	9
	Mean	1.78	1.54	2.18	1.32	1.69	1.67

The K-W exact test found no statistical correlation between sex and expression of the trait for any of the molars of either the baboon or macaque sample. Finding no significant differences in interconulus scores between the sexes, male and female individuals were pooled to create larger sample sizes. Additionally, individuals of unknown sex from the

MVZ, the AMNH and the NMNH data were added to the sample pool. Molars with an expression score of 0, representing an absence of the interconulus or a damaged sample, were not included in this study. As a threshold trait, expression of the interconulus varies on a quasi-continuous scale. However, absence of the trait suggests that threshold of expression was not attained, and therefore absence cannot be included in the scaled assessment of presence expression (e.g. Scott and Turner II 1997). A maximum of 42 baboons and 136 macaques were included in the sample (Table 6).

Table 6. Number of *Papio* and *Macaca* individuals represented at each tooth position.

Papio		***Macaca***	
Molar Position	N=	Molar Position	N=
1	37	1	136
2	42	2	129
3	40	3	112

The independent samples Jonckheere-Terpstra (J-T) exact test was used to compare expression of the interconulus with position of the tooth within the dental arcade. The J-T exact test was chosen because it is used to test for an ordered pattern using the median of the categorized data (Field 2000). The J-T test is comparable to the K-W exact test in that it searches for differences in the medians of groups. However, the J-T test was used here because it attempts to see if the order in these differences is meaningful (Field, 2000). The J-T test was relevant in this situation because position was compared to expression in order to determine if ordered metameric variation in the expression of the interconulus exists in this sample.

The relationship between position and expression was tested in the sample. Ideally the tests would be run with ungrouped expression data. However, due to small sample sizes, a secondary analysis was performed where expression categories were grouped to lend greater weight to the statistical comparisons. In the baboon and macaque samples, expression scores of 3, 4 and 5 were combined, leaving three overall expression categories: 1, 2 and 3 (3-5). Combining the scores produces three categories of expression with more equalized sample sizes.

General frequency statistics were run for direct comparison with the numbers published by Hlusko (2002a). Hlusko had a much larger sample size (n=329) of baboons and concluded that ordered metameric variation was statistically present in the sample. In her study, Hlusko assessed metameric variation using descriptive statistics such as median and standard deviation. While the independent samples K-W and J-T tests were a better choice for this data due to non-standard distribution and small sample sizes, comparable descriptive statistics were also used here for direct comparison to Hlusko's results.

Finally, frequency statistics were run on the expression of the interconulus separately by species for macaques, and by subspecies for baboons. The populations were pooled in this study to generate larger sample sizes. However additional frequency statistics were run to identify whether it is possible for significant differences in the pattern of interconulus expression to exist at the species and subspecies level in the *Cercopithecidae* family. Means were generated for each tooth position to see if ordered metameric variation of expression was present in some populations and absent in others.

RESULTS

For this study, the expression of the interconulus trait was assessed in a sample of baboons and macaques. The interconulus expresses between the protocone and the hypocone of the maxillary molars. The expression of the interconulus was scored using a dental model developed by Hlusko (2002a). A maximum of 42 baboons and 136 macaques were included in the study. The macaque sample showed statistically significant ordered metameric variation in the expression of the interconulus. The baboon sample showed no ordered metameric variation. Some evidence presented for the existence of variable interconulus expression patterns between taxa.

Baboons

The expression of the interconulus was assessed on a sample of 42 baboons across four subspecies. Sexes were pooled, and 119 teeth were scored and included in the baboon dataset. The data were analyzed as 5 expression categories. Due to small sample size, some of the expression categories, especially high expression, had limited representation. In order to provide additional power to the statistics, a secondary analysis was performed with the 3 highest expression categories being condensed, forming a grouped dataset with only 3 categories of expression. Neither the ungrouped or grouped baboon samples showed statistically significant ordered metameric variation in the expression of the interconulus.

Ungrouped Baboon Sample. The ungrouped baboon sample failed to show ordered metameric variation in the interconulus expression of the maxillary molars. The mean expression scores for the ungrouped baboon sample were XM1=1.595, XM2=1.500, and XM3=1.800 (Table 7). The independent samples K-W exact test was used to analyze the distribution of interconulus expression score across tooth position for the ungrouped baboon sample. The K-W statistic was run with a significance level of $p<0.05$. The significance score for correlation between expression and position in the ungrouped sample of baboons was $p=0.815$. The high p score indicates that the Null hypothesis cannot be rejected: the distribution of expression scores is the same across tooth position (Table 8).

Table 7. Description of interconulus expression by molar position in *Papio* (score 1-5).

Molar Position	N	Minimum Score	Maximum Score	Mean Score	Std. Deviation
XM1	37	1.00	5.00	1.5946	.92675
XM2	42	1.00	5.00	1.5000	.86250
XM3	40	1.00	5.00	1.8000	1.26491

Table 8. Kruskal-Wallis test summary for comparison of interconulus expression and tooth position in *Papio* (score 1-5). Significance level is 0.05.

Null Hypothesis	Test	Significance	Decision
Distribution of Expression Scores is the same across categories of Position	Independent Samples Kruskal-Wallis Test	0.815	Retain Null
The medians of Expression Scores are the same across categories of Position	Independent Samples Median Test	0.906	Retain Null

Grouped Baboon Sample. When the data was grouped into 3 expression categories, the baboons still did not exhibit ordered metameric variation in expression of the interconulus. The mean expression scores for the grouped baboon sample were XM1=1.514, XM2=1.429, and XM3=1.575 (Table 9). A K-W exact test was run on the baboon sample with the grouped categories of expression (1-3). The significance level on the K-W test was $p<0.05$. The significance score for the comparison of expression and position of the grouped categories was $p=0.818$. Therefore the Null hypothesis cannot be rejected: the distribution of expression scores is the same across categories of position (Table 10).

Table 9. Description of interconulus by molar position in *Papio* (grouped, score 1-3).

Molar Position	N	Minimum Score	Maximum Score	Mean Score	Std. Deviation
XM1	37	1.00	3.00	1.5135	.69208
XM2	42	1.00	3.00	1.4286	.63025
XM3	40	1.00	3.00	1.5750	.81296

Table 10. Kruskal-Wallis test summary for comparison of interconulus expression and tooth position in *Papio* (grouped, score 1-3). Significance level is 0.05.

