Reassessing Extant and Fossil Papionin Taxonomy Utilizing a Novel Non-Metric Analysis of Maxillary Molar Morphology

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by

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Under the Direction of Frank L'Engle Williams PhD

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ABSTRACT

Members of the papionin tribe of cercopithecoid monkeys have had historically contested taxonomic assignments. Assessments of cranial and molar dimension as well as genetic data have limited potential for determining phylogenetic signals, possibly due to instances of hybridization and notable inter-taxon variation. This study aims to reassess papionin taxonomy by means of establishing a standardized methodology to associate absence or degree of presence of non-metric dental traits of papionin maxillary molars and evolutionary relationships. Images and dental casts of papionin dentition were utilized and the seven traits were given appropriate scores according to the criteria outlined in this study. The results of this analysis posit lingual dental trait expression as the most informative regarding phylogenetic signal while features of the occlusal surface vary more among individuals. Covariance of interconulus and novel mesiolingual accessory feature scores in papionins produced the highest predicted probabilities between extant *Papio,* possibly supporting a species designation between *Papio ursinus* and *Papio anubis*. Results did not support species designation between *Parapapio whitei, Parapapio broomi,* and *Parapapio jonesi*, especially when accounting for temporal distribution. This analysis also identified lingual cingulum expression as a means to assess affinity for an ancestral *Papio* condition in extant baboons, which supports a much earlier divergence of southern African baboon taxa.

INDEX WORDS: *Papio*, *Parapapio*, Molar Morphology, Taxonomy, Fossil Primates, Non-Metric Dental Traits

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DEDICATION

This thesis is dedicated to the entire village of individuals who make such a body of work possible. This endeavor is not one I could have accomplished on my own. I want to thank my parents, who always abided my unconventional Christmas lists of microscopes or robotic dinosaurs. I would especially like to credit my mother for never discouraging me from studying the past and staying up late to read countless dinosaur books to me as a child.

Appreciation falls short of expressing my gratitude for my fiancée, Solomon. Without your unwavering support amidst sleepless nights and countless roadblocks, I could not have crossed this finish line.

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INTRODUCTION

1.1 Old World Monkeys: Classification Debates

The taxonomy of the Old World monkeys is highly contested and continuously evolving, especially given the new insights that genetic data provide in understanding evolutionary relationships. Phylogeny, or the concerted study of evolutionary relationships, is therefore of particular interest for redressing historic taxonomic classifications of cercopithecoids. In extant cercopithecoid taxa, morphology, coloration, geographic ranges, dietary niche, and behavior have been the primary historic basis for establishing phylogenetic relationships within the super-family. For fossil taxa, anatomical descriptions have persisted as a primary method for establishing phylogenetic relationships among the cercopithecoids. Delson (1975) argues that morphology of the craniofacial region and dentition have provided the most quantifiable data in terms of establishing these phylogenies.

Extensive literature exists analyzing the craniodental as well as post-cranial anatomy of Old World Monkeys (Delson 1975; Szalay and Delson 1979; Delson and Dean 1993), though historic analysis of such data has opposed findings from molecular data. In more recent anatomical analysis, considerations of allometry have provided findings that align with radiation events and evolutionary relationships established through various genetic techniques (Frost et al. 2003; Gilbert and Rossie 2007; Gilbert 2014). Unlike molecular studies, anatomical insights are still inherently limited by fossil record preservation bias as anatomical structures must be relatively complete in order to provide reliable data points.

Landmark-based analysis of shape, or geometric morphometrics, is another methodology employed to assess phylogenetic relationships of Old World monkeys (Collard and O'Higgins 2002; Collard and Wood 2001). These analyses attempt to quantify differences in complex shapes by utilizing landmarks in anatomical regions of interest, while considering evolutionary allometries (Nishimura et al. 2019). Most recent geometric morphometric analyses align with molecular data in describing the radiation events and phylogenies of extant papionin clades.

Molar dimensions and morphology have also been extensively analyzed as models for Old World Monkey phylogeny. Overall molar size and dimension can be affected by confounding factors such as sexual dimorphism, a characteristic of papionin taxa, as well as individual and clinal variation (Frost et al. 2003; Delson 1975; Swindler 2002). Heritability data also support that shape is a more heritable factor in molariform teeth than size (Harbin 2018).

The taxonomy of papionins is difficult to assess given the lack of agreement regarding species classification, especially in *Papio* (Delson 1973, 1975; Szalay and Delson 1979; Jolly 1993). Much of this disagreement in taxonomy stems from deciding which species concept(s) to employ in both extant and fossil contexts. The Biological Species Concept has been frequently utilized to determine such demarcations on the basis of reproductive isolation. Usage of the Biological Species Concept (BSC) has proved difficult in the case of African papionins as there are observations of wild and captive baboons hybridizing between populations thought to be separate species as well as with *Theropithecus gelada* (Jolly 1997; Jolly et al. 2011). This behavioral observation as well as perceptible clinal variation in modern baboon population morphology has resulted in some researchers classifying all baboons within a single species, *Papio hamadryas*, and demarcated at the subspecies level (Frost et al. 2003).

Given the hybridization across genera observed in *Papio* and *Theropithecus*, others argue that reproductive isolation is not an accurate means of establishing formal taxonomy (Gilbert et al. 2018). The Phylogenetic Species Concept (PSC) is supported by measures of morphological variation in taxa and, in the case of papionins, more readily supports the existence of six extant baboon species: *Papio ursinus, Papio anubis, Papio hamadryas, Papio cynocephalus, Papio kindae,* and *Papio papio* (Gilbert et al. 2018). Even with the aid of molecular techniques, assigning *Papio* populations to the species or subspecies level is not straightforward (Newman et al. 2004).

