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Comparison of Occlusal Area and Postcanine Mesiodistal Length in Old World and New World Monkeys

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COMPARISON OF OCCLUSAL AREA AND POSTCANINE MESIODISTAL
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ABSTRACT

The purpose of this study is to discover the relationship between the number of teeth and the postcanine occlusal area and postcanine mesiodistal length in select OWM and NWM species. New World monkeys (NWM) have 12 premolars, whereas Old World monkeys (OWM) have 8. Four species are studied: *Cercopithecus albogularis* and *Colobus guereza* (OWM), and *Cebus capucinus* and *Alouatta palliata* (NWM). Two pairs of species are chosen because they are classified as having the same general folivorous and omnivorous diet: *Co. guereza* and *A. palliata*, and *Cer. albogularis* and *Ceb. capucinus*, respectively. Adult, wild caught, female specimens from the Smithsonian, National Museum of Natural History are studied. Sample sizes are as follows: 20 *Co. guereza, A. palliata* and *Ceb. capucinus*, and 14 *Cer. albogularis.*

The null hypothesis is there will be no difference in the overall occlusal area of the premolar and molar rows between the compared species, and that the occlusal area on the premolar row will be distributed differently among OWMs' and NWMs' individual teeth. Results show that an extra premolar in the NWMs increases the postcanine occlusal area and postcanine mesiodistal length contributed by the premolar row to the overall postcanine row. In NWMs, premolars make up 40-50% of the postcanine mesiodistal length and occlusal area while in OWMs, the premolars make up only 30%. Each premolar is close to the same length of 33% of the premolar row for NWMs; whereas in OWMs, each premolar is about of 50% of the premolar row. Therefore, in terms of postcanine length, the loss of P2 in OWM species leads to a uniform increase in postcanine length of P3 and P4. Likewise, when P2 is present, there is the same mesiodistal postanine length of about 33% on each premolar. Therefore, retention or loss of P2 does not seem to affect proportionate size of premolars.

INTRODUCTION

The research in this paper focuses on primate dentition, specifically that of Old World monkeys (OWMs) and New World monkeys (NWMs). This paper studies the relationship between number of postcanine teeth and their occlusal area (i.e., chewing surface or the surface on a tooth that comes into contact with other teeth) as well as postcanine mesiodistal length (i.e., the space occupied by the first premolar, after the canine, to the last molar). This issue is important because NWMs have an extra premolar tooth in each quadrant of their mouth compared to OWMs. If NWMs and OWMs shared a recent common ancestor before their evolutionary divergence, then one lineage either gained or lost a premolar. Did this gain or loss of a premolar change occlusal area or did the change in number of teeth simply result in different sizes of the teeth but occlusal area remained unchanged?

All primates' mouths can be divided into quadrants. In many extant species, these quadrants consist of the following permanent teeth: 2 incisors, 1 canine, 2 or 3 premolars, and 3 molars. There are many differences between NWMs and OWMs. Some of these differences include NWMs being typically smaller in body mass than OWMs, some NWMs possess a prehensile, or grasping, tail and NWMs' nostrils are farther apart and open to the side, while OWMs' nostrils are closer together and open downward. Another difference that is the focus in this study is the number of their permanent teeth.

Living primates vary in their number of teeth. For instance, OWMs, apes, and humans (catarrhines) have 32 permanent teeth consisting of 8 incisors, 4 canines, 8 premolars, and 12 molars, producing a dental formula of 2.1.2.3 (i.e., number of each type of tooth per quadrant of the mouth). In contrast, the NWM species (platyrrhines) from the *Cebidae*, *Pitheciidae*, *Aotidae* and *Atelidae* families have 36 permanent teeth with the same number of incisors, canines, and

molars as catarrhines; however, due to an extra premolar in each mouth quadrant, NWMs have 12 premolars producing a dental formula of 2.1.3.3. *Callitrichidae* is a family of NWM platyrrhines that deviates from other NWMs in their dental formula; they have 2 molars in each mouth quadrant instead of 3.

Premolars and molars are both used in mastication to shear and break down food. Together, they can be considered the postcanines or cheek teeth. For this study, only postcanines are used to study occlusion as well as postcanine mesiodistal length. Occlusion refers to the way in which the teeth fit together. This includes the relationship between the teeth in the same jaw, and the relationship between the set of teeth in the mandible and maxilla (Hillson 2005).

The premolars in OWMs are known as the first premolar or P3, and the second premolar or P4. In contrast, the premolars in NWMs are known as the first premolar or P2, the second premolar or P3, and the third premolar or P4. P2 is the premolar tooth that is lost in the ancestor of all OWMs but retained in the NWMs. The molars in OWMs and NWMs are known as first, second and third molar or M1, M2, and M3, respectively. The premolar and molar rows/fields are the amount of space in the postcanine length taken up by the premolars or molars in that mouth quadrant, respectively.

Two issues are addressed in this study. Firstly, do the compared species of OWMs and NWMs, which share a similar diet, differ in the distribution of their occlusal area on postcanine teeth due to a difference in number of teeth? Secondly, do the compared species differ in the distribution of their postcanine mesiodistal length due to a difference in their number of teeth?

Both issues are tested by the paired samples: two OWM species (*Cercopithecus albogularis* and *Colobus guereza*) and two NWM species (*Alouatta palliata* and *Cebus capucinus*) are studied. Two pairs of species are chosen because they are reported as having the

same general diet and being of comparable body mass: folivory for *Colobus guereza* and *Alouatta palliata* (Dasilva 1992; Fleagle 2013), and omnivory for *Cercopithecus albogularis* and *Cebus capucinus* (Teaford 2005; Fleagle 2013). To eliminate the effects of sexual dimorphism, only female specimens are chosen for this study.

This study will also look for a direct proportional relationship between cranial and palatal length in comparison to occlusal area and postcanine mesiodistal length in the four species studied. This comparison is done in order to determine if cranial and palatal length can be used to standardize postcanine tooth comparisons. In this study, the postcanine occlusal area of the premolar and molar rows is expected to be the same in both compared OWM and NWM species.

LITERATURE REVIEW

Primate Teeth

  The primate tooth consists of various parts which are comprised of different structures that perform different functions. The crown, which is covered in protective and highly mineralized enamel, makes up the part of the tooth above the gum line. Dental pulp, composed of soft tissues containing blood vessels and nerves that enter the tooth through the apical foramen, makes up the center of the tooth. Dentine, a moderately mineralized substance, surrounds the dental pulp and root. The tooth root is covered by dentine and cementum and the root is attached to the periodontal ligament. The periodontal ligament anchors the tooth into the jaw and covers the root of the tooth up to the cementoenamel junction (Swindler 2002).

  The development of primate teeth begins in utero. A germ cell is organized into three parts that will eventually form all parts of the teeth: enamel organ (comes from the oral ectoderm and dental lamina and will eventually form the enamel), dental papilla (comes from the ectomesenchyme and will eventually form the dentine and dental pulp) and dental follicle (comes from the ectomesenchyme and will eventually develop into the cementum, periodontal ligament and alveolar bone). The development of teeth can be divided into three stages: bud stage, cap stage, and bell stage. During the bud stage, the dental lamina develops and tooth buds composed of oral epithelial structures form (Ungar 2010). During the cap stage, the dental papilla begins to form and cells are differentiated into more specialized layers. During the bell stage, the crown of the tooth, as well as enamel and dentine, develops into the shape of the future tooth.

  The development of mammalian teeth and mastication are processes that have been evolving for more than 225 million years. The first mammals likely evolved from a cynodont, mammal-like reptile, ancestor sometime in the Middle to early Late Triassic Periods (Ungar

2010). With the evolution of mammals come more complex and specialized dental and jaw

adaptations, some of which are not present in any of the earlier and more primitive taxa, such as

the pre-mammalian reptiles (Ungar 2010). Described below are some adaptations that provide

examples of some of the characteristics that make mammals unique or have played important

roles in the evolution of mammal mastication.

Heterodonty, dentition with different types of teeth, is not unique to the class *Mammalia*

but plays an important role in increasing food processing efficiency as well as a dietary

specialization (Ungar 2010). Conversely, the development of a temporomandibular joint, in

place of the articulate quadrate joint, is unique to *Mammalia* (Ungar 2010). The

temporomandibular jaw, combined with the reorganization of the adductor muscles in the

mandible, allows for mastication. Mastication is uniquely mammalian and allows for more

flexibility and precise occlusion between the teeth during chewing. This flexibility is due to a

transverse chewing pattern, which allows for a more even alignment of the teeth, rather than the

simple up-and-down motion allowed by the articulate quadrate joint (Ungar 2010).

In primates, the hard palate is the thin bony plate located on the roof of the mouth. The

primary palate is the part of the hard palate that is located behind the maxillary central incisors.