Null Hypothesis	Test	Significance	Decision
Distribution of Expression Scores (grouped) is the same across categories of Position	Independent Samples Kruskal-Wallis Test	0.818	Retain Null
The medians of Expression Scores (grouped) are the same across categories of Position	Independent Samples Median Test	0.906	Retain Null

Subspecies Variation in Papio Expression of the Interconulus. Examining the expression of the interconulus at the subspecies level suggests that the pattern of metameric expression may vary across populations. Mean expression scores for *P. anubis* were XM1=1.3333, XM2=1.5625, and XM3=1.8667, for a sample of n=16 individuals

(Table 11), and could reflect ordered metameric variation in the interconulus. None of the other *Papio* subspecies demonstrated ordered metameric variation in mean expression scores.

Table 11. Subspecies variation in mean expression of the interconulus for *Papio*, by molar position.

SPECIES	Molar Position	N	Minimum Score	Maximum Score	Mean Score	Std. Deviation
P. anubis	1	12	1.00	2.00	1.3333	.49237
	2	16	1.00	3.00	1.5625	.62915
	3	15	1.00	4.00	1.8667	1.18723
P. hamadrayas	1	11	1.00	5.00	2.2727	1.34840
	2	12	1.00	5.00	1.8333	1.33712
	3	11	1.00	5.00	2.6364	1.62928
P. papio	1	1	2.00	2.00	2.0000	.
P. ursinus	1	13	1.00	2.00	1.2308	.43853
	2	14	1.00	2.00	1.1429	.36314
	3	14	1.00	2.00	1.0714	.26726

Macaques

The expression of the interconulus was assessed on a maximum of 136 macaques across 10 species. Indeterminate macaque species were also included. A maximum of 377 teeth were scored and included in the macaque sample. The data was analyzed with 5 interconulus expression categories, according to the Hlusko (2002a) model. Some of the expression categories, especially high expression, had limited representation in the macaque dataset. Like the baboons, the macaques were analyzed with the 3 highest expression categories being condensed to form a grouped dataset as part of a subsample. The macaque specimens showed significant metameric variation in interconulus expression regardless of whether the data was grouped.

Ungrouped Macaque Sample. The ungrouped macaque sample demonstrated statistically significant metameric variation in the expression of the interconulus. When expression of the interconulus was assessed according to the five-category model established by Hlusko (2002a), the mean expression scores for macaques were XM1=1.120, XM2=1.4651, and XM3=1.7500 (Table 12). The independent samples J-T exact test was used to analyze the distribution of interconulus expression across tooth position. The J-T statistic was run with a significance level of $p<0.05$. The macaque individuals showed a significance of $p=0.00$, meaning that the Null hypothesis must be rejected: the distribution of interconulus scores varies by tooth position (Table 13).

Table 12. Description of interconulus expression by molar position in *Macaca* (score 1-5).

Molar Position	N	Minimum Score	Maximum Score	Mean Score	Std. Deviation
XM1	136	1.00	2.00	1.1250	.33194
XM2	129	1.00	4.00	1.4651	.75048
XM3	112	1.00	5.00	1.7500	1.02667

Table 13. Jonckheere-Terpstra test summary for comparison of interconulus expression with molar position in *Macaca* (score 1-5). Significance level is 0.05.

Null Hypothesis	Test	Significance	Decision
Distribution of Expression Scores is the same across categories of Position	Independent Samples Jonckheere-Terpstra Test for Ordered Alternatives	0.000	Reject Null

Grouped Macaque Sample. When the macaque data was grouped into three categories of expression, ordered metameric variation in expression of the interconulus was also evident. Using the J-T exact test produced mean expression scores of XM1=1.1250, XM2= 1.4419, and XM3=1.6339 (Table 14). Like with the ungrouped macaque sample, the independent samples J-T exact test was used to analyze the distribution of interconulus expression score across tooth position. The J-T statistic was run with a significance level of $p<0.05$. The macaque individuals with grouped expression scores also showed a significance of $p=0.00$, meaning that the Null hypothesis must be rejected: the distribution of interconulus scores varies by tooth position (Table 15).

Table 14. Description of interconulus expression by molar position in *Macaca* (grouped, score 1-3).

Molar Position	N	Minimum Score	Maximum Score	Mean Score	Std. Deviation
XM1	136	1.00	2.00	1.1250	.33194
XM2	129	1.00	3.00	1.4419	.68359
XM3	112	1.00	3.00	1.6339	.74731

Table 15. Jonckheere-Terpstra test summary for comparison of interconulus expression with molar position in *Macaca* (grouped, score 1-3). Significance level is 0.05.

Null Hypothesis	Test	Significance	Decision
Distribution of Expression Scores (grouped) is the same across categories of Position	Independent Samples Jonckheere-Terpstra Test for Ordered Alternatives	0.000	Reject Null

Species variation in Macaca expression of the interconulus. Ordered metameric variation was also present at the species level in the macaque sample, although not among all species examined. All *Macaca* species with at least seven representative individuals per tooth position demonstrated ordered metameric variation in expression of the interconulus with the exception of *M. fascicularis* (Table 16). *M. mordax, M. mulatta,* and *M. villosa* all demonstrated ordered metameric variation in the mean expression score of the interconulus. *M. mordax* exhibited mean expression scores of XM1=1.125, XM2=1.542, and XM3=1.750 with a subsample of n=24. The mean expression scores for *M. mulatta* were XM1=1.075, XM2=1.284, XM3=1.700 in a subsample of n=67 macaques. And *M. villosa* exhibited mean expression scores of XM1=1.000, XM2=1.429, and XM3=2.000 with a maximum of n=7 individuals. The *M. fascicularis* subsample did not demonstrate ordered metameric variation in the expression of the interconulus. The mean expression scores for *M. fascicularis* were XM1=1.185, XM2=1.905, and XM3=1.867 in a subsample of n=27.

Table 16. Species variation in mean expression scores of the interconulus for *Macaca*, by molar position.