The lack of agreement in papionin classification extends into the fossil record as well. Reproductive isolation and, by extension, the Biological Species Concept, cannot be assessed in fossil material, meaning most insights are reliant upon morphological insights. The phylogenetic relationships ascertained from various morphological methods do not always align with the estimates provided from molecular techniques. As in any evolutionary context, the lack of fossils which depict exact divergence and radiation events is common, possibly explaining such incongruences.

This study builds on this existing corpus of research to address the complicated phylogeny of papionins using non-metric dental trait score frequencies. This methodology could provide useful data points for assessing evolutionary relationships between fossil and extant papionins which are non-destructive to limited fossil specimens and do not require the financial costs associated with full-genome sequencing.

1.2 Radiations and Fossil Evidence

The formal taxonomy of the “Old World” monkeys is comprised of the super-family Cercopithecoidea, which includes all extant and fossil Old World monkeys (Gray 1821). Within the super-family are the Cercopithecidae, which contain the two subfamilies Cercopithecinae and Colobinae (Gray 1821, Blyth 1875). Colobinae is comprised of the African Colobini tribe and the Asian Presbytini tribe. Within the Cercopithecinae subfamily are two tribes, Cercopithecini and Papionini (Gray 1821, Burnett 1828), the former containing African forest guenons and the latter baboons, mandrills, geladas, mangabeys, and macaques. While this study focuses solely on baboons and their closest relatives, or the subtribe Papionina (Burnett 1828), understanding the phylogeny and taxonomy of the Old World monkeys at large is crucial for assessing phylogenies and radiation events.

Due to the large-bodied nature of most extant and fossil papionins as well as their proclivity for drier environmental niches, there is likely a degree of preservation bias compared to the forest cercopithecids of Africa (Jablonski 2002). This preservation bias of papionin fossils stems from differential taphonomy, or the process by which remains of organisms are preserved and become fossilized at different frequencies depending on environmental factors. More robust skeletal elements in drier environments are more likely to become fossilized due to a reduced rate of decomposition, quicker desiccation, and a decreased likelihood of being scavenged. Smaller skeletal elements in moisture-rich environments, as exemplified by the smaller-bodied forest cercopithecids, are not only more likely to be scavenged, but also have a reduced likelihood of becoming preserved as fossils due to soil acidity, insect density, and other factors characteristic of forest environments which increase the rate of decomposition. Given this disproportionate degree of preservation, fossil representations of major papionin radiation events would presumably be numerous but debate as to how populations are classified is ever evolving. Considering taphonomy and the stringent requirements that must be met for organisms to become fossilized, it is statistically unlikely that the earliest representations of papionins in the fossil record are direct evidence of the earliest radiation events.

The most agreed upon estimates of the radiation of various papionin lineages, therefore, lie in molecular data. Genetic studies have placed the divergence of Papionini and Cercopithecini at an estimated 9-10 million years ago (Ma) (Page et al. 1999), thus demarcating the first radiation of papionins in Africa. However, there is still a lack of consensus regarding papionin phylogeny, and the timing of divergence and radiation events. Liedigk et al. (2014) estimated the *Theropithecus – Lophocebus- Papio* clade to have diverged from the *Mandrillus – Cercocebus* clade around 4-5 Ma. Others have placed this divergence between 6-10 Ma with *Theropithecus, Lophocebus,* and *Papio* separating 4-5 Ma (Disotell and Raaum 2002; Gilbert 2013; Pozzi et al. 2014). While it is typically expected that morphological analysis of the fossil record will underestimate divergence dates and radiation events, large discrepancies between morphological and molecular analysis prevail in many instances.

The earliest representations of Cercopithecoid monkeys in the fossil record are contested as there are few fossil individuals from the Early to Middle Miocene that are undoubtably attributable to the super-family. Fossil individuals from the Fayum region of Egypt such as *Parapithecus* and *Apidium* have been presumed as possible ancestors to the cercopithecoids (Simmons 1967), but the seemingly derived ape-like dentition has excluded them as direct ancestors to the members of Cercopithecoidea (Delson 1975). Several species of the genus *Victoriapithecus* found in East Africa present papionin-like molars and possible post-cranial adaptations for terrestrial proclivities, but derived dental characteristics for leaf-eating likely places it as ancestral to colobines (Delson 1975; Gilbert 2013). Fossil evidence of cercopithecoid monkeys in the middle to late Miocene is poorly represented and therefore most inferences of radiation events are from genetic estimates (Gilbert 2013; Liedgk et al. 2014; Newman et al. 2004).

It has been estimated that papionins emerged and began to occupy semi-terrestrial niches throughout Africa in the Middle Miocene, though fossil evidence of undisputed papionins from this era is scarce, with most accepted individuals dating to the Pliocene (Delson 1975). The earliest papionin fossils are represented by macaque-like ancestral forms found throughout North Africa and Southern Europe with species such as *Macaca libyca* and *Macaca sylvanus prisca* (Gervais 1859; Delson 1975, 1980; Jablonski 2002). Asian radiations of the *Macaca* lineage appear in the Plio-Pleistocene, represented by several proposed and debated species, such as *Procynocephalus* and *Paradolichopithecus*.

Parapapio, a probable direct ancestor to *Papio*, is estimated to be the earliest genus of the Papionina sub-tribe (Jablonski 2002; Page et al. 1999). *Parapapio lothagamensis* is one of few papioninans of the Late Miocene represented in the fossil record with specimens in Kenya and Ethiopia dating between 11-3.6 Ma (Leakey et al. 2003). *Parapapio ado*, localized to Pliocene Tanzania and Kenya, and *Parapapio whitei* are represented in East African fossil deposits and are described as possessing more ancestral craniodental traits compared to the South African species (Jablonski 2002). The majority of *Parapapio* fossil species are represented in South Africa at Makapansgat, Bolt's Farm, Sterkfontein, Swartkrans, Kromdraai, and Taung. Species found in South African sites include *Parapapio antiquus, Parapapio broomi, Parapapio jonesi,* and *Parapapio whitei,* the only species found in both East and South African sites (Jones 1937; Broom 1940; Haughton 1925; Hopwood 1936).