The primary palate develops during embryonic development and separates the oral cavity from

the nasal cavities. The development of the secondary bony palate is also important for

mastication among mammals, and is located posterior to the primary palate. The secondary bony

palate serves as a hard surface for the tongue to manipulate food against as needed, acts to

separate the food and air passages in the mouth, and creates a vacuum to aid in swallowing or

suction of food material (Ungar 2010). In addition, diphyodonty also separates mammals from

other vertebrates. Rather than having multiple sets of teeth that are lost and gained throughout a

lifetime, mammals are diphyodonts and are restricted to usually no more than two sets of teeth. In most cases, mammals possess a set of deciduous and permanent teeth. However, the timing of when they possess each set is variable and unique among species.

Primate Origins

Many advances have been made in the field of primate evolution within the last 20 years. This advancement is due to a combination of research in comparative biology among species, molecular biology (especially genomics), and the expansion of the existing fossil record. Before modern molecular studies, the widely held scientific belief was that primates originated approximately 65 Ma during the Cretaceous/Tertiary boundary. However, more recent research suggests the divergence of primates from other mammals to have been 85 Ma and the divergence of strepsirrhines from haplorhines to have been 77 Ma (Miller et al. 2005). Living primates are currently classified into three major lineages: strepsirhines (lemurs, lorises and bushbabies), tarsiers, and anthropoids (NWMs, OWMs, humans and apes) (Beard 2013). Tarsiers and anthropoids (both more closely related to each other than to strepsirhines) can additionally be collectively grouped into the clade, haplorhine, to emphasize their special evolutionary relationship (Beard 2013).

A popular theory today on the origin of anthropoids is that an initial split of haplorrhines from strepsirrhines led tarsiers and anthropoids to then evolve side by side as "sister clades." This theory casts doubt on the African origin hypothesis for anthropoids, due to the lack of fossil evidence for tarsiers anywhere in Africa. This view could lend support to an Asian origin hypothesis for anthropoids. The anthropoids and tarsier clades may have evolved side by side for a time, and then only the anthropoid clade migrated into Africa with tarsiers remaining in Asia. Looking at the fossil evidence alone, the earliest known definitive anthropoid fossil from Asia is

Eosimias sinensis and dates to the Middle Eocene (45 Ma); the earliest definitively known

African anthropoid, *Biretia piveteaui*, dates to the late Middle Eocene (37 Ma) (Beard 2013).

The exact origin of platyrrhines is still a debate in the paleoanthropological community.

Platyrrhines may have derived from a parapithecid ancestor from the Oligocene Epoch. Two

parapithecida taxa, *Parapithecus grangeri* and *Apidium moustafaii*, are both Oligocene

anthropoids discovered in the Fayum Province of Egypt that possess a third premolar in their

adult permanent dentition (Kay and Simons 1983). Some researchers (Takai et al. 2000) argue

that the dental morphology of parapithecids is too specialized for them to be the likely ancestors

for platyrrhines. Takai et al. (2000) instead theorize *Proteopithecus sylviae*, from the

Proteopithecidae family, as a likely platyrrhine ancestor due to its morphological similarities

with *Branisella boliviana*, the earliest discovered platyrrhine fossil from the Late Oligocene of

Salla, Bolivia. *Proteopithecus sylviae*, like *Branisella boliviana*, had a dental formula of 2.1.3.3.

The extinct Eocene primates of North America and Europe are often divided into two

families: *Omomyidae,* typically linked with anthropoids and tarsiers, and *Adapidae,* typically

linked with strepsirrhines (Fleagle 2013). A.L. Rosenberger and F.S. Szalay hypothesize that

primitive "protoanthropoids" are derived from omomyids and that platyrrhines originated in

North America (Ciochon and Fleagle 1987). In constrast to this view, Philip Gingerich believes

that anthropoids are derived from an Eocene (54-34 Ma) adapoid ancestor, and Gingerich

considers southern Asia to be the most likely continent of origin (Ciochon and Fleagle 1987). In

regards to platyrrhines, Gingerich hypothesizes "protosimians" may have crossed into North

America from Asia by way of the Bering Land Bridge (Ciochon and Fleagle 1987).

During the Eocene Epoch, the primitive primate dental formula 2.1.4.3 characterized

many adapoid primates (Fleagle 2013). The primitive adapoid genera *Cantius*, *Nothartus* and

Adapis all possessed four premolars (Fleagle 2013). P1 is the premolar that was lost in the evolution of some early primate species between the Eocene Epoch and the Oligocene Epoch (34-23 Ma).

If OWMs and NWMs shared a common ancestor with 2.1.3.3 dental formula, that means that somewhere along their evolutionary history, the catarrhine lineage lost a premolar (P2), while the platyrrhine lineage retained it. Most extant species do not have more teeth than their ancestors because it is far more likely to lose a tooth in evolutionary history than it is to gain one (Ungar 2010).

Contemporary Related Studies

Rosenberger (1992) suggested that the reduction in molars from 3 to 2 in the NWM callitrichids actually increases the occlusal pressure for piercing chitin. The occlusal pressure is increased by decreasing the unit area over which force is applied and/or enlarging tooth embrasures to expose perimeter shearing blades and puncturing surfaces (Rosenberger 1992). Smaller molars also decrease resistance when closing the jaws on food, and thereby enhance the force applied on the anterior premolar row (Rosenberger 1992). In the case of the *Callitrichadae*, a reduction in the number of molars proves dietarily beneficial to mastication of insects, which make up a large component of their diet.

Ribeiro et al. (2013) studied the relative molar and premolar fields among males in 11 species of primates, including both OWMs and NWMs. Ribeiro et al. (2013) studied one specimen from each species revealing that there was a limit for the size of the premolar field in relation to the secondary palate and molar field among the species studied. Ribeiro et al. (2013) demonstrated that species possessing the 2.1.2.3 dental pattern had an increased molar to secondary palate ratio, as well as smaller premolar to secondary palate ratio than that of species

with a 2.1.3.3 dental formula. Therefore, the number of premolars in these species impacts the size proportions among the premolars, molars and secondary palate. Fewer premolars in the premolar field led to a larger molar field than premolar field, in a ratio comparison to the secondary palate.

Rodent dentition can be viewed as an example of reduction in evolution. Many species of Oligocene rats have P4. Labonne et al. (2012) believe the loss of P4 in rat descendants may have released constraint on M1 development, leading to an elongation of M1. Most rodent lineages today have lost their premolars (Labonne et al. 2012). Labonne et al. (2012) studied 510 rodent specimens from 178 species, in 24 subfamilies, including examples of 3 extinct (*Eomyidae*, *Theromyoidae* and *Allomyidae*) and 7 extant (*Castoridae*, *Cricetidae*, *Dipodidae*, *Gliridae*, *Muridae*, *Spalacidae* and *Sciuridae*) families over a time period spanning 40 million years. One of the issues Labonne et al.'s research addressed is the loss of P4 and its associated impact on molars. Labonne et al. (2012) found there are three main dental molar phenotypes among the specimens studied (M1>M2>M3, M1<M2<M3, and M1<M2>M3). The fourth, and far less common, phenotype is M1>M2<M3, and is found in only 2% of the individuals studied (2 families with P4, *Theromyoidae* and *Sciuridae*, and 1 family without P4, *Cricetidae*; this phenotype is also rare in other mammal species) (Labonne et al. 2012).

The results from Labonne et al.'s (2012) study indicate that the subfamily *Arvicolinae* from the family *Cricetidae*, in which M1 is the largest, is also a subfamily that is missing P4. Despite occasional individual variations, the trend in the results is for the subfamilies in which P4 is present to have, on average, a smaller M1. The pattern is for the loss or retention of P4 to have an impact on the development of the adjacent molar, and then indirectly, the entire molar

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row. In this same way, the loss or retention of P2 among primate species may similarly impact the adjacent P3 or canine tooth.

Scott (2011) believes, in many cases, that facial size is a more appropriate constant than body mass for standardizing postcanine measurement comparisons. Scott (2011) states that facial size is strongly correlated with postcanine area when body mass is held constant, but the same is not true for body mass when facial size is held constant. Scott (2011) argues that larger postcanine teeth could be a consequence of larger faces and independent of body mass. Scott's (2011) research included 29 anthropoid species, including 5 platyrrhines, 8 cercopithecines, 8 colobines and 8 hominoids. Scott (2011) determined the postcanine area for each specimen by summing the products of the mesiodistal and buccolingual diameters, or lengths, for each tooth. The four facial measurements referred to and used for postcanine comparison included: dorsal facial length, mandibular length, posterior facial height and jaw width. Scott's (2011) results indicated that species with larger postcanine teeth relative to facial size were not necessarily the same as those with larger postcanine teeth relative to body mass, and that facial size has a strong effect on postcanine size independent of body mass.

Premolar and Molar Function

A premolar's primary purpose is to assist in the mastication of food and to help maintain the vertical dimension of the face (Scheid 2007). The premolars are situated between the canines and molars in each of the four mouth quadrants. They are the fourth, fifth, and sometimes sixth (i.e., in NWMs) tooth from the midline. Premolars display variation among different species. Depending upon the dietary habits and evolutionary history of a species, they take on a variety of shapes and sizes, from single-cusped structures in shrews, to more substantive structures that can be used for crushing like those seen in hyenas (Ungar 2010).