SPECIES	Molar Position	N=	Minimum Score	Maximum Score	Mean Score	Std. Deviation
M. albobarbatus	1	1	2.00	2.00	2.0000	.
	2	1	2.00	2.00	2.0000	.
	3	1	2.00	2.00	2.0000	.
M. fascicularis	1	27	1.00	2.00	1.1852	.39585
	2	21	1.00	3.00	1.9048	.76842
	3	15	1.00	5.00	1.8667	1.06010
M. maura	1	1	2.00	2.00	2.0000	.
	2	1	2.00	2.00	2.0000	.
	3	1	2.00	2.00	2.0000	.
M. mordax	1	24	1.00	2.00	1.1250	.33783
	2	24	1.00	4.00	1.5417	.88363
	3	20	1.00	5.00	1.7500	1.25132
M. mulatta	1	67	1.00	2.00	1.0746	.26477
	2	67	1.00	4.00	1.2836	.69208
	3	60	1.00	5.00	1.7000	1.01347

SPECIES	Molar Position	N=	Minimum Score	Maximum Score	Mean Score	Std. Deviation
M. nemestrina	1	3	1.00	2.00	1.6667	.57735
	2	3	1.00	2.00	1.6667	.57735
	3	3	1.00	3.00	2.0000	1.00000
M. nigra	1	1	1.00	1.00	1.0000	.
	2	1	1.00	1.00	1.0000	.
	3	1	1.00	1.00	1.0000	.
M. radiata	1	1	1.00	1.00	1.0000	.
	2	1	1.00	1.00	1.0000	.
	3	1	1.00	1.00	1.0000	.
M. sylvana	1	1	1.00	1.00	1.0000	.
	2	1	1.00	1.00	1.0000	.
	3	1	1.00	1.00	1.0000	.
M. villosa	1	6	1.00	1.00	1.0000	.00000
	2	7	1.00	2.00	1.4286	.53452
	3	7	1.00	3.00	2.0000	1.00000
Macaca	1	4	1.00	1.00	1.0000	.00000
	2	2	2.00	2.00	2.0000	.00000
	3	2	2.00	2.00	2.0000	.00000

DISCUSSION

This thesis aimed to characterize the expression of the interconulus, a nonmetric dental trait, in two genera of Old World Monkey. The distribution of the interconulus trait was assessed in 42 baboons and 136 macaques by comparison to a dental cast model developed by Hlusko (2002a). The baboons and macaques were sampled from three museum collections and represented specimens of distinct geographical and temporal origins. The interconulus trait was assessed because dental traits play a critical role in our interpretation of relationships of both extinct and extant individuals. Studying the distribution of expression of the interconulus trait can contribute data to the current understanding of extant primate dentition and shed light on ordered metameric variation in the dental arcade.

Dental traits are recognized as highly heritable and represent a unique way of tracking populations and identifying information about individuals, both contemporary and ancient (e.g. Johanson 1974; Pilbrow 2003; Scott and Turner II 1997). The interconulus is a nonmetric dental trait with a range of expression that has been assessed in only a few studies (Hlusko 2002a; Saheki 1966; Swindler 1976). This study aimed to assess whether the interconulus expresses with ordered metameric variation, increasing distally along the molar row, in baboons and macaques.

The interconulus is a metameric trait, or a duplicate trait that occurs as part of a serial structure (Hlusko 2002a; Saheki 1966). The implications for metameric variation in the molars have been explored in many studies on mammalian dentition (Braga et al. 2010; Hlusko 2002a; Olejniczak, Martin and Ulhaas 2004; Smith et al. 2005). Current research suggests that metameric variation in the dental arcade develops as the result of environmental effects associated with the activation of developmental pathways, generating a field of variation across the tooth class (Koh et al. 2010; Rizk et al. 2009). As a trait that expresses in multiples, the interconulus offers insight into the gene processes and mechanisms that underlie development and metameric variation in the dental arcade.

Metameric Variation in the Expression of the Interconulus

This thesis hypothesized that the distribution of the interconulus exhibits ordered metameric variation in the dental arcade of baboons and macaques. Based on previous assessments of metameric variation in the maxilla (Hlusko 2002a; Saheki 1966), this thesis predicted that the expression of the interconulus varies with increasing expression from XM1 to XM3. Due to the heritable nature of dental traits (e.g. Johanson 1974; Scott and Turner II 1997), this thesis also hypothesized that patterns of expression of the interconulus vary across taxa.

Expression of the Interconulus in Papio. Analysis of 42 baboons did not reveal statistically significant ordered metameric variation in the expression of the interconulus. While variation in the expression of the interconulus exists across molar number in almost all individuals, this thesis does not find data to suggest that this variation is ordered or can be correlated with molar position in baboons. These results differ from Hlusko's (2002a) previous assessment of metameric variation in *Papio* (Table 17).

Table 17. Comparison of interconulus expression with Hlusko's (2002a) results.

Descriptive Statistics for *Papio* (Monson 2011)					Descriptive Statistics for *Papio* (Hlusko 2002a)		
Molar Position		N	Mean	Std. Deviation	N	Mean	Std. Deviation
XM1	Expression Score	37	1.59	0.93	318	1.59	0.71
XM2	Expression Score	42	1.50	0.86	320	1.64	0.90
XM3	Expression Score	40	1.80	1.27	305	2.09	1.24

There are several possible explanations for why the results of this study did not replicate Hlusko's (2002a) results. First, the sample size in this study was very small, and the power of the statistics was therefore greatly reduced (Field 2000). Hlusko's (2002a) sample size in assessment of the interconulus was approximately eight times larger than this study, and any ordered metameric variation may be more likely to appear in larger sample sizes. Additionally, Hlusko assessed the expression of the interconulus on a population of pedigreed baboons at the Southwest Foundation for Biomedical Research. The baboons at the Southwest Foundation are genetically related and may therefore exhibit different patterns of variation. The genetic management of the population means that all samples were taken from non-inbred animals. Despite this, due to the heritability of many dental traits, it is possible that the genetic relationship between the individuals sampled affected the expression of the interconulus. Hlusko and Mahaney (2007) suggest that there is no difference in dental shape between wild and captive populations. However, their study focused on metric traits of the molars and did not consider presence or expression strength of nonmetric, or quasi-continuous, dental traits. The heritability of the interconulus trait suggests that it may be more likely to express in a small population where genes for the trait are circulating.

Expression of the Interconulus in Macaca. The presence of the interconulus in species of *Macaca* has been noted in other studies (Saheki 1966; Swindler 1976). This study found that the sample of 136 macaques, from 10 distinct species, express the interconulus with ordered metameric variation. The expression of the interconulus increased distally across the molar class with the M3 exhibiting the greatest average expression of the interconulus in the macaque sample. Although Saheki's (1966) study only assessed presence or absence of the interconulus, he did find that the M3 had the greatest frequency of interconulus presence in the sample suggesting that the M3 is most likely to express the interconulus. And this study shows that for macaques expressing the interconulus, the M3 is the molar likely to have greatest expression. This is a finding that has been generated for a wide range of dental traits in other studies of metameric variation in the molars (e.g. Garn 1966b; Kondo and Townsend 2006).