The earliest fossils of *Theropithecus* are dated to 3.5-4 Ma in Kenya (Delson 1975), but eventually range throughout Asia, Europe, and Africa. The presence of subgenera is debated with *Theropithecus* (*Theropithecus*), which includes the extant gelada, and *Theropithecus* (*Omopithecus*) on the basis of craniofacial morphology (Delson 1993; Jablonski 2002). Possible distinctions of subgenus aside, fossil *Theropithecus* includes 5 species: *T. darti, T. oswaldi, T.*

baringensis, *T. brumpti* and *T. quadratirostris* (Andrews 1916; Broom and Jensen 1946; Leakey 1969; Delson 1993).

Fossil evidence of *Cercocebus* and *Lophocebus* is relatively sparse and is represented primarily by fragmentary remains (Jablonski 2002). Both *Cercocebus* and *Lophocebus* fossils are found in East African Plio-Pleistocene deposits, with some *Cercocebus* discovered at Makapansgat. Two taxa, *Dinopithecus ingens* and *Gorgopithecus major,* are hypothesized as South African descendants of *Parapapio* with specialized enamel structure, though *Gorgopithecus* is represented by relatively small amounts of fossil material, causing debate regarding the denotation of a separate genus (Freedman 1957; Jablonski 1994, 2002).

The fossils of the genus *Papio,* as in the extant taxa, are contested in classification. Individuals assigned to *Papio* have been frequently reassigned to *Parapapio* and *Theropithecus* (Delson and Dean 1993; Jablonski 2002) and re-classification on the species and subspecies level occurs frequently. Four fossil *Papio* species/subspecies that are widely accepted include *Papio izodi, Papio* [?*hamadryas*] *angusticeps, Papio* [?*hamadryas*] *robinsoni,* and *Papio* [?*hamadryas*] *botwswanae* (Gilbert et al. 2018). While the majority of fossil *Papio* material is found in South Africa at sites including Swartkrans, Cooper's Cave, Kromdraai, Bolt's Farm, Taung, and Sterkfontein, some remains attributed to *Papio* sp. indet, have been found in Pliocene deposits from Tanzania and Kenya.

Assessing chronology of the fossil-bearing sites in South Africa has important implications for estimating age ranges of various papionin taxa. Given the lack of volcanic activity in southern Africa, geochronology in South African contexts is difficult to ascertain as most typical radiometric dating methods, which rely on volcanic elemental signatures, cannot be employed (Frost et al. 2022). Since these South African localities produce hominin fossils, the geochronology has been assessed frequently utilizing the cercopithecoid taxa as comparative proxies. This provides a wealth of information regarding dating and distribution of papionin taxa within these South African contexts.

Makapansgat (2.8-2.0 Ma) is estimated to be the oldest fossil site, containing such taxa as *Theropithecus darti, Parapapio jonesi, Parapapio broomi,* and *Parapapio whiteii* (Frost et al. 2022). Members 2 and 4 of Sterkfontein are dated similarly and, excluding *T. darti*, contain the above-mentioned *Parapapio* taxa with the addition of a smaller-bodied *Papio*: *Papio izodi*. Later members of Sterkfontein (Member 5) contain *Theropithecus oswaldi* and possibly *Papio robinsoni* (Heaton 2006). Swartkrans Member 1 (2.1- 1.7 Ma) has produced *T. oswaldi, D. ingens, P. robinsoni,* and *Gorgopithecus major*. It is important to note that the genus *Parapapio* is no longer present in sites more recent than pit 23 at Bolt's Farm (2.6-2.0 Ma) except for *Parapapio jonesi* at Swartkrans. More recent sites such as Kromdraai A and B contain *P. robinsoni, P. h. angusticeps, G. major* and *T. oswaldi*.

1.3 **Study Aims, Design, and Hypotheses**

This study utilizes both dental casts and images of extant and fossil papionins from the Georgia State University dental microwear lab. The extant taxa represented in this study include (see appendix) *Papio ursinus* (n = 22), *Papio anubis* (n = 27), *Papio kindae* (n = 12), and *Papio cynacephalus* (n = 15). Given the possible designation of all extant *Papio* taxa into *Papio hamadryas*, the inclusion of this taxon for future datasets is crucial to further test the efficacy of the methodology employed. This taxon, as well as *Papio papio*, were only excluded due to lack of representation of maxillary dentition in the dental cast collection. The extinct *Parapapio* genus is represented here by *Parapapio broomi* (n = 7), *Parapapio whitei* (n = 4), and *Parapapio jonesi* (n = 3). Extinct *Papio* is represented in this study solely by *Papio robinsoni* (n =4).

Debate still exists as to whether extant baboon taxa belong to a single species, *Papio hamadryas,* with multiple subspecies, or if these populations represent differentiation on the species level. While there is significant phenotypic and behavioral variation among these groups, the ability to inbreed questions the validity of a true species demarcation. The four extant taxa selected vary significantly in geographic distribution as well as size, providing a decent proxy to test whether the distribution of non-metric dental traits is affected by any of these extenuating factors. The extant *Theropithecus gelada* is not included in this study, not as an intentional measure, but due to lack of representation in the present dental cast collection. Future efforts would hope to include this species.

Parapapio whitei, Parapapio jonesi, and *Parapapio broomi* have been included in this analysis due to continuously evolving controversy regarding the placement of these taxa into separate species categories. *Papio robinsoni* is of particular interest in its possible classification as a subspecies to the modern *Papio* species (*Papio hamadryas robinsoni*). Substantial overlap in frequency of non-metric dental traits may illustrate a sub-species classification rather than the typical species classification.

Temporal differences between these South African fossil sites can possibly influence how the results of this study are interpreted. It has been observed that species may experience degrees of microevolutionary change that is expressed anatomically. *Parapapio whitei,* for example, has been recovered from Pliocene fossil deposits in Kenya and East Africa as well as in Plio-Pleistocene deposits in South Africa. The *Parapapio whitei* individuals from East Africa have been described as possessing more primitive craniodental traits while the South African individuals appear more derived in their morphology (Jablonski 2002).