Molars can also display a wide array of variation dependent upon a families' or individual species' diet and evolutionary history. In some families, such as *Delphinoidae* (dolphins) and *Bradypodidae* (sloths), the molars are simple and peglike, whereas in other families, such as *Elephantidae* (elephants), molars are more complex and elaborate structures (Ungar 2010). Primate molars have an occlusal surface that typically contains three to five cusps, and molar chewing surfaces are the largest of the four types of teeth (Scheid 2007). The prominent four molar cusps are known as the paracone (mesial-buccal), protocone (mesial-lingual), metacone (distal-buccal), and hypocone (distal-lingual). Similar to premolars, molars play a large role in the mastication of food (they are primarily used for grinding).

Old World and New World Monkey Species

The four species in this study are: (1) (OWM) *Colobus guereza,* from the family *Cercopithecidae*; (2) (NWM) *Alouatta palliata*, from the family *Atelidae*; (3) (OWM) *Cercopithecus albogularis*, from the family *Cercopithecidae*; and (4) (NWM) *Cebus capucinus,* from the family *Cebidae*. *Colobus guereza,* more commonly known as the black-and-white colobus monkey, is an OWM that lives in the forests of equatorial Africa. The black-and-white colobus is the largest of the African colobine monkeys and displays considerable sexual dimorphism in body mass. Unlike many other species of monkey, *Colobus guereza*'s diet is restricted to vegetation. They have developed a specialized labyrinthine stomach that allows them to extract the greatest amount of nutrients possible from their food (Eimerl and De Vore 1965). This type of specialized diet helps to limit the competition for food between sympatric primate species.

Alouatta palliata, commonly referred to as the mantled howler monkey, is a NWM that is found in parts of Mesoamerica and northern South America. Like most howlers, the mantled

howler is one of the larger species of NWM and is very sexually dimorphic. *Alouatta palliata* is considered a mixed folivore (Estrada et al. 1999). *Alouatta palliata*'s diet consists of month-to-month seasonal variations but is mostly comprised of leaves, with flowers and fruits being the next most common components (Deane 2012).

Cercopithecus albogularis, also known as the white-throated guenon, is an OWM found in sub-Saharan Africa. *Cercopithecus albogularis*' diet consists predominantly of fruits and insects. However, during certain parts of the year, leaves also become a part of *Cercopithecus albogularis*' diet. Sexual dimorphism is moderate within this species and can be best seen in the canine teeth. The males (as with all sexually dimorphic primates) have larger canine teeth than the females.

Cebus capucinus, commonly referred to as the white-throated capuchin, is the only species of capuchin that lives in Central America. The omnivorous *Cebus capucinus* diet includes numerous types of fruits, small vertebrates, and invertebrates. They display marked sexual dimorphism in canine and body mass.

MATERIALS AND METHODS

The species in this study exhibit sexual dimorphism, with the males displaying larger canines and/or body mass. Therefore, to mitigate the effects of sexual dimorphism on dental size and body mass in this study, only adult (with permanent dentition), wild-caught female specimens were studied. Only specimens without extensively worn teeth were used so that the cusps could be identified. Not all results reflect all specimens from that respective species, due to some individual teeth being partially or completely lost postmortem or individual teeth being too damaged for inclusion in the analysis. Sample sizes were 20 specimens each for *Colobus guereza, Alouatta palliata* and *Cebus capucinus*, and 14 specimens for *Cercopithecus albogularis* from the Smithsonian's National Museum of Natural History (NMNH) in Washington, D.C. Information on available individuals' sex, body mass and body length was obtained from NMNH's online records.

All measurements were taken with standard digital sliding calipers. Maximal cranial length and palatal length were recorded on each specimen and analyzed to see if these measurements could be used a constant for comparing postcanine teeth. Maximum cranial length was measured from glabella to opisthocranion (Figure 1). Length of the palate was measured from the point closest to the prosthion, behind and between the maxillary central incisors, to alveolon (Figure 2).
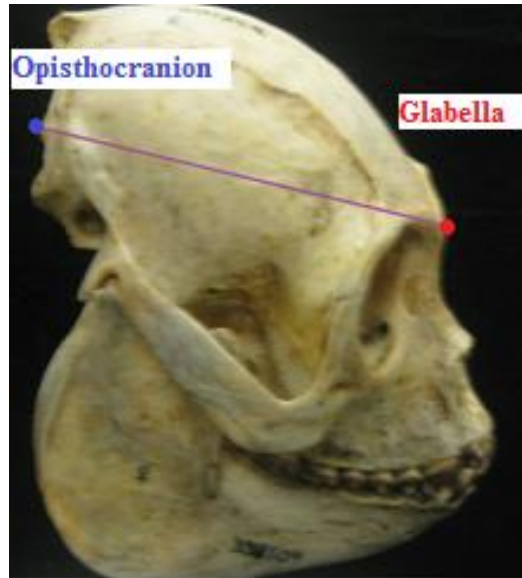
Figure 1. Maximum Cranial Length from Opisthocranion to Glabella (*A. palliata* skull)
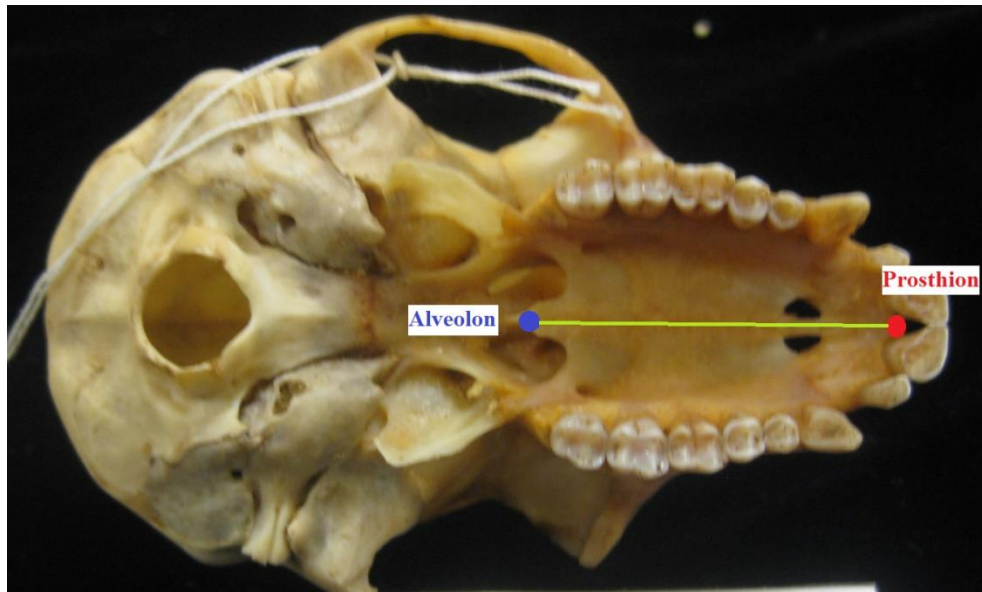
Figure 2. Length of the Palate from Alveolon to Point Closest to the Prosthion (*Cer. albogularis* skull)

In this study, a numeric superscript denotes a tooth from the maxilla (i.e., M^1) while a numeric subscript indicates a tooth from the mandible (i.e., M_2). The lack of a numeric superscript or subscript (i.e., M3) indicates a referral to teeth that occupy both the maxilla and mandible of the species or specimen, unless stated otherwise in a table.

There are multiple methods for measuring postcanine teeth, with some of the most common including tooth height, mesiodistal length, buccolingual length, and crown module (Bass 2005). The dental measurements, taken on the crown surface of the teeth, for this study were as follows: length between posterior buccal and lingual cusps, length between anterior buccal and lingual cusps, maximum mesiodistal length and maximum buccolingual width of tooth (Scott 2011).

Many researchers calculate the occlusal area of a tooth using the standard formula of multiplying length times width (i.e., rectangle). In this study, various standard statistical formulae were used for calculating the occlusal area of the different teeth of OWMs and NWMs, because the teeth display a wide variation in shape. The statistical formulae used were chosen based on each type of tooth's individual shape. A summary of these formulae is in Table 1.