It is important to note that the use of the *Papio* scoring standard for assessment of the interconulus in *Macaca* may have affected the results. The application of discrete categories to a nonmetric trait results in the loss of data (Scott and Turner II 1997). As a quasi-continuous trait, limiting quantifiable expression of the interconulus to only five categories of expression restricts the power of the data. Additionally, a great range of variation existed in the *Macaca* specimens between scores 1 and 2 in the *Papio* model (See Methods). Many of the macaques expressed the interconulus in the range between a slight groove and a small cuspule. It would be beneficial to have a model with more categories of expression in this range. The ability to better quantify the range of expression in the discrete category model used to assess the interconulus in *Macaca* could generate more significant and powerful data.

Variation at the Subspecies and Species Levels. While ordered metameric variation was not present in this *Papio* sample, analysis of mean expression scores suggest that variation may occur at other taxonomic levels. A comparison of mean interconulus scores between baboon subspecies suggests that some populations may demonstrate ordered metameric variation of the interconulus. In this study, the mean scores of the interconulus for *P. anubis* expressed with ordered metameric variation. This lends support to the hypothesis that expression of the interconulus will vary between populations due to significant heritability.

The *Macaca* sample also showed variation in the expression of the interconulus across taxonomic classes. Of the macaque species sampled, most showed ordered metameric variation in interconulus expression. All macaque species with more than seven representative individuals showed ordered metameric variation with the exception of *M. fascicularis*. This suggests that variation in interconulus expression occurs at population levels with some groups demonstrating ordered metameric variation as a trait of the population. It is unclear what role behavior and environment may play in these population differences. Hlusko and Mahaney (2003) demonstrated the heritability of the interconulus, finding that the heritability of the interconulus, like the phenotype itself, expressed with ordered metameric variation. According to their study, the M3 has the highest heritability coefficient for the interconulus (Table 18).

Table 18. Heritability estimates for the interconulus. From Hlusko and Mahaney (2003).

	LM1	LM2	LM3	RM1	RM2	RM3
Heritability estimates	0.333	0.442	0.541	0.393	0.499	0.725

Because the interconulus demonstrates a significant level of heritability, it is subjected to the pressures of natural selection. Ordered variation in the expression of the interconulus differs at the population level. This variation in expression is likely to be at least partially a result of genetic pressures and heritability. The developmental environment may also play a role. By studying ordered expression of the interconulus, it may be possible to better understand variation in mammalian dentition and the role that metameric variation has played in primate evolution.

CONCLUSION

This study characterized the expression of the interconulus in a sample of baboons and macaques. The interconulus is a nonmetric dental trait that expresses in the maxillary molars of some Old World Monkeys. This thesis hypothesized that baboons and macaques demonstrate ordered metameric variation in the expression of the interconulus. This thesis also hypothesized that variation in patterns of expression will occur across taxonomic units. Metameric variation is found in numerous parts of the metazoan body. This project aimed to characterize the metameric variation seen in the Old World Monkey dentition and contribute to a more general understanding of the role that metameric variation has played and continues to play in primate evolution.

The macaques demonstrated significant metameric variation in the expression of the interconulus. Expression of the interconulus in macaques increased distally along the molar row, with M3 having the greatest expression of the trait (M1=1.12, M2=1.46, M3=1.75). The macaques also demonstrated variation in the pattern of expression at the population level. All macaques analyzed with a species sample of n>7 demonstrated metameric variation in the expression of the interconulus, with the exception of *M. fascicularis*. The baboons did not show significant metameric variation in the expression of the interconulus trait (M1=1.59, M2=1.50, M3=1.80). However, assessment of mean expression scores at the subspecies level suggests that the pattern of metameric expression may differ across populations. Specifically, *P. anubis* exhibited ordered metameric variation in expression of the interconulus (M1=1.33, M2=1.56, M3=1.87).

Heritability of Metameric Variation

In mammals, teeth increase in complexity rather than number. Metameric variation allows for this increase in complexity and has been postulated to be at the root of new cusp formation (e.g. Harris 2007; Jernvall and Jung 2000; Weiss 1990). Therefore, it can be hypothesized that the genetic basis for metameric variation of the dentition is present in most, if not all, mammalian species. The ordered expression of a trait must be heritable for natural selection to act on it as a phenotype. Jernvall and Jung (2000) note that in case of hybrid seal populations, an intermediate tooth form with intermediate cusp number and configuration is present. This indirect evidence suggests that the association between trait expression and tooth position, as a result of metameric variation and cascading effects, is a heritable trait.

The interconulus, a product of metameric variation, has only evolved in a few primate species. While the interconulus trait is most likely heritable (Hlusko and Mahaney 2003), it is unclear whether increasing expression of the interconulus along the dental arcade of an individual can be inherited as a vector trait. The vector trait can be defined as the correlation between molar position and interconulus expression. For macaques in this study, the interconulus vector is M1<M2<M3, but it may be possible to further quantify this relationship in other primates.

It is possible that ordered variation in the expression of the interconulus, with expression increasing distally along the molar row, is a heritable phenotype. This would explain why some populations have ordered variation in the trait and others do not. However, even if ordered expression of the interconulus exists at the population level, it is still possible that the vector trait is an accumulation of genetic drift rather than a result of the heritability of the vector. The pattern of ordered metameric variation in the expression of the interconulus that was seen for *Macaca* could be a result of drift acting on the heritability of the interconulus on a single molar rather than a significant relationship between the three molars.

Developmental Effects on Metameric Variation. It is very likely that the developmental environment plays a significant role in tooth morphology (see Rizk et al. 2010). Later developing teeth may be more plastic due to repeated activation of the clonal developmental module. It has been suggested that repeated activation of these pathways can alter the biochemical environment and lead to the accumulation of minor traits and ordered variation (e.g. Grine et al. 2005; Harris 2007). The interconulus may be a trait that expresses with ordered variation as a product of the developmental environment. The heritability of the interconulus as shown in previous studies (Hlusko and Mahaney 2003) could be a reflection of the heritability of the underlying developmental mechanism.

The third molar accumulates the most variation and has greatest expression of the interconulus because it is the last tooth to develop (e.g. Garn 1966b). The fact that the M3 is the last tooth to develop, in combination with having the most variation, may suggest that it is the least important molar in the tooth class. Third molars have been noted to accumulate variation in many dental studies (e.g. Harris 2007; Kondo and Townsend 2006). This variation could accumulate as a result of relaxed controls over teeth at the edge of the field. It is also possible that there is a greater chance for changes to the biochemical environment to occur when the developmental pathways for the molars have already been activated (Grine et al. 2005, Rizk et al. 2010).