With microevolution in mind, the temporal factor must be considered when interpreting the statistical results. Individuals from Sterkfontein and Makapansgat are decidedly older than those from Swartkrans, Kromdrai, Cooper’s, and Bolt’s Farm. Trends in non-metric dental traits may depict a change of frequency over time rather than taxonomic classification. While this is a notable caveat to consider, significantly different results between taxa from a similar temporal distribution could be considered a more powerful indicator of phylogeny.

1.4 Justification for Non-Metric Dental Scoring Systems

The Arizona State University Dental Anthropology System (ASUDAS), a standardized scoring system, has utilized non-metric dental traits in anatomically modern humans as a research method to assess population movements and genetic drift in modern and past populations (Turner et al. 1991). Several studies have utilized the ASUDAS to assess phylogenetic relationships in fossil hominins, indicating a precedent for using this methodology outside of the species *Homo sapiens* (Louail and Prat 2018; Liao et al. 2019). Hlusko and Mahaney (2003) have similarly used the ASUDAS as a reference to create non-metric dental trait scoring criteria for non-human primates. The traits utilized in these scoring systems have been selected with the assumption of being not only heritable, but also relatively selectively neutral, meaning that they persist as indicators of genetic drift rather than natural selection (Scott et al. 2018).

Frequencies of these various traits can then be statistically analyzed to express possible evolutionary relationships between and among primate species and populations (Pilbrow 2013). Applications of such classification systems to fossil materials typically include comparison to extant populations with known, or at least better understood, phylogenetic relationships. This comparison may pose difficulty given the aforementioned lack of agreement on formal classification of extant papionins, though it could be useful in assessing such controversial phylogenies in the extant members sampled.

Several assessments of the heritability of dental traits have occurred in the biomedical field with implications for human orthodontia (Santana et al. 2020; Paul et al.

2022). These studies have assessed cusp size, overall tooth dimension, and dental arcade shape with varying results regarding heritability. Analysis of the heritability of molar dimensions in *Macaca mulatta* illustrate that the majority of cheek-teeth dimensions are under a high degree of genetic control with the exception of P3, likely attributed to the role of this premolar in the development of the sexually dimorphic honing complex (Hardin 2018).

The presence of a cingular remnant of the mandibular and maxillary molars is observed to be the ancestral mammalian and primate condition (Hlusko and Mahaney 2003). The fossil record indicates a reduction of this trait through time (Hartwig 2002) and the feature is variably expressed throughout the various primate radiations. In anthropoids, the varied expression of well-documented features such as Carabelli's cusp, the parastyle, and the protostyle are estimated to be remnants of the ancestral cingulum (Scott and Turner 1997; Hillson 1986; Swindler 2002). Hlusko and Mahaney (2003) examined the interconulus and interconulid of *Papio anubis* (*Papio hamadryas anubis*) and *Papio cynocephalus* (*Papio hamadryas cynocephalus*) to determine heritability of this possible representation of the primitive cingular remnant using a ranked, non-metric approach. Given the high degree of heritability observed in Hlusko and Mahaney's (2003) study, the methodology for scoring the interconulus is adopted in the present study to assess trait score frequency in relation to phylogenetic signal.

Aside from limitations of the interpretation of dental traits in assessing taxonomy, there are inherent limitations when analyzing fossil material. These traits are only informative in taxa that are represented by dentition that includes intact molar crown structure. Heavy attrition on the occlusal surface of the molars can obscure crown morphology, thus limiting the sample size to young adults, subadults and juveniles with unworn permanent crown morphology. Some traits can, at times, be unaffected by occlusal wear, but missing or incomplete data are often incompatible with several statistical analyses for non-parametric data. With traits that have proven to be highly heritable and used as a model for phylogeny, such as the interconulus and novel mesiolingual accessory features (analogous to Carabelli's cusp), these individuals can likely still be scored and analyzed.

Papionin maxillary molars have four cusps and are bilophodont with moderate shearing crests (Swindler 2002). Bilophodonty appears to be the ancestral condition of cercopithecoid teeth, with bunodonty being a more derived form in papionins (Jablonski 2002). The relatively low shearing crests compared to colobines likely reflects dietary proclivity, as the terrestrial baboons and relatives are observed to consume more hard objects rather than foliage. While having lower shearing crests than other cercopithecoids, the crests are significantly higher than those seen in humans and hominins.

Utilizing a non-metric analysis of bilophodont papionin teeth is difficult in the sense that the majority of scoring systems are based upon the hominoid molar condition. Certain dental landmarks observed in the frugivorous ape dentition do not appear in any of the sampled papionin dentition. Analogous features do exist, though are not necessarily identical in presentation, and have utility in assessing evolutionary relationships.

In attempting to analyze papionin phylogenetic relationships with applications to the fossil record, creating a methodology focused on dentition aligns with the preservation bias of teeth. The exceptionally resilient composition of the enamel matrix of vertebrate dentition allows for much higher rates of preservation compared to other skeletal elements (Pilbrow 2003). Aside from cases with exceptional antemortem attrition and wear, dentition can be more informative than other skeletal elements in fragmentary contexts. Where a fragmentary skeletal element requires projection estimations and levels of bias in reconstruction, a singular tooth, if intact, could more clearly be assigned to a taxonomic identifier. In fact, most of the vertebrate fossil record is comprised of dental elements.