Table 1. Formulae Used to Compute Occlusal Area on Each Type of Old World Monkey and New World Monkey Tooth[1]

Tooth Type	Old World monkey	New World monkey
M3,M2,M1	$\text{Trapezoid} = \frac{L(W_1+W_2)}{2}$	$\text{Trapezoid} = \frac{L(W_1+W_2)}{2}$
P4	$\text{Ellipse} = \pi(\frac{W_3}{2})(\frac{L}{2})$	$\text{Ellipse} = \pi(\frac{W_3}{2})(\frac{L}{2})$
P3	$\text{Circle} = \frac{\pi L^2}{4}$	$\text{Ellipse} = \pi(\frac{W_3}{2})(\frac{L}{2})$
P2		$\text{Ellipse} = \pi(\frac{W_3}{2})(\frac{L}{2})$

The trapezoidal formula was used on all species' molars because all molars displayed a similar shape and the comparative lengths of the measurements taken fit best with this formula. For the first, second, and third molars in OWMs and NWMs the measurements taken included

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[1] L stands for mesiodistal length of the tooth.
W_1 stands for buccolingual width between posterior cusps of the tooth.
W_2 stands for buccolingual width between anterior cusps of the tooth.
W_3 stands for maximum buccolingual width between the sides of the tooth.

the mesiodistal length of the tooth (L) (Figure 3), the width (W_1) between the posterior buccal and lingual cusps, and the width (W_2) between the anterior buccal and lingual cusps (Figure 4).

$$\text{Area for all molars} = \frac{L(W_1 + W_2)}{2}$$

Figure 3. Measurement of the Mesiodistal Length of Third Molar (mandible from *Cer. albogularis*)
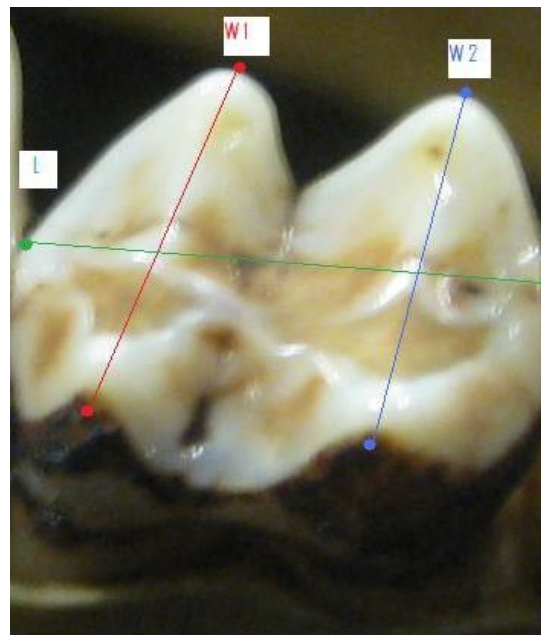
Figure 4. Measurements Taken on Molar for the Trapezoidal Formula (molar of *Co. guereza*)

For the OWMs' (*Co. guereza* and *Cer. albogularis)* second premolars (P4) and the

NWMs' (*A. palliata* and *Ceb. capucinus*) first, second, and third premolars (P2, P3 and P4) the

same two measurements were used: maximum buccolingual width between the sides of the tooth

(W_3), and the mesiodistal length of the tooth (L). The formula for an ellipse was used to compute

the area.

$$\text{Area} = \pi(\frac{W_3}{2})(\frac{L}{2})$$

The first premolar (P3) in OWMs was different in shape than the other premolars;

therefore, a different formula was used to calculate its occlusal area. For determining area in the

first premolars (P3) of OWMs' (*Co. guereza* and *Cer. albogularis)*, mesiodistal length of the

tooth (L) and the formula for area of a circle was used.

$$\text{Area} = \frac{\pi L^2}{4}$$

Student's t-tests were conducted on the paired species to determine, through a direct

comparison, whether there was a difference between OWMs and NWMs in the way occlusal area

and postcanine mesiodistal length was distributed amongst the premolars and molars due to a

difference in the number of teeth. Student's t-tests were run on the postcanine occlusal area and

postcanine mesiodistal length for tooth-by-tooth comparisons as well as comparisons between

types of teeth. All measurements were from the right side of the jaw, unless otherwise stated in a

table or text, on both the mandibular and maxillary postcanines. Level of significance was set at

$P \leq 0.05$ for this study.

RESULTS

Ten *A. palliata* specimens were re-measured, 1 month after initial measurements, to determine intra-observer error through the technical error of measurement (TEM). TEM= $\sqrt{(\Sigma d^2)/2N}$, where *d* is the difference between measurements made on a given object on two different occasions, and *N* is the sum of the total number of measurements made on those separate occasions (Lewis 1999). In this study, *N* is 20 (10 re-measurements of mesiodistal length for M[3] and the 10 initial measurements) and TEM is 0.29%. Labonne et al. (2012) determined their TEM to be 0.25% for M1, 2.49% for M2, and 0.31% for M3, and these researchers considered those errors to be negligible. Correspondingly, the TEM in this study of 0.29% is considered negligible.

Paired species were selected for this study based on expectations that they are of comparable body mass. However, samples in this study are not comparable in either body mass or body length (Table 2). Due to few available specimens and a large standard deviation among them, median of body mass and body length, rather than mean is reported. For the paired species of *Co. guereza* and *A. palliata*, *Co. guereza* is larger in both body mass (7,421 g vs. 5,670 g) and body length (561 mm vs. 516 mm). For the paired species of *Cer. albogularis* and *Ceb. capucinus*, *Cer. albogularis* is larger in both body mass (5,557 g vs. 2,540 g) and body length (470 mm vs. 388 mm).

Table 2. Median Body Mass and Body Length[2]

Species	Median Body Mass (*n*)	Median Body Length (*n*)
Cer. albogularis	5,557 g (7)	470 mm (9)
Co. guereza	7,421 g (4)	561 mm (8)
Ceb. capucinus	2,540 g (1)	388 mm (5)
A. palliata	5,670 g (2)	516 mm (8)

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[2] Data from online records of National Museum of Natural History.

Student's t-tests are run for comparing both maxillary and mandibular postcanine occlusal areas for M3, M2, M1, P4, and P3 of both sets of paired species (Table 3). For *Co. guereza* and *A. palliata,* M_1 and M_2 have a nonsignificant difference. *A. palliata* is significantly larger than *Co. guereza* for the maxillary and mandibular P4 as well as M^2, M^1 and P^3. In contrast, *Co. guereza* has significantly larger M^3, M_3 and P_3 than *A. palliata*.

Compared to *Ceb. capucinus*, *Cer. albogularis* has significantly more occlusal area for both the maxillary and mandibular M3, M2, M1 as well as P_3. In contrast, *Ceb. capucinus* has significantly more occlusal area on P_4 and P^3 than *Cer. albogularis*. The difference for P^4 is nonsignificant.

Student's t-tests are run for comparing postcanine mesiodistal length in the M3, M2, M1, P4, and P3 on both the mandible and maxilla between *A. palliata* and *Co. guereza* as well as *Ceb. capucinus* and *Cer. albogularis* (Table 4). In the first paired species comparison (*A. palliata* and *Co. guereza*), both the maxillary and mandibular mesiodistal length for M3 and P4, as well as P_3, are significantly larger in *Co. guereza* than in *A. palliata*. M_2 mesiodistal length is significantly larger in *A. palliata* than in *Co. guereza*. M^2, M^1, P^3 and M_1 are not significantly different between the species. The second species comparison shows that *Cer. albogularis* has significantly longer mesiodistal length than *Ceb. capucinus* for all 10 postcanine teeth evaluated.

Student's t-test is run comparing both postcanine occlusal area (Table 5) as well as postcanine mesiodistal length (Table 6) on summed types of teeth on the maxilla and mandible. The summation of premolars P3 and P4 is compared in the paired species (as well as a second comparison of premolars, including P2, for the NWM species). The summation of M3, M2, and M1 is compared between the paired species. Lastly, a comparison of all postcanine teeth is made (with and without P2 for the NWMs) between the paired species.

Table 3. Summary Statistics for Occlusal Area (mm^2) of Postcanine Teeth, with Results of Student's t-Test Comparing *A. palliata* with *Co. guereza*, and *Ceb. capucinus* with *Cer. albogularis*; 2-Tailed Test of Significance (sd = standard deviation)

Teeth	*A. palliatta* (a)			*Co. guereza* (b)			*Ceb. capucinus* (c)			*Cer. albogularis* (d)			Prob. a:b	Prob. c:d
Maxilla	mean	sd	*n*	mean	sd	*n*	mean	sd	*n*	mean	sd	*n*		
P2	21.8	2.1	20				18.4	1.5	20					
P3	25.6	2.1	19	19.0	3.9	20	17.9	1.5	20	11.4	1.6	14	<0.001	<0.001
P4	27.0	1.6	20	24.9	2.3	20	16.8	1.3	20	15.9	1.8	12	<0.001	0.10
M1	40.6	3.8	20	35.7	4.7	18	18.0	2.3	20	25.8	3.3	14	<0.001	<0.001
M2	44.8	4.3	20	40.4	5.7	18	15.5	1.9	20	27.8	4.0	14	0.01	<0.001
M3	31.8	3.6	20	37.9	7.2	20	8.7	1.4	20	20.9	4.0	14	<0.001	<0.001
Mandible														
P2	20.5	2.7	20				17.4	2.2	19					
P3	20.2	1.6	20	30.7	4.8	20	15.2	1.4	19	20.3	3.3	14	<0.001	<0.001
P4	24.1	1.7	20	20.6	2.1	20	14.7	1.4	20	13.5	1.9	14	<0.001	0.04
M1	34.4	3.3	20	34.9	3.9	16	18.1	1.9	20	23.9	2.7	14	0.69	<0.001
M2	42.4	4.7	20	39.9	3.7	19	15.5	1.7	20	28.4	3.8	14	0.07	<0.001
M3	44.2	6.1	20	50.5	6.6	16	11.8	1.5	19	26.2	3.8	14	0.01	<0.001