There is some suggestion that the interconulus trait responds to a threshold model in the developmental environment. Based on current knowledge of dental development and tooth classes, it can be hypothesized that the interconulus is the non-functional product of a developmental pathway (e.g. Bei 2009). As a non-essential product within the dental arcade, it can be theorized that the interconulus is only able to develop in circumstances of excess resources. This is one explanation for why a pedigreed population of baboons showed significant ordered variation in the expression of the interconulus while this study showed no ordered metameric variation in the wild specimens.

Correlating the Interconulus with Other Dental Traits

Even if developmental resources and biochemical environments directly affect the expression of the interconulus, heritability studies have shown that a genetic basis for the trait exists (Hlusko and Mahaney 2003). Currently, the genes responsible for the interconulus, and many other dental traits, remain unknown. There have been attempts to investigate the genetic basis of dental traits by correlating the traits with other characteristics in order to more readily quantify the genetics responsible for one or both traits (Tucker and Sharpe 1998; Kangas et al. 2004). Cusp traits like the interconulus have been suggested to correlate with enamel thickness (Grine 2007, Kono 2004), molar size (Harris 2007; Garn et al. 1963, 1966b) and developmental time (Kondo and Townsend 2006).

Harris (2007) measured molar size in 300 American whites to study the relationship between molar size and expression of Carabelli's trait. His study found that Carabelli's cusp expresses preferentially in larger molars and is directly related to crown size. Harris uses this evidence to support the prominent theory that increasing tooth size can be associated with greater crown complexity (e.g. Garn, Lewis and Vicinus 1963; Kondo and Townsend 2006). However, the macaques tend to have third molars that are smaller than second molars (Swindler 1976, Warwick 1960). The macaques in this study showed significant ordered metameric variation in the expression of the interconulus. Therefore, while molar size may vary metamerically in primates, there is no evidence to suggest that interconulus expression correlates with molar size in macaques.

Metameric variation in molar size has also been associated with variation in enamel thickness (Grine 2005) and developmental time (Kondo and Townsend 2006). While this correlation may be significant in studies of *Papio* dental traits, the ordered expression of the interconulus in the macaque sample does not correlate with molar size. Therefore, it is unlikely that variation in enamel thickness in *Macaca* can be correlated with ordered metameric variation in the expression of the interconulus. However, it is still unclear how molar enamel thickness varies in the maxillary molar class of *Papio.* It is possible that the interconulus expression can be correlated with enamel thickness in baboons.

Developmental time is another trait that has been suggested to create variation in the dental class. Kondo and Townsend (2006) examined 308 standardized occlusal photographs from a population of Australians, all of European descent. They quantitatively assessed the cusp area of each molar cusp and examined the amount of variability present within the population. Overall, they discovered that the cusps that develop earlier had less variability in area. Ordered variation in the expression of the interconulus may be a reflection of development times and patterned changes in the developmental environment. In baboons and macaques, molar development time follows the same M1<M2<M3 pattern as interconulus expression (Swindler and Meekins 1991). Therefore, one would expect that both *Papio* and *Macaca* would show ordered

expression of the interconulus increasing from M1 to M2 if the interconulus were more likely to occur in later developing teeth. The macaque sample did follow this trend, however, the *Papio* sample did not show ordered expression of the interconulus correlating with permanent dentition development times. It is possible that a study with a larger *Papio* sample would reveal a correlation between interconulus expression and molar development, especially since metameric variation in the expression of the trait has been detected in previous studies (Hlusko 2002a).

Future Directions

Based on previous studies, and variation in expression at the population level, it is likely that the interconulus is a heritable trait. However, it is currently unclear whether ordered variation of the interconulus is a phenotypic trait inherited as a vector. Assessing the heritability of the ordered variation of interconulus expression could help identify target gene areas that result in metameric variation. In order to assess heritability of the expression vector, it is necessary to quantify the relationship that exists between the three molars. It would then be possible to assess heritability of the molar expression vector within a population of known pedigree. This method would allow for analysis of the heritability of metameric expression of the trait. This could provide information not only about the interconulus trait, but also about the heritability of metameric variation as a distinct mechanism.

The assessment of the heritability of the trait relationship within an individual arch is an important step for identifying quantitative trait loci (QTL). These QTL are gene stretches directly responsible for the production of the phenotype. If the ordered variation of the interconulus is a heritable trait, it may be possible to correlate the trait within a pedigreed population in a way that identifies potential QTL. By characterizing the heritability of the vector of expression, these correlations can begin to be assessed. Describing a method for quantifying this ordered variation as a single phenotype is the launching point for future heritability assessments.

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Appendix 1. Raw data on interconulus expression from the Museum of Vertebrate Zoology, baboons.

SPECIMEN ID	SEX	LM1	LM2	LM3	RM1	RM2	RM3	ORIGIN	DATE	SPECIES
149507	M	1	1	1		1	1	NIGER	1972	*P. anubis*
124254	M	4	5	5	3	4	5	UGANDA	1958	*P. ham*
19290	M	2			2			unknown	1913	*P. papio*
106562	M	1	1	1	1	1	1	unknown - Arabia? Sudan?	1947	*P. ham*
154147	M	2	2	3	2	1	2	ETHIOPIA	unknown	*P. ham*
154145	M	2	1		2	2		ETHIOPIA	unknown	*P. ham*
119810	F	1	1	2	1	1	4	unknown	1955	*P. ham*
120929	M	1	1	1	1	1	1	unknown	1956	*P. ham*
106563	M	3	4	5	2	4	5	Africa	1947	*P. ham*
154146	M	3	1	4	3	2	4	ETHIOPIA	unknown	*P. ham*
149509	M		1	1		1	1	NIGER	1972	*P. anubis*
149512	F	1	2	1	1	2	1	NIGER	1972	*P. anubis*
149511	M		2	4	2	2	3	NIGER	1972	*P. anubis*
149510	M	1	1			1	1	NIGER	1972	*P. anubis*
149508	M	1	2	2		1	2	NIGER	1972	*P. anubis*
149506	F	2			3			NIGER	1972	*P. anubis*
149505	F		1	1		1	1	NIGER	1972	*P. anubis*
149504	F		1	1		1	1	NIGER	1972	*P. anubis*
149503	F	1	1	1	2	1	1	NIGER	1972	*P. anubis*
149502	F		1	1		1	2	NIGER	1972	*P. anubis*
149501	unknown	2			2			NIGER	1972	*P. anubis*
149500	F	1	1	2		1	2	NIGER	1972	*P. anubis*