In primates and most other heterodont mammals, the molars and cheek teeth possess a high degree of complexity compared to the incisors and canines (Pilbrow 2003). The morphology of molars in humans and Old World monkeys have been assessed to be under a high degree of genetic control, likely due to implications for successful mastication within ecological dietary niches (Hardin 2019; Santana et al. 2020; Stojanowski 2022). These high degrees of heritability give molars exceptional utility for assessing phylogenetic relationships. Overall molar size shows a lesser degree of heritability than expressions of shape, further justifying the use of non-metric analysis for assessing phylogenies from dentition (Hardin 2018). The complex occlusal morphology of molars provides more intricate patterns of genetic expression and therefore a greater degree of information about phylogeny than other teeth such as single-cusped incisors and canines.

The ASUDAS has relied on the assumption that many of the dental traits assessed are likely to be selectively neutral rather than increasing or decreasing the reproductive fitness of individuals (Scott et al. 2018). While these traits appear to be highly heritable, the complexity of features do not undergo significant change under minor selective pressures (Hardin 2018; Hlusko and Mahaney 2003). By following methodologies presented in the ASUDAS, maxillary molar traits in papionins would likely represent phylogenetic signal and exclude more volatile components of morphology that are influenced by various environmental selective pressures. Therefore, an in-depth analysis of non-metric trait score frequencies for papionin dentition, as developed in the present study, has the potential to assess the complex phylogenetic history of this primate group in a way that solely focuses on selectively neutral traits.

2 MATERIALS AND METHODS

2.1 Dental Traits Selected for Analysis

Many dental traits utilized in scoring systems like the ASUDAS do not have direct analogues in papionin dentition due to the presentation of bilophodont molar crown structure and high shearing crests. The sulcus obliquus (distolingual groove), distoconulus, protoconule, and centroconule, as outlined by Swindler (2002), and the crista obliqua (Louail and Prat 2018) are not represented in any of the eight taxa sampled.

A split hypocone (Bailey et al. 2017), otherwise described as a bifurcated hypocone (Scott et al. 1991; Scott and Irish 2017) or double cusp 6 (Louail and Prat 2018), is observed in the papionins sampled and scored based upon absence or presence. Degree of lingual and buccal cingulum expression are also directly analogous to the molar morphology expressed by papionins. Other features including Carabelli's trait/cusp as well as the mesial and distal foveae have analogous structures seen in papionins, but this study employs a novel scoring of trait expression designed for papionin molar structure. This study also utilizes scoring of the interconulus, a proposed expression of the cingular remnant, which has previously been used to assess heritability of dental traits in modern baboon populations (Hlusko and Mahaney 2003).

2.1.1 Mesiolingual accessory feature (Carabelli's trait/cusp analogue)

Carabelli's trait/cusp is observed on the mesiolingual region of maxillary molars in humans and hominoids. While papionins across taxa present a variable expression of a mesiolingual element, the criterion in the ASUDAS does not adequately represent the variation seen in papionin dentition. The shape of papionin molars does not facilitate a cingulum-protocone crest nor a free apex. The criterion for this mesiolingual element in papionin molars is based on indentation shape/size and whether the accessory feature creates a complete ring.

0: Absence of an accessory feature

1: Incomplete ring formed, interrupted by oblong shaped indentation

2: Incomplete ring formed, interrupted by slender indentation

3: Mostly complete ring, slight/no interruption with central slender indentation

4: Complete ring with only a small circular indentation contained within

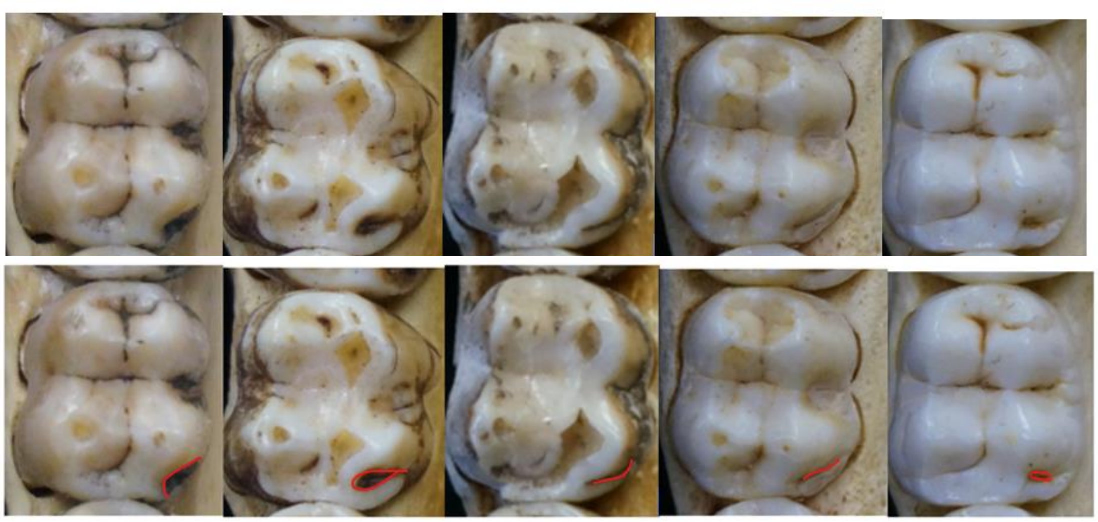

Figure 1 Papio molars showing five expressions of the mesiolingual accessory feature. Trait stages are demarcating in red on the bottom row; the top row shows the same molars without demarcation of the features.

2.1.2 Interconulus

The interconulus is located at the most lingual margin of the lingual groove. This is an accessory feature resting inferior to the occlusal surface of the molar and is scored on its absence or degree of presence utilizing a similar scoring pattern as Hlusko and Mahaney (2003). Scores for this feature are based on the number and intensity of supernumerary cusps.