Table 4. Summary Statistics for Mesiodistal Length of Postcanine Teeth (mm), with Results of Student's t-Test Comparing *A. palliata* with *Co. guereza*, and *Ceb. capucinus* with *Cer. albogularis*; 2-Tailed Test of Significance (sd = standard deviation)

Teeth	*A. palliata* (a)			*Co. guereza* (b)			*Ceb. capucinus* (c)			*Cer. albogularis* (d)			Prob. a:b	Prob. c:d
Maxilla	mean	sd	*n*	mean	sd	*n*	mean	sd	*n*	mean	sd	*n*		
P2	4.5	0.34	20				3.7	0.21	20					
P3	4.7	0.31	19	4.9	0.49	20	3.5	0.22	20	3.8	0.27	14	0.25	<0.001
P4	4.7	0.18	20	5.0	0.32	20	3.4	0.17	20	4.4	0.29	13	<0.001	<0.001
M1	6.9	0.35	20	6.7	0.49	20	4.3	0.22	20	5.9	0.51	14	0.19	<0.001
M2	7.1	0.37	20	7.2	0.42	20	4.1	0.26	20	6.2	0.42	14	0.68	<0.001
M3	5.6	0.34	20	7.1	0.68	20	2.9	0.26	20	5.5	0.43	14	<0.001	<0.001
Mandible														
P2	4.5	0.38	20				4.1	0.32	19					
P3	4.5	0.27	20	6.2	0.49	20	3.7	0.22	19	5.1	0.41	14	<0.001	<0.001
P4	4.9	0.34	20	5.8	0.31	20	3.7	0.20	20	4.7	0.33	14	<0.001	<0.001
M1	6.8	0.32	20	6.8	0.29	20	4.8	0.18	20	6.0	0.27	14	0.78	<0.001
M2	7.6	0.38	20	7.2	0.38	20	4.3	0.22	20	6.4	0.40	14	<0.001	<0.001
M3	8.1	0.62	20	9.1	0.75	20	3.9	0.23	19	6.3	0.38	14	<0.001	<0.001

Table 5. Statistics for Summed Occlusal Area (mm^2) of Postcanine Teeth, with Results of Student's t-Test Comparing *A. palliata* with *Co. guereza*, and *Ceb. capucinus* with *Cer. albogularis*; 2-Tailed Test of Significance (sd = standard deviation)

Teeth	*A. palliata* (a)			*Co. guereza* (b)			*Ceb. capucinus* (c)			*Cer. albogularis* (d)			Prob. a:b	Prob. c:d
Maxilla	mean	sd	*n*	mean	sd	*n*	mean	sd	*n*	mean	sd	*n*		
∑ P3, P4	52.6	3.2	19	44.0	5.4	20	34.7	2.6	20	27.5	2.9	12	<0.001	<0.001
∑ P2, P3, P4	74.4	4.7	19	44.0	5.4	20	53.1	3.9	20	27.5	2.9	12	<0.001	<0.001
∑ M1, M2, M3	117.3	10.2	20	113.4	13.9	18	42.3	4.7	20	75.1	9.7	13	0.34	<0.001
∑ P3, P4, M1, M2, M3	169.9	12.1	19	158.0	17.9	18	77.0	5.4	20	101.5	10.1	12	0.02	<0.001
∑ P2, P3,P4 M1, M2, M3	191.7	12.8	19	158.0	17.9	18	95.3	6.2	20	101.5	10.1	12	<0.001	0.04
Mandible														
∑ P3, P4	44.3	3.0	20	51.3	5.6	20	29.9	2.6	19	33.9	3.8	14	<0.001	<0.001
∑ P2, P3, P4	64.7	5.0	20	51.3	5.6	20	47.3	4.2	19	33.9	3.8	14	<0.001	<0.001
∑ M1, M2, M3	121.1	11.7	20	124.8	14.7	16	45.0	4.0	19	78.5	9.4	14	0.43	<0.001
∑ P3, P4, M1, M2, M3	165.3	12.3	20	176.6	16.6	16	75.5	5.6	19	112.4	11.3	14	0.03	<0.001
∑ P2, P3,P4 M1, M2, M3	185.8	13.0	20	176.6	16.6	16	92.8	6.1	19	112.4	11.3	14	0.09	<0.001

Table 6. Statistics for Summed Mesiodistal Length of Postcanine Teeth (mm), with Results of Student's t-Test Comparing *A. palliata* with *Co. guereza*, and *Ceb. capucinus* with *Cer. albogularis*; 2-Tailed Test of Significance (sd = standard deviation)

Teeth	*A. palliata* (a)			*Co. guereza* (b)			*Ceb. capucinus* (c)			*Cer. albogularis* (d)			Prob. a:b	Prob. c:d
Maxilla	mean	sd	*n*	mean	sd	*n*	mean	sd	*n*	mean	sd	*n*		
∑ P3, P4	9.4	0.36	19	9.9	0.73	20	6.9	0.34	20	9.1	0.59	13	0.02	<0.001
∑ P2, P3, P4	13.9	0.56	19	9.9	0.73	20	10.6	0.48	20	9.1	0.59	13	<0.001	<0.001
∑ M1, M2, M3	19.6	0.89	20	21.0	1.4	20	11.4	0.49	20	17.6	1.1	14	<0.001	<0.001
∑ P3, P4, M1, M2, M3	29.0	1.2	19	30.9	1.9	20	18.3	0.75	20	26.6	1.6	13	<0.001	<0.001
∑ P2, P3,P4 M1, M2, M3	33.5	1.3	19	30.0	1.9	20	22.0	0.89	20	26.6	1.6	13	<0.001	<0.001
Mandible														
∑ P3, P4	9.4	0.54	20	12.0	0.61	20	7.4	0.34	19	9.8	0.58	14	<0.001	<0.001
∑ P2, P3, P4	13.9	0.75	20	12.0	0.61	20	11.6	0.53	19	9.8	0.58	14	<0.001	<0.001
∑ M1, M2, M3	23.4	1.12	20	23.5	1.46	20	13.0	0.48	19	18.6	0.92	14	0.71	<0.001
∑ P3, P4, M1, M2, M3	32.8	1.30	20	35.5	1.87	20	20.4	0.72	19	28.4	1.3	14	<0.001	<0.001
∑ P2, P3,P4 M1, M2, M3	37.3	1.42	20	35.5	1.87	20	24.6	0.79	19	28.4	1.3	14	<0.001	<0.001

For occlusal area on summed types of teeth, *A. palliata* is significantly larger than *Co. guereza* for $\sum P^3,P^4$ and $\sum P^3,P^4,M^1,M^2,M^3$. In contrast, *Co. guereza* is significantly larger for $\sum P_3,P_4$ and $\sum P_3,P_4,M_1,M_2,M_3$. $\sum M1,M2,M3$ is nonsignificantly different between the species. When P2 is included in *A. palliata*'s summation of the postcanines $\sum P2,P3,P4,M1,M2,M3$, *A. palliata* has a larger occlusal area on the maxilla but is nonsignificantly different on the mandible in comparison to the postcanines of *Co. guereza* (191.7 mm^2 vs. 158.0 mm^2, and 185.8 mm^2 vs. 176.6 mm^2, respectively).

For occlusal area on summed types of teeth, *Cer. albogularis* is significantly larger than *Ceb. capucinus* for $\sum P_3,P_4$, $\sum M1,M2,M3$ and $\sum P3,P4,M1,M2,M3$. In contrast, *Ceb. capucinus* is larger than *Cer. albogularis* for $\sum P^3,P^4$. When P2 is included in *Ceb. capucinus'* summation of the postcanines, $\sum P2,P3,P4,M1,M2,M3$, there is still a smaller occlusal area on both the maxilla and mandible in comparison to the postcanines of *Cer. albogularis* (95.3 mm^2 vs. 101.5 mm^2 and 92.8 mm^2 vs. 112.4 mm^2, respectively).

For summed mesiodistal length of postcanine teeth, *Co. guereza* is significantly longer than *A. palliata* for $\sum P3,P4$, $\sum M^1,M^2,M^3$ and $\sum P3,P4,M1,M2,M3$. The $\sum M_1,M_2,M_3$ is not significantly different between the species. When P2 is included in *A. palliata*'s summation of the postcanines, $\sum P2,P3,P4,M1,M2,M3$, *A. palliata* has a longer postcanine mesiodistal length on both the maxilla and mandible in comparison to *Co. guereza* (33.5 mm vs. 30.9 mm, and 37.3 mm vs. 35.5 mm, respectively). For summed mesiodistal length of postcanine teeth, *Cer. albogularis* is significantly longer on $\sum P3,P4$, $\sum M1,M2,M3$ and $\sum P3,P4,M1,M2,M3$ than *Ceb. capucinus*. When P2 is included in *Ceb. capucinus'* summation of the postcanines, $\sum P2,P3,P4, M1,M2,M3$, there is still a significantly smaller postcanine mesiodistal length on both the

maxilla and mandible in comparison to the postcanines of *Cer. albogularis* (22.0 mm vs. 26.6 mm, and 24.6 mm vs. 28.4 mm, respectively).