SPECIMEN ID	SEX	LM1	LM2	LM3	RM1	RM2	RM3	ORIGIN	DATE	SPECIES
152835	M		2	4		2	4	NIGER	1972	*P. anubis*
155549	F	2	3		2	2		KENYA	1972	*P. anubis*
154148	M	2	2	2	2	2	2	ETHIOPIA	unknown	*P. ham*
184531	M	5	2	4	5	3	4	CONGO BASIN	1960	*P. ham*
149514	F	1		2	1	2	2	NIGER	1972	*P. anubis*
149513	F		2	4	1	2	4	NIGER	1972	*P. anubis*
149515	M	2	2	2		2	2	NIGER	1972	*P. anubis*
122418	unknown	1			2			unknown	1957	*P. papio*
117258	unknown	1			2			SOUTH AFRICA	1948	*P. ursinus*
117256	unknown	1			1			SOUTH AFRICA	1948	*P. ursinus*
117255	unknown							SOUTH AFRICA	1948	*P. ursinus*
117249	F	1	2	1	2	2	2	SOUTH AFRICA	1948	*P. ursinus*
117264	unknown	1	1	1	2	1	1	SOUTH AFRICA	1948	*P. ursinus*
117244	M	1	1	1	1	1	1	NAMIBIA	1948	*P. ruacana*
117250	M		1	1	1	1	1	SOUTH AFRICA	1948	*P. ursinus*
117262	F		1	1		1	1	SOUTH AFRICA	1948	*P. occidentalis*
4891	M	1	1		1	1		SOUTH AFRICA	unknown	*P. ursinus*
117263	M	1	1	1	1	1	1	SOUTH AFRICA	1948	*P. ham*
117260		1	1		2	1		SOUTH AFRICA	1948	*P. occidentalis*
117246	F	1	1		1	1		SOUTH AFRICA	1948	*P. ruacana*
117247	F	2						SOUTH AFRICA	1948	*P. ruacana*
117248	F			1				SOUTH AFRICA	1948	*P. ruacana*
118062	F		1	1	2	1	1	BOTSWANA	1950	*P. occidentalis*
117243	F		1	1		1	1	SOUTH AFRICA	1948	*P. ruacana*
117252	F	1		1		1	1	SOUTH AFRICA	1948	*P. ursinus*
117253								SOUTH AFRICA	1948	*P. ursinus*
117261	F	1	1	1	1	1	1	SOUTH AFRICA	1948	*P. occidentalis*
117245	F		1	1		1	1	SOUTH AFRICA	1948	*P. ruacana*

SPECIMEN ID	SEX	LM1	LM2	LM3	RM1	RM2	RM3	ORIGIN	DATE	SPECIES
117254								SOUTH AFRICA	1948	*P. ursinus*
117257		1						SOUTH AFRICA	1948	*P. ursinus*
121456					2			unknown	1956	*Papio*
117242	M	1	1	2	1	1	2	SOUTH AFRICA	1947	*P. ruacana*
117259	M	2	1	1	1	1	1	SOUTH AFRICA	1948	*P. ursinus*
117251	M	1	2	1	1	1		SOUTH AFRICA	1948	*P. ursinus*
117265		1	1	2		1	1	SOUTH AFRICA	1948	*P. ursinus*
81571	M		1	1	1	1		SOUTH AFRICA	unknown	*P. orientalis*
47164		2	1		1	1		SOUTH AFRICA	1948	*P. ursinus*
122416	M		1	1		1	1	unknown	1957	*P. ham*

Appendix 2. Raw data on interconulus expression from the Museum of Vertebrate Zoology, macaques.

SPECIMEN ID	SEX	LM1	LM2	LM3	RM1	RM2	RM3	ORIGIN	DATE COLLECTED	SPECIES
40990		1	2		1	2		MALAYA	1928	M. fascicularis
20898	M	2	2	2	2	2	2	E. INDIES	1914	M. maura
31341	M	2			2			unknown	1920	M. fascicularis
44179	F	2	2	2	2	2	2		1930	M. albobarbatus
109738	F	1	2	3	1	1	2	PHILIPPINES	1945	M. fascicularis
122335	M	1	1	1	1	1	1	INDIA	1958	M. nigra
132531	F	1	1		1	1		unknown	1963	M. mulatta
106181	M		1	1	1	1	2	unknown	1944	M. radiata
24341	M	2	2		2	2		PHILIPPINES	1916	M. fascicularis
24343	M	1			1			PHILIPPINES	1916	M. fascicularis
24344	F	1	2	1	1	2	2	PHILIPPINES	1916	M. fascicularis
24345	M	1			1			PHILIPPINES	1916	M. fascicularis
24346	M	1			1			PHILIPPINES	1916	M. fascicularis
24340	F								1916	M. fascicularis
24339	F	2			2			PHILIPPINES	1916	M. fascicularis
24338	M	1	2		1	2		PHILIPPINES	1916	M. fascicularis
154161								INDIA	1970	M. mulatta
154162	M	1	2		2	2		unknown	1970	M. mulatta
19553	M	2	2		1	2		JAVA	1913	M. mulatta
8949		1			1			INDIA	1905	M. mulatta
154160		2	4	5	2	4	4	unknown	1970	M. mulatta
154159		2	2	2	2	2	2	unknown	1970	M. mulatta
183645	M	1	1	1	1	1	1	SINGAPORE	unknown	M. fascicularis
8948		2			1			unknown	1905	M. fascicularis
40991								unknown	unknown	M. fascicularis

SPECIMEN ID	SEX	LM1	LM2	LM3	RM1	RM2	RM3	ORIGIN	DATE COLLECTED	SPECIES
63313		2			1			unknown	1932	M. fascicularis
119377	M	1	2	2	1	2	2	SINGAPORE	1953	M. fascicularis
24348	F	1	2		1	2		PHILIPPINES	1916	M. fascicularis
24347	M	1			1			PHILIPPINES	1916	M. fascicularis
106869	F	1			1			PHILIPPINES	1946	Macaca
106870	M	1			1			PHILIPPINES	1946	Macaca
116826		2	3	2	2	3	2		1952	Macaca
119479	F								1953	Macaca
106866	F	1	2	2	1	2	2	PHILIPPINES	1946	Macaca
106867	M	1	2	2	1	2	2	PHILIPPINES	1946	Macaca
20899	M	2	2	3	2	2	2	E. INDIES	1914	M. nemestrina
125936	F	1	1	1	1	1	2	unknown	1959	M. sylvanus
134148	M	2	1	1	2	1	2	MALAYSIA	1964	M. nemestrina
130098	M	1	2	2	1	2	2	KUALA LAMPUR	1963	M. nemestrina

Appendix 3. Raw data on interconulus expression from the American Museum of Natural History.