0: No supernumerary cusps formed

1: One supernumerary cusp formed

2: Two supernumerary cusps formed, relatively flat with no apex on cusps

3: Two supernumerary cusps formed, raised appearance with at least one cusp having an

apex

4: Three or more supernumerary cusps formed

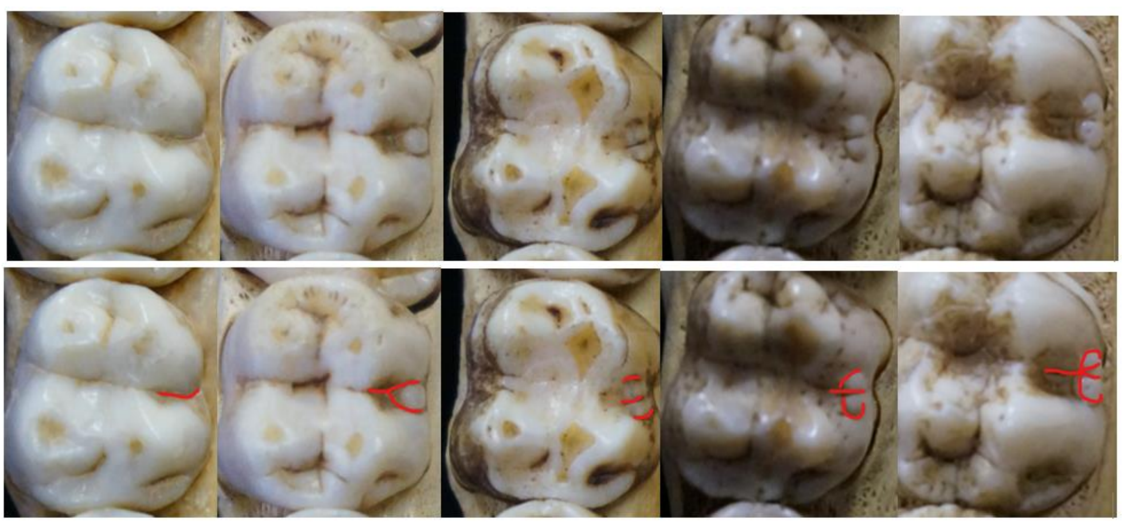

Figure 2 Papio molars showing five expressions of the interconulus. Morphology shown above and demarcation of traits shown below in red.

2.1.3 Mesial Fovea

The mesial fovea is a feature characteristic of papionin molar morphology, although varying degrees of expression were observed. This trait is scored on the complete or incomplete ring formed around the indentation feature.

1: Incomplete ring, caused by any interrupting ridge or indentation

2: Complete ring with no interruptions

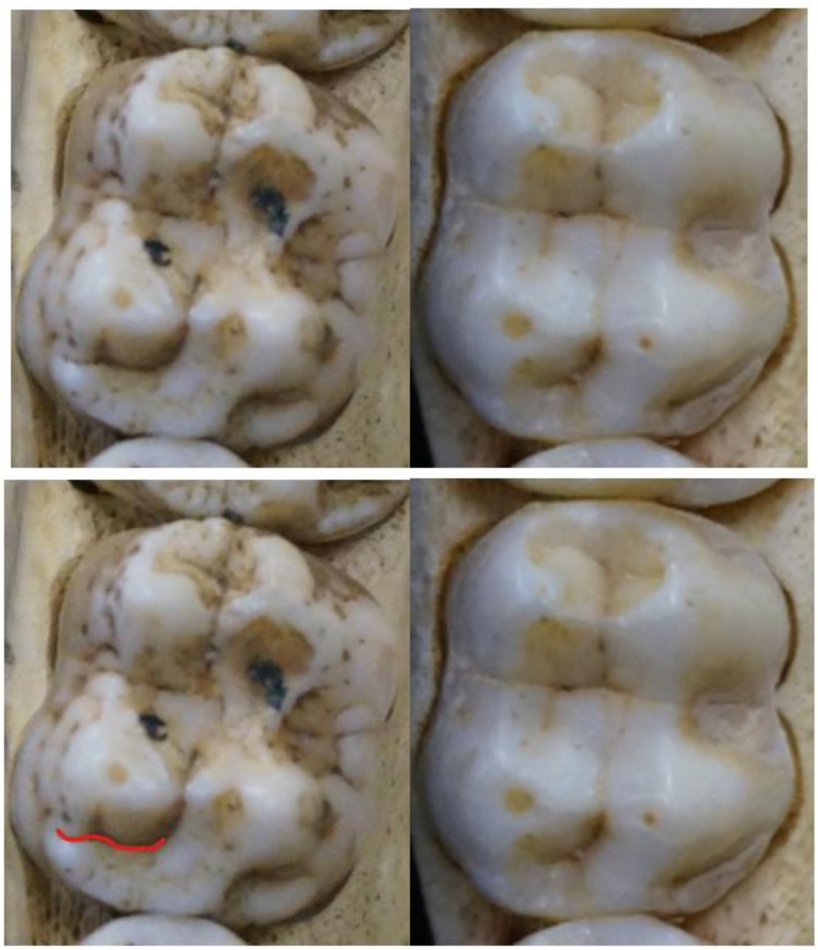

Figure 3 Papio molars showing two expressions of the mesial fovea. The left shows a score of 1 and the right shows a score of 2.

2.1.4 Distal Fovea

See above, but distal.