The mean overall postcanine occlusal area was calculated for each species by summing the occlusal area of every tooth from all mouth quadrants of each specimen and finding the mean for each respective species. The mean overall postcanine occlusal area is 12% larger in *A. palliata* compared to *Co. guereza* (755.6 mm^2 vs. 671.7 mm^2, respectively); this difference is due to *A. palliata'*s 46% larger occlusal area in premolars (278.9 mm^2 vs. 190.9 mm^2, respectively) (Table 7). *Cer. albogularis* has a 12% larger overall postcanine occlusal area than *Ceb. capucinus* (426.9 mm^2 vs. 380.6 mm^2, respectively), but *Ceb. capucinus* has a 65% larger premolar occlusal area than *Cer. albogularis* (202.6 mm^2 vs. 122.6 mm^2, respectively).

Table 7. Mean Postcanine Occlusal Area in All Combined Maxillary and Mandibular Teeth, Right and Left Side of Jaw

Species	Mean Occlusal Area in mm^2 (%)		
	postcanine teeth (*n*)	Premolars (*n*)	Molars (*n*)
Cer. albogularis	426.9 (12)	122.6 (29%) (12)	304.3 (71%) (14)
Co. guereza	671.7 (16)	190.9 (28%) (20)	480.8 (72%) (16)
Ceb. capucinus	380.6 (19)	202.6 (53%) (19)	178.0 (47%) (19)
A. palliata	755.6 (19)	278.9 (37%) (19)	476.7 (63%) (20)

Cer. albogularis and *Co. guereza* both have about 60% of their maxillary premolar row occlusal area on P4 and 60% of their mandibular premolar row occlusal area on P3 (Table 8). Therefore, with both the maxilla and mandible, there is an uneven occlusal area distribution between the two OWMs' premolar rows. Both OWMs display $P^4>P^3$ and $P_3>P_4$ in premolar area occlusal distribution.

Cer. albogularis displays $M^2>M^1>M^3$ and $M_2>M_3>M_1$ in occlusal area. *Co. guereza* displays $M^2>M^3>M^1$ and $M_3>M_2>M_1$. Both OWMs have their M^2 as their molar displaying the

most occlusal area; however, *Cer. albogularis*' second largest is M^1 while *Co. guereza*'s is M^3.

For the mandible, *Cer. albogularis* displays M_2 as having the largest occlusal area followed by

M_3. In contrast, *Co. guereza*'s largest occlusal area is on M_3, followed by M_2.

Table 8. Mean Maxillary and Mandibular Occlusal Area Distribution in Old World Monkeys'
Postcanine Teeth (mm^2), (percentage per type of tooth)

Maxilla	M3 (*n*)	M2 (*n*)	M1 (*n*)	P4 (*n*)	P3 (*n*)
Cer. albogularis	20.9 (28%) (14)	27.8 (37%) (14)	25.8 (35%) (14)	15.9 (58%) (12)	11.4 (42%) (14)
Co. guereza	37.9 (33%) (20)	40.4 (35%) (18)	35.7 (32%) (18)	25.0 (57%) (20)	19.0 (43%) (20)
Mandible					
Cer. albogularis	26.2 (33%) (14)	28.4 (36%) (14)	23.9 (31%) (14)	13.5 (40%) (14)	20.3 (60%) (14)
Co. guereza	50.5 (40%) (16)	39.9 (32%) (19)	35.0 (28%) (16)	20.6 (40%) (20)	30.8 (60%) (20)

In contrast to the uneven occlusal area distribution in the OWMs' premolars, both NWMs

(*Ceb. capucinus* and *A. palliata*) have their premolar occlusal area more evenly distributed

(ranging from 29% to 37% per tooth) among each of their three premolars in their premolar row

(Table 9). *Ceb. capucinus* displays $P^2>P^3>P^4$ and $P_2>P_3>P_4$ in occlusal area. *A. palliata* displays

$P^4>P^3>P^2$ and $P_4>P_2>P_3$.

For the NWMs' molars, *Ceb. capucinus* displays $M^1>M^2>M^3$ and $M_1>M_2>M_3$ in occlusal

area with the molars becoming larger from back to front on both the maxilla and mandible. *A.*

palliata displays $M^2>M^1>M^3$ and $M_3>M_2>M_1$. For the maxilla, M^2 is the molar with the most

occlusal area for *A. palliata* followed by M^1. For the mandible, the molars become smaller from

back to front in regards to occlusal area.

Table 9. Mean Maxillary and Mandibular Occlusal Area Distribution in New World Monkeys'
Postcanine Teeth (mm^2), (percentage per type of tooth)

Maxilla	M3 *(n)*	M2 *(n)*	M1 *(n)*	P4 *(n)*	P3 *(n)*	P2 *(n)*
Ceb. capucinus	8.7 (21%) (20)	15.5 (37%) (20)	18.0 (42%) (20)	16.8 (32%) (20)	17.9 (33%) (20)	18.4 (35%) (20)
A. palliata	31.8 (27%) (20)	44.8 (38%) (20)	40.6 (35%) (20)	27.0 (36%) (20)	25.6 (34%) (19)	21.8 (29%) (20)
Mandible						
Ceb. capucinus	11.8 (26%) (19)	15.5 (34%) (20)	18.1 (40%) (20)	14.8 (31%) (20)	15.2 (32%) (19)	17.4 (37%) (19)
A. palliata	44.2 (37%) (20)	42.4 (35%) (20)	34.4 (28%) (20)	24.1 (37%) (20)	20.2 (31%) (20)	20.5 (32%) (20)

A comparison is also made between all of the species' mandibular and maxillary P3 and P4 occlusal areas (with P2 in NWMs being excluded from this analysis; Table 10). Based on Labonne et al. (2012), who showed that M1 is elongated in the absence of P4 in rats, we might expect to see an elongation and increase in occlusal area on P3 in the OWMs compared to NWMs. For OWMs, P_3 has more occlusal area than P_4 (60% vs. 40%, respectively), but the opposite is seen for the maxilla with more occlusal area on P^4 than P^3 (58% for *Cer. albogularis* and 57% for *Co. guereza)*. For NWMs, *Ceb. capucinus* has 48% of its maxillary occlusal area on P^4, while *A. palliata* has 51% of its occlusal area on P^4. Similarly, *Ceb. capucinus* has 49% of its mandibular occlusal area on P_4. The biggest difference is in *A. palliata's* mandible, which has 54% of occlusal area on P_4 and 46% on P_3.

Table 10. Mean Maxillary and Mandibular Comparison of P4 and P3 Occlusal Area (mm^2), (percentage per type of tooth)

Species	(n)	Maxilla		(n)	Mandible	
		P4	P3		P4	P3
Cer. albogularis	(12)	15.9 (58%)	11.4 (42%)	(14)	13.5 (40%)	20.3 (60%)
Co. guereza	(20)	25.0 (57%)	19.0 (43%)	(20)	20.6 (40%)	30.8 (60%)
Ceb. capucinus	(20)	16.8 (48%)	17.9 (52%)	(19)	14.8 (49%)	15.2 (51%)
A. palliata	(19)	27.0 (51%)	25.6 (49%)	(20)	24.1 (54%)	20.2 (46%)

The jaw is also divided between molars and premolars (including P2 for NWMs) and percentage of occlusal area contributed by these teeth is shown in Table 11. OWMs have more occlusal area on their molars than their premolars. The maxillary and mandibular molars in OWMs account for between 70-73% of their occlusal area, while premolars account for 27-30%. The NWMs have between 44-65% of their occlusal area on molars and 35-56% on their premolars.

Table 11. Mean Occlusal Area (mm^2), (percentage per type of teeth)

Species	Maxilla		Mandible	
	Molars (n)	Premolars (n)	Molars (n)	Premolars (n)
Cer. albogularis	74.5 (73%) (14)	27.3 (27%) (12)	78.5 (70%) (14)	33.8 (30%) (14)
Co. guereza	114 (72%) (18)	44 (28%) (20)	125.4 (71%) (16)	51.4 (29%) (20)
Ceb. capucinus	42.2 (44%) (20)	53.1 (56%) (20)	45.4 (49%) (19)	47.4 (51%) (19)
A. palliata	117.2 (61%) (20)	74.4 (39%) (19)	121 (65%) (20)	64.8 (35%) (20)

The mean and percentage contribution for postcanine mesiodistal length of the premolars and molars is given for each type of tooth on the mandible and maxilla (Tables 12 and 13). Both OWMs display $P^4 > P^3$ but $P_3 > P_4$ in premolar mesiodistal length (*Cer. albogularis* displays 53% on P^4 but 48% on P_4; *Co. guereza* displays 51% on P^4 but 48% on P_4). The NWMs display different distributions in their premolar mesiodistal lengths. *Ceb. capucinus* displays both $P^2 > P^3 > P^4$ and $P_2 > P_3 > P_4$. *A. palliata* displays $P^3 > P^4 > P^2$ but $P_4 > P_3 > P_2$.