Genus species	Specimen #		LM1	LM2	LM3	LM1	LM2	LM3
M. fascicularis fascicularis	102765	1	1	1	2	1	1	2
		2	1	1	2	1	1	2
		avg	1	1	2	1	1	2
M. fascicularis fascicularis	102211	1	2	2	2	2	2	2
		2	2	2	2	2	2	2
		avg	2	2	2	2	2	2
M. fascicularis fascicularis	102763	1	1	3	0	2	3	1
		2	1	3	0	2	3	1
		avg	1	3	0	2	3	1
M. fascicularis fascicularis	102764	1	1	3	2	1	1	2
		2	1	3	2	1	1	2
		avg	1	3	2	1	1	2
M. fascicularis fascicularis	102786	1						
		2						
		avg						
M. fascicularis fascicularis	102767	1	2	3	2	2	3	2
		2	2	3	2	2	3	2
		avg	2	3	2	2	3	2
M. fascicularis fascicularis	102769	1	1	1	1	1	1	2
		2	1	1	1	1	1	2
		avg	1	1	1	1	1	2
M. fascicularis fascicularis	102770	1	1	3	5	1	3	5
		2	1	3	5	1	4	5
		avg	1	3	5	1	4	5
M. fascicularis fascicularis	102766	1	1	3	2	1	3	3
		2	1	2	2	1	3	3
		avg	1	3	2	1	3	3

Genus species	Specimen #		LM1	LM2	LM3	LM1	LM2	LM3
M. fascicularis mordax	107562	1	1	2	1	1	2	2
		2	1	2	1	1	2	2
		avg	1	2	1	1	2	2
M. fascicularis mordax	107557	1	1	2	2	1	2	1
		2	1	2	2	1	2	1
		avg	1	2	2	1	2	1
M. fascicularis mordax	107556	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1
M. fascicularis mordax	107555	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1
M. fascicularis mordax	107561	1	2	3	4	2	3	4
		2	2	3	4	2	3	4
		avg	2	3	4	2	3	4
M. fascicularis fascicularis	102909	1	1	1	1	1	2	2
		2	1	1	1	1	1	2
		avg	1	1	1	1	1	2
M.. fascicularis fascicularis	102907	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1
M. fascicularis mordax	107564	1	1	1	2	1	0	2
		2	1	1	2	1	0	2
		avg	1	1	2	1	0	2
M. fascicularis fascicularis	102908	1	1	2	2	1	1	2
		2	1	2	2	1	1	2
		avg	1	2	2	1	1	2

Genus species	Specimen #		LM1	LM2	LM3	LM1	LM2	LM3
M. fascicularis fascicularis	102910	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1
M. fascicularis fascicularis	102906	1	1	1	0	1	1	0
		2	1	1	0	1	1	0
		avg	1	1	0	1	1	0
M. fascicularis fascicularis	102904	1	1	2	0	1	2	0
		2	1	2	0	1	2	0
		avg	1	2	0	1	2	0
M. fascicularis mordax	107568	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1
M. fascicularis mordax	107566	1	1	4	0	1	4	0
		2	1	4	0	1	4	0
		avg	1	4	0	1	4	0
M. fascicularis mordax	107567	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1
M. fascicularis mordax	107558	1	1	1	1	1	1	1
		2	1	1	1	1	2	1
		avg	1	1	1	1	2	1
M. fascicularis mordax	101809	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1
M. fascicularis mordax	107559	1	1	3	4	1	3	4
		2	1	3	4	1	3	5
		avg	1	3	4	1	3	5

Genus species	Specimen #		LM1	LM2	LM3	LM1	LM2	LM3
M. fascicularis mordax	107560	1	1	3	0	1	2	0
		2	1	3	0	1	2	0
		avg	1	3	0	1	2	0
M. fascicularis mordax	101810	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1
M. mordax	101811	1	1	1	1	1	2	1
		2	1	1	1	1	2	1
		avg	1	1	1	1	2	1
M. fascicularis mordax	101891	1	1	1	1	2	1	2
		2	1	1	1	2	1	2
		avg	1	1	1	2	1	2
M. fascicularis mordax	102020	1	2	2	5	2	3	5
		2	2	2	5	2	3	5
		avg	2	2	5	2	3	5
M. fascicularis mordax	102022	1	1	1	3	1	1	3
		2	1	1	3	1	1	3
		avg	1	1	3	1	1	3
M. fascicularis mordax	102021	1	2	2	2	2	2	2
		2	2	2	2	2	2	2
		avg	2	2	2	2	2	2
M. fascicularis mordax	102015	1	1	1	1	1	1	3
		2	1	1	1	1	1	3
		avg	1	1	1	1	1	3
M. fascicularis mordax	102017	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1

Genus species	Specimen #		LM1	LM2	LM3	LM1	LM2	LM3
M. fascicularis mordax	102019	1	1	1	0	1	1	0
		2	1	1	0	1	1	0
		avg	1	1	0	1	1	0
M. fascicularis mordax	102016	1	1	1	0	1	1	0
		2	1	1	0	1	1	0
		avg	1	1	0	1	1	0
M. fascicularis mordax	102018	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1

Appendix 4. Raw data on interconulus expression from the National Museum of Natural History.

Genus species	Specimen #		LM1	LM2	LM3	LM1	LM2	LM3
M. mulatta	537233	1	1	1	1	1	1	1
		2	1	1	2	1	1	1
		avg	1	1	2	1	1	1
M.mulatta	537210	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1
M. mulatta	537235	1	1	1	2	1	1	1
		2	1	1	2	1	1	1
		avg	1	1	2	1	1	1
M. mulatta	537238	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1
M. mulatta	537246	1	1	3	4	1	4	4
		2	1	3	4	1	4	4
		avg	1	3	4	1	4	4
M. mulatta	537247	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1
M. mulatta	537242	1	1	2	2	1	1	2
		2	1	2	2	1	1	2
		avg	1	2	2	1	1	2
M. mulatta	537249	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1

Genus species	Specimen #		LM1	LM2	LM3	LM1	LM2	LM3
M. mulatta	537250	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1
M. mulatta	537255	1	1	1	2	1	1	2
		2	1	1	2	1	1	2
		avg	1	1	2	1	1	2
M. mulatta	537259	1	2	3	2	1	2	2
		2	2	3	2	1	2	2
		avg	2	3	2	1	2	2
M. mulatta	537260	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1
M. mulatta	589096	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1
M. mulatta	537271	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1
M. mulatta	537256	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1
M. mulatta	537281	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1
M. mulatta	537225	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1