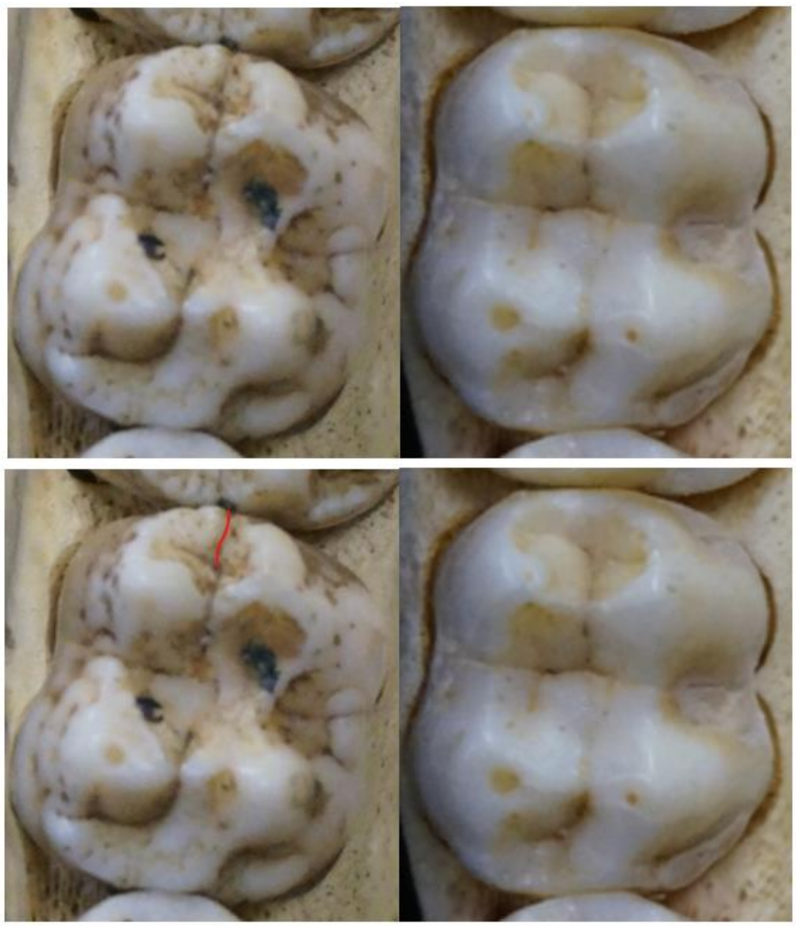

Figure 4 Papio molars showing two expressions of the distal fovea. The left shows a score of 1 while the right shows a score of 2.

2.1.5 Split hypocone

A split hypocone is observed when a ridge interrupts the apex of the hypocone and is scored as being either absent or present.

0: Absence of split hypocone

1: Presence of split hypocone

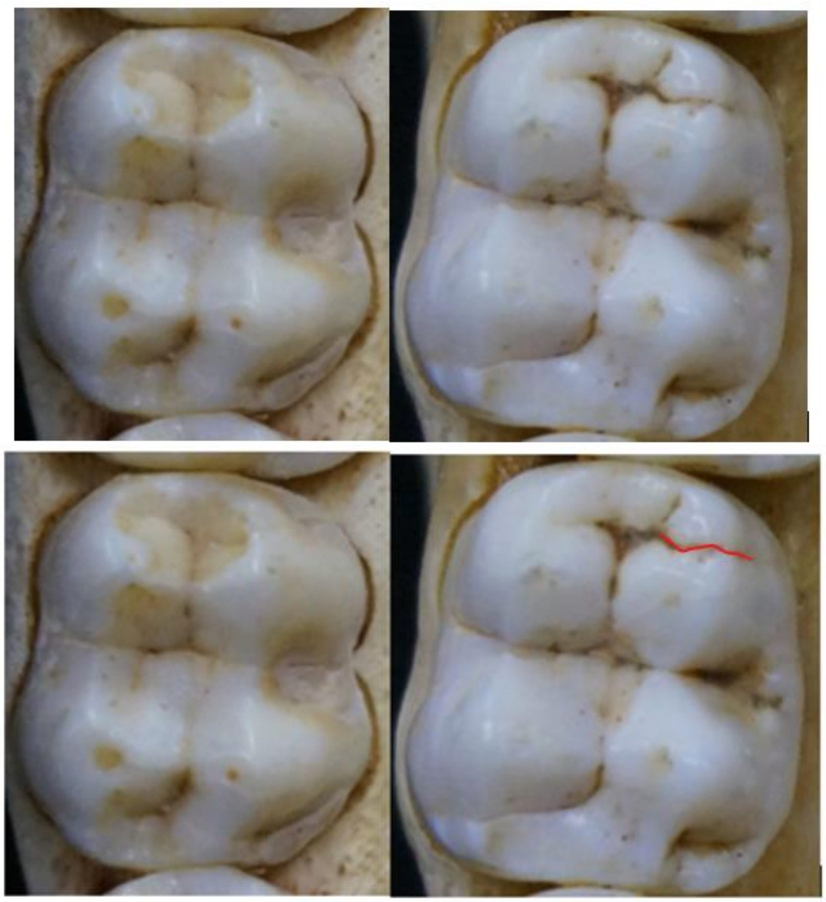

Figure 5 Papio molars showing absence or presence of a split hypocone. The left illustrates absence, or a score of 0, while the right shows a score of 1, or presence.

2.1.6 Lingual Cingulum

Ridge observed on the lingual edge of maxillary molars. The lingual cingulum houses the mesiolingual accessory. This feature is scored on absence or degree of presence. In this instance, degree of presence is quantified based on how far distally the feature reaches.

Increased scores for these traits essentially correspond to length of the feature, and do not account for width.

0: Absence of lingual cingulum

1: Cingulum does not extend beyond the most lingual point of the protocone

2: Cingulum extends to the lingual groove, but does not connect to hypocone

3: Cingulum extends to the most lingual aspect of the hypocone but does not pass this

point.