Cer. albogularis displays $M^2 > M^1 > M^3$ and $M_2 > M3 > M1$ in molar mesiodistal length. *Co. guereza* displays $M^2 > M^3 > M^1$ and $M_3 > M_2 > M_1$. It was observed that in both species of OWMs, M^2 is the longest maxillary molar but *Cer. albogularis'* second longest is M^1, while *Co. guereza's* is M^3. For the mandible, *Cer. albogularis'* longest molar is M_2, followed by M_3. In contrast, *Co. guereza's* longest is M_3, followed by M_2.

Ceb. capucinus displays $M^1 > M^2 > M^3$ and $M_1 > M_2 > M_3$ in molar mesiodistal length. *A. palliata* displays $M^2 > M^1 > M^3$ and $M_3 > M_2 > M_1$. For the maxilla, M^2 is the longest molar for *A. palliata* followed by M^1. For the mandible, the molars become shorter in mesiodistal length from back to front.

Table 12. Mean Maxillary and Mandibular Postcanine Mesiodistal Length in Old World Monkeys (mm), (percentage per type of tooth)

Maxilla	M3 (n)	M2 (n)	M1 (n)	P4 (n)	P3 (n)
Cer. albogularis	5.5 (31%) (14)	6.2 (35%) (14)	5.9 (34%) (14)	4.3 (53%) (13)	3.8 (47%) (14)
Co. guereza	7.1 (33.5%) (20)	7.2 (34.5%) (20)	6.7 (32%) (20)	5.0 (51%) (20)	4.9 (49%) (20)
Mandible					
Cer. albogularis	6.3 (33.5%) (14)	6.4 (34.5%) (14)	5.9 (32%) (14)	4.7 (48%) (14)	5.0 (52%) (14)
Co. guereza	9.1 (39%) (20)	7.2 (31%) (20)	6.8 (30%) (20)	5.8 (48%) (20)	6.2 (52%) (20)

Table 13. Mean Maxillary and Mandibular Postcanine Length in New World Monkeys (mm), (percentage per type of tooth)

Maxilla	M3 (*n*)	M2 (*n*)	M1 (*n*)	P4 (*n*)	P3 (*n*)	P2 (*n*)
Ceb. capucinus	2.9 (26%) (20)	4.1 (36%) (20)	4.3 (38%) (20)	3.4 (32%) (20)	3.5 (33%) (20)	3.7 (35%) (20)
A. palliata	5.6 (29%) (20)	7.1 (36%) (20)	6.9 (35%) (20)	4.6 (33.5%) (20)	4.7 (34%) (19)	4.4 (32.5%) (20)
Mandible						
Ceb. capucinus	3.9 (30%) (19)	4.3 (33%) (20)	4.8 (37%) (20)	3.6 (31.5%) (20)	3.7 (32.5%) (19)	4.1 (36%) (19)
A. palliata	8.1 (36%) (20)	7.6 (34%) (20)	6.8 (30%) (20)	4.9 (35%) (20)	4.6 (33%) (20)	4.5 (32%) (20)

Postcanine mesiodistal lengths are also added together for all of the premolars and molars; the percentage contributions of the different types of teeth are then cross-compared among the four species (Table 14). Both OWMs' postcanine mesiodistal length has a premolar contribution of 33%, while 67% is contributed by molars. An increase in the percentage contribution by premolars is displayed in both NWMs over OWMs. *Ceb. capucinus* displays a 48% contribution by premolars, while 52% is contributed by molars. *A. palliata* has 40% of postcanine mesiodistal length contributed by the premolars with the remaining 60% being contributed by molars. The postcanine mesiodistal length is 6% larger in *A. palliata* than *Co. guereza* (139.9 mm vs. 132.5 mm, respectively) and 30% larger in *Cer. albogularis* than *Ceb. capucinus* (108.3 mm vs. 93.8 mm, respectively).

Table 14. Mean Maxillary and Mandibular Postcanine Mesiodistal Length of Teeth and Contribution Per Type of Tooth, Right and Left Side of Jaw

Species	Mean Postcanine Mesiodistal Length in mm (%)		
	Postcanine Row (n)	Premolar Row (n)	Molar Row (n)
Cer. albogularis	108.3 (13)	36.0 (33%) (13)	72.4 (67%) (14)
Co. guereza	132.5 (20)	43.7 (33%) (20)	88.8 (67%) (20)
Ceb. capucinus	93.8 (19)	44.7 (48%) (19)	49.1 (52%) (19)
A. palliata	139.9 (19)	55.5 (40%) (19)	84.5 (60%) (20)

A comparison is made between all of the species' mandibular and maxillary P3 and P4 mesiodistal lengths (with P2 in NWMs being excluded because of the absence of a homologue in OWMs; Table 15). A similar display for postcanine mesiodistal length is seen as with occlusal area in that there is a difference between the percentage contributions made by each premolar to the premolar row, but it is less of a difference in percentage distribution than that seen for occlusal area. P_3 is longer than P_4 (52% for OWMs), but the opposite is seen for the maxilla with P^4 longer than P^3 (53% for *Cer. albogularis* and 51% for *Co. guereza*). For NWMs, *Ceb. capucinus* has 49% of its maxillary premolar mesiodistal length on P^4, while *A. palliata* has 50% on P^4. *Ceb. capucinus* and *A. palliata* have 50% and 52%, respectively, of their mandibular premolar mesiodistal length on P_4.

Table 15. Mean Maxillary and Mandibular Postcanine Mesiodistal Length for P4 and P3 (mm), (percentage per type of tooth)

Species	(n)	Maxilla		(n)	Mandible	
Maxilla		P4	P3		P4	P3
Cer. albogularis	(13)	4.3 (53%)	3.8 (47%)	(14)	4.7 (48%)	5.0 (52%)
Co. guereza	(20)	5.0 (51%)	4.9 (49%)	(20)	5.8 (48%)	6.2 (52%)
Ceb. capucinus	(20)	3.4 (49%)	3.5 (51%)	(19)	3.7 (50%)	3.7 (50%)
A. palliata	(19)	4.7 (50%)	4.7(50%)	(20)	4.9 (52%)	4.6 (48%)

Mesiodistal length and percentage of postcanine mesiodistal length of molars and premolars (including P2 for NWMs) for the maxilla and mandible are presented in Table 16 for all species. OWMs exhibit more of their postcanine mesiodistal length percentage on their molars (66-68%) than their premolars (32-34%). NWMs exhibit a more evenly distributed range, with 52-62% on their molars and 38-48% on their premolars.

Table 16. Mean Postcanine Mesiodistal Length (mm), (percentage per type of tooth)

Species	Maxilla		Mandible	
	Molars (*n*)	Premolars (*n*)	Molars (*n*)	Premolars (*n*)
Cer. albogularis	17.6 (68%) (14)	8.1 (32%) (13)	18.6 (66%) (14)	9.7 (34%) (14)
Co. guereza	21 (68%) (20)	9.9 (32%) (20)	23.1 (66%) (20)	12 (34%) (20)
Ceb. capucinus	11.3 (52%) (20)	10.6 (48%) (20)	13 (53%) (19)	11.4 (47%) (19)
A.palliata	19.6 (59%) (20)	13.7 (41%) (19)	22.5 (62%) (20)	14 (38%) (20)

Table 17 presents mean cranial lengths and palatal lengths. Mean maximum cranial length is longest in *Co. guereza* (79.2 mm), followed by *Ceb. capucinus* (75.4 mm), *Cer. albogularis (*73.9 mm) and lastly *A. palliata* (71.4 mm). The average palatal length is longer in both OWMs (39.3 mm in *Cer. albogularis* and 47.2 mm in *Co. guereza*) than it is in NWMs (33.3 mm in *Ceb. capucinus* and 37.8 mm in *A. palliata*).

Table 17. Mean Cranial and Palatal Measurements

Species	(*n*)	Maximum Cranial Length (mm)	Palatal Length (mm)
Cer. albogularis	(14)	73.9	39.3
Co. guereza	(20)	79.2	47.2
Ceb. capucinus	(20)	75.4	33.3
A. palliata	(20)	71.4	37.8

DISCUSSION

This research presents information in regard to the way postcanine occlusal area and mesiodistal length are distributed among and between four species' premolars and molars. Results are summarized in Table 18.