Genus species	Specimen #		LM1	LM2	LM3	LM1	LM2	LM3
M. mulatta	537270	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1
M. mulatta	537277	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1
M. mulatta	537265	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1
M. mulatta	537267	1	1	1	3	1	1	3
		2	1	1	3	1	1	3
		avg	1	1	3	1	1	3
M. mulatta	537241	1	1	1	2	1	1	2
		2	1	1	2	1	1	2
		avg	1	1	2	1	1	2
M. mulatta	537274	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1
M. mulatta	537221	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1
M. mulatta	537263	1	1	1	2	1	1	2
		2	1	1	2	1	1	2
		avg	1	1	2	1	1	2
M. mulatta	537279	1	1	4	5	1	4	5
		2	1	4	5	1	4	5
		avg	1	4	5	1	4	5

Genus species	Specimen #		LM1	LM2	LM3	LM1	LM2	LM3
M. mulatta	537266	1	1	1	2	1	1	2
		2	1	1	2	1	1	2
		avg	1	1	2	1	1	2
M. mulatta	537261	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1
M. mulatta	537272	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1
M. mulatta	537262	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1
M. mulatta	537280	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1
M. mulatta	537257	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1
M. mulatta	537275	1	0	0	1	0	0	1
		2	0	0	1	0	0	1
		avg	0	0	1	0	0	1
M. mulatta	537229	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1
M. mulatta	537224	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1

Genus species	Specimen #		LM1	LM2	LM3	LM1	LM2	LM3
M. mulatta	537232	1	1	1	2	1	2	2
		2	1	1	2	1	2	2
		avg	1	1	2	1	2	2
M. mulatta	537234	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1
M. mulatta mulatta	267851	1	1	1	4	1	1	4
		2	1	1	4	1	1	4
		avg	1	1	4	1	1	4
M. mulatta	300017	1	1	1	0	1	1	0
		2	`1	1	0	1	1	0
		avg	1	1	0	1	1	0
M. mulatta villosa	173813	1	1	1	1	1	1	0
		2	1	1	1	1	1	0
		avg	1	1	1	1	1	0
M. mulatta mulatta	279191	1	1	1	0	1	1	0
		2	1	1	0	1	1	0
		avg	1	1	0	1	1	0
M. mulatta	307715	1	2	3	3	2	3	3
		2	2	3	3	2	3	3
		avg	2	3	3	2	3	3
M. mulatta	296917	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1
M. mulatta	320780	1	1	2	3	1	1	2
		2	1	1	2	1	1	2
		avg	1	2	2	1	1	2

Genus species	Specimen #		LM1	LM2	LM3	LM1	LM2	LM3
M. mulatta	320781	1	1	1	2	1	1	1
		2	1	1	2	1	1	1
		avg	1	1	2	1	1	1
M. mulatta	353187	1	1	1	2	1	1	2
		2	1	1	1	1	1	1
		avg	1	1	2	1	1	2
M. mulatta	353186	1	1	1	2	1	1	2
		2	1	1	2	1	1	2
		avg	1	1	2	1	1	2
M.. mulatta villosa	399285	1	1	1	2	1	1	3
		2	1	2	3	1	1	3
		avg	1	2	3	1	1	3
M. mulatta	268944	1	1	1	0	1	2	0
		2	1	1	0	1	2	0
		avg	1	1	0	1	2	0
M. mulatta	240486	1	1	2	0	1	1	0
		2	1	2	0	1	1	0
		avg	1	2	0	1	2	0
M. mulatta mulatta	240704	1	2	2	0	2	2	0
		2	2	2	0	2	2	0
		avg	2	2	0	2	2	0
M. mulatta mulatta	241160	1	1	1	2	1	1	2
		2	1	1	2	1	1	2
		avg	1	1	2	1	1	2
M. mulatta mulatta	258184	1	0	0	0	0	0	0
		2	0	0	0	0	0	0
		avg	0	0	0	0	0	0

Genus species	Specimen #		LM1	LM2	LM3	LM1	LM2	LM3
M. mulatta villosa	173812	1	0	1	2	0	1	2
		2	0	1	2	0	1	2
		avg	0	1	2	0	1	2
M. mulatta villosa	173814	1	1	1	3	1	1	3
		2	1	1	3	1	1	3
		avg	1	1	3	1	1	3
M. mulatta villosa	020123/A35488	1	1	2	1	1	1	1
		2	1	2	1	1	1	1
		avg	1	2	1	1	1	1
M. mulatta villosa	020124/A35489	1	1	2	3	1	2	3
		2	1	2	3	1	2	3
		avg	1	2	3	1	2	3
M. mulatta villosa	63471	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1
M. mulatta	537273	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1
M. mulatta	537278	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1
M.mulatta	537282	1	1	1	1	0	1	2
		2	1	1	1	0	1	2
		avg	1	1	1	0	1	2
M. mulatta	537276	1	2	4	4	2	3	4
		2	2	4	3	2	3	4
		avg	2	4	4	2	3	4

Genus species	Specimen #		LM1	LM2	LM3	LM1	LM2	LM3
M. mulatta	537254	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1
M. mulatta	537231	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1
M. mulatta	537244	1	1	2	5	1	2	5
		2	1	2	5	1	2	5
		avg	1	2	5	1	2	5
M. mulatta	537269	1	1	1	2	1	1	1
		2	1	1	2	1	1	1
		avg	1	1	2	1	1	1
M. mulatta	537236	1	1	1	3	1	1	3
		2	1	1	3	1	1	3
		avg	1	1	3	1	1	3
M. mulatta	537243	1	1	1	2	1	1	2
		2	1	1	2	1	1	2
		avg	1	1	2	1	1	2
M. mulatta	537252	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1
M. mulatta	537226	1	1	1	2	1	2	2
		2	1	1	2	1	2	2
		avg	1	1	2	1	2	2
M. mulatta	537248	1	1	1	2	1	1	1
		2	1	1	2	1	1	1
		avg	1	1	2	1	1	1

Genus species	Specimen #		LM1	LM2	LM3	LM1	LM2	LM3
M. mulatta	537264	1	1	1	2	1	1	3
		2	1	1	2	1	1	3
		avg	1	1	2	1	1	3
M. mulatta	537237	1	1	1	1	1	1	1
		2	1	1	1	1	1	1
		avg	1	1	1	1	1	1