Table 18. Summary of Results of Student's t-Test

Summary of Results	First Paired Species		Second Paired Species	
Postcanine Occlusal Area Per Tooth				
Species	*A. palliata*	*Co.guereza*	*Ceb. capucinus*	*Cer. albogularis*
Significantly larger	$P4,M^2,M^1$ and P^3	M3 and P_3	P_4 and P^3	M3,M2,M1 and P_3
Postcanine Mesiodistal Length Per Tooth				
Species	*A. palliata*	*Co.guereza*	*Ceb. capucinus*	*Cer. albogularis*
Significantly larger	M_2	M3,P4 and P_3	None	M3,M2,M1,P4,P3
Summed Occlusal Area				
Species	*A. palliata*	*Co.guereza*	*Ceb. capucinus*	*Cer. albogularis*
Significantly larger	$\sum P^3,P^4$ and $\sum P^3,P^4,M^1,M^2,M^3$	$\sum P_3,P_4$ and $\sum P_3,P_4,M_1,M_2,M_3$	$\sum P^3,P^4$	$\sum P_3,P_4,$ $\sum M1,M2,M3$ and $\sum P3,P4,M1,M2,M3$
Summed Postcanine Mesiodistal Length				
Species	*A. palliata*	*Co.guereza*	*Ceb. capucinus*	*Cer. albogularis*
Significantly larger	None	$\sum P3,P4,$ $\sum M^1,M^2,M^3$ and $\sum P3,P4,M1,M2,M3$	None	$\sum P3,P4,$ $\sum M1,M2,M3$ and $\sum P3,P4,M1,M2,M3$

Comparing summed postcanine occlussal area on both the maxilla and mandible of *A. palliata* and *Co. guereza* show that there is significantly larger occlusal area on the maxilla of *A. palliata* in comparison to *Co. guereza*. There was also significantly larger occlusal area on the

mandible of *Co. guereza* in comparision to *A. palliata*. This shift in results between the maxilla and mandible is surprising given *Co. guereza's* overall larger body mass and palatal length.

Comparing postcanine mesiodistal length on the M3, M2, M1, P4, and P3 on both the mandible and maxilla of the paired species, results show that between *Cer. albogularis* and *Ceb. capucinus,* the OWM (*Cer. albogularis*) consistently has a larger mesiodistal length per type of tooth for all teeth. This may be due to *Cer. albogularis'* 119% larger body mass in comparison to *Ceb. capucinus.* For the summation of molar mesiodistal length, *A. palliata* is not significantly different from *Co. guereza* on the mandible. This result is surprising, given that *Co. guereza* is 31% larger in body mass than *A. palliata*.

In this study, species with similar diets differ in both the distribution of their postcanine occlusal area and their postcanine mesiodistal length due to a difference in their number of premolars and how this difference affects their postcanine row. *Ceb. capucinus* and *A. palliata* both have more occlusal area and postcanine mesiodistal length on their premolar row than *Cer. albogularis* and *Co. guereza*. Therefore, an extra premolar in the NWMs increases both the occlusal area and mesiodistal length contributed by the premolar row to the overall postcanine row. This result shows more premolars take up a greater proportion of the jaw in NWM than OWMs, rather than the same amount of space being divided differently.

This study shows that the occlusal area for premolars in both OWMs (*Cer. albogularis* and *Co. guereza*) is not evenly distributed between their two teeth. In contrast, for NWMs (*Ceb. capucinus* and *A. palliata*) the occlusal area is fairly evenly distributed among each of the three premolars. This indicates that there is a difference in the way NWMs' occlusal area is distributed across their premolar row due to their retention of P2. Namely, the occlusal area is divided

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differently among NWMs premolars (with the retention of P2) than the OWMs (with only P3 and P4).

This study shows that NWMs have more percentage of their total postcanine occlusal area and mesiodistal length contributed by their premolars than do OWMs. In the case of *Ceb. capucinus*, there is also more occlusal area on the premolar row than the molar row. More occlusal area and mesiodistal length in the premolars of NWMs compared to OWMs may be due to their P2. Perhaps when OWMs lost their P2, in order to capitalize on the empty space freed up by P2's absence, there was a shift to greater occlusal area on the molar row.

In this study, palatal length and cranial length were measured to see if they can be used to standardize length of postcanine teeth of different species. *Cer. albogularis* has a 15% larger postcanine mesiodistal length as well as an 18% larger palatal length than *Ceb. capucinus*. However, *Cer. albogularis* shows a 2% smaller maximum cranial length than *Ceb. capucinus*. *A. palliata* has a 6% larger postcanine mesiodistal length than *Co. guereza*, but *Co. guereza* has a 24% larger palatal length and 11% larger maximum cranial length than *A. palliata.* Therefore, palatal length and cranial length do not seem to have a consistent and reliable relationship with mesiodistal length of postcanines.

Results show that OWMs have a larger percentage of their total postcanine mesiodistal length contributed by their molar row than their premolar row, as was the case with occlusal area. In NWMs, a larger percentage of their total postcanine mesiodistal length is contributed to the premolar row than in OWMs; however, there is still more postcanine mesiodistal length contributed to the molar row in both NWM species than the premolar row (unlike the occlusal area, which had more on the premolar row than molar row for *Ceb. capucinus*).

The most meaningful result is that each premolar is close to the same mesiodistal length of 33% of the premolar row for NWMs, whereas in OWMs each premolar is about of 50% of the premolar row. Therefore, in terms of premolar mesiodistal length, the loss of P2 in OWM species leads to a uniform increase in mesiodistal length of P3 and P4. Likewise, when P2 is present, there is the same mesiodistal length of about 33% on each premolar. Therefore, retention or loss of P2 does not seem to affect proportionate size of premolars and their proportionate contribution to the premolar row.

Labonne et al. (2012) demonstrated how the loss of a tooth can lead to elongation of adjacent teeth in rats. Therefore, it is possible that the loss of P2 experienced by the ancestor species of OWMs in turn favored elongation of their P3 and P4. Early African anthropoids of the Oligocene feature three premolars in some species (*Parapithecus grangeri* and *Apidium moustafai)* but two premolars in others (*Propliopithecus haeckeli* and *Aegyptopithecus zeuxis*). Perhaps simply by coincidence, only the species that retained the third premolar migrated to the Americas, giving rise to the NWMs we see today.

The loss of P2 in catarrhines may be a result of evolutionary constraints on the development of postcanine teeth. Ribeiro et al. (2013) revealed that there is a limit for the size of the premolar field in proportional relation to the secondary palate and molar field, and that the loss of P2 may be associated with an inhibitory effect preventing the formation of P2 produced by the other premolars during tooth development. Therefore, perhaps some yet to be identified evolutionary constraint resulted in the loss of P2 in OWMs and retention in NWMs.

Ribeiro et al. (2013) also stated that species with P2 demonstrated, on average, a larger M1 but an associated smaller M2 and M3, consequently leaving more room for the premolar field than in those species observed without P2. Results in this study are not fully in accord with

this result in Ribiero et al. (2013). Whereas *Ceb. capucinus* has M1 as the largest molar for occlusal area and mesiodistal length, *A. palliata* has M2 as largest of the molars for both occlusal area and mesiodistal length.

A possible explanation for the loss of P2 among catarrhines and retention among platyrrhines includes dietary specializations. Rosenberger (1992) demonstrated how the NWM *Callitrichidae's* loss of M3 is dietarily beneficial in the mastication of insects. Platyrrhines display a variety of diets, though most are largely frugivorous. Perhaps the retention of P2 in platyrrhines has proved advantageous with the available fruit and plant species in the New World (in some cases tougher leaves and harder nuts and seeds (Rosenberger 1992)). Meanwhile, evolution has favored the loss of P2 among catarrhine species subsisting on Old World fruit and plant species. If 3 premolars are advantageous to *Callitrichidae* in masticating the hard exoskeltons of insects, likewise, perhaps three premolars are advantageous with some of the tougher plants and/or harder nuts and seeds found among some New World plant species.

The null hypothesis, that there would be no difference in occlusal area between the paired species' premolar row is not supported. Though the proportional contributions of the individual premolars to occlusal area does not change between the species, NWMs premolar rows contribute more to the overall occlusal area than in the OWM comparisons. In regards to molars, three of the species (with the exception of *Ceb. capucinus*) have their molar row contributing the majority of their occlusal area. All species have the proportional contribution of individual molars to the molar row varying by individual tooth.

Future research on the comparison of postcanine occlusal area and postcanine mesiodistal length between OWMs and NWMs would benefit from species that are closer in body mass and tooth size. Also, measures of standardization, such as jaw length, could prove beneficial when

comparing species. Other areas of future research on this topic could include 1) further analysis on *Ceb. capucinus*' distinctively large premolar field, and 2) whether loss of P2 is associated with enlargement of canine and incisor teeth.

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VITA

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Her academic achievements while attending graduate school include conference presentations at the American Association of Physical Anthropologists (AAPA) and American Anthropological Association (AAA). Her paper presentation earned her an "honorable mention" for the AAA's Biological Anthropology Section Student Award. After earning her M.A. in anthropology, she would like to continue seeking higher education by entering a Ph.D. program in the field of biological anthropology.