4: Cingulum extends beyond the hypocone, reaching the distal edge

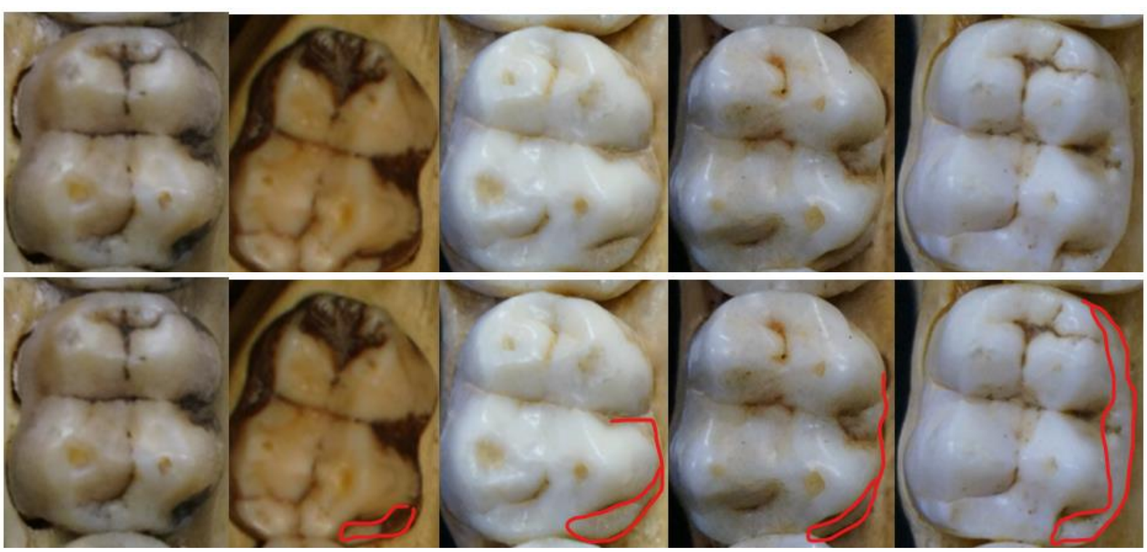

Figure 6 Papio molars illustrating five expressions of the lingual cingulum. Morphology shown above with demarcations in red below.

2.1.7 Buccal Cingulum

The buccal cingulum follows the same patterns seen in the lingual cingulum and uses equidistant buccal landmarks. Like the lingual cingulum, this trait is an expression of length, rather than width or shape.

0: Absence of buccal cingulum

1: Cingulum is limited to the most mesiobuccal region, does not extend beyond the

paracone

2: Cingulum reaches buccal groove but does not connect to the metacone

3: Cingulum extends to most buccal edge of the metacone, but does not surpass this point

4: Cingulum extends beyond the metacone, reaching distal edge

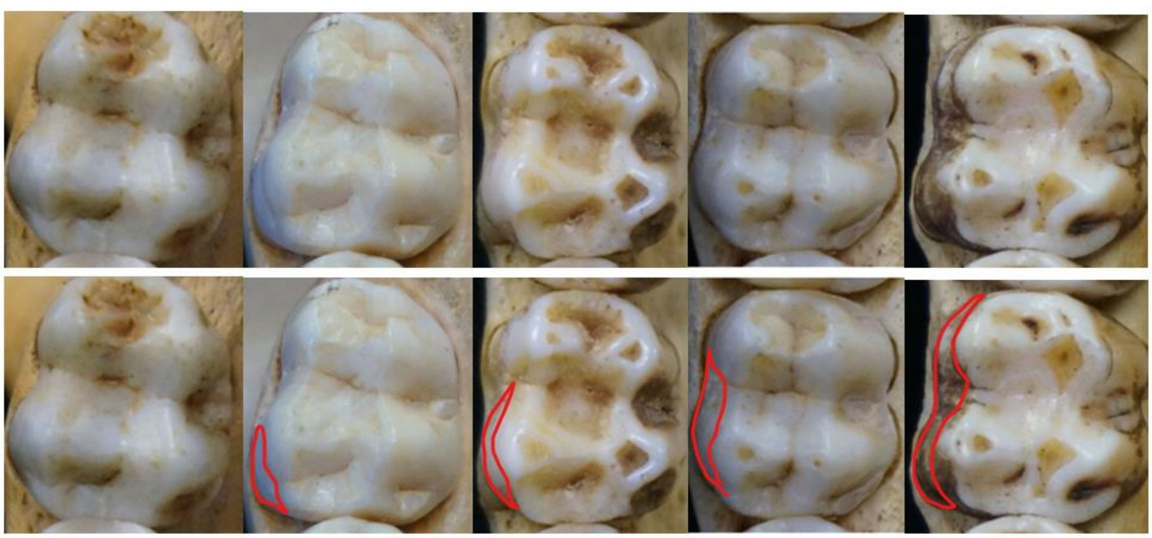

Figure 7 Papio molars showing five expressions of the buccal cingulum. Morphology shown above with demarcations in red below.

2.2 Statistical Methods Employed

2.2.1 Univariate Tests

Univariate analysis of these scores can explain the extent to which one specified dental trait is phylogenetically informative. Traits that are related to the primitive lingual cingulum, for example, have been assessed as highly heritable and not mediated by dietary proclivity. These traits would be important in assessing relatedness. Univariate analysis, while explaining phylogenetic trends regarding specific traits, serve as a proxy to assess which traits vary significantly between taxa, but do not account for covariance with other dental features.

The ranked, categorical data associated with a score-based analysis are non-parametric by nature. While most non-parametric tests are less statistically powerful than the parametric measures, the applications to inferences of fossil material result in a more robust analysis (Vrbin 2022). The Kruskal-Wallis H test is used in this analysis as a means to determine significant difference between the central tendency of taxa. This test is crucial for reassessing species and subspecies assignments of both fossil and extant papionins. Before a Kruskal-Walis H test could be performed, shape of distributions had to be assessed to determine whether median or mean rank was the appropriate test statistic for the data. Due to high variability in sample size for each taxon and non-normal distribution, mean rank was assessed as the most appropriate measure to not violate assumptions of the Kruskal-Walis H test. Subsequent significance values for both the Kruskal Wallis tests and pairwise comparisons in this analysis are based on mean rank of scores for each trait.

A Chi-Square test is also employed in this study to assess the observed expression of specified dental traits versus the expected value. Chi-squared tests have frequently been utilized to justify species designation in the fossil record, especially when assessing ranked or scored data.

2.2.2 Multivariate Tests

A multivariate analysis includes multiple dependent variables, or in this case, the scores of multiple traits for each individual. While multivariate analysis gives an idea of the efficacy of individual traits in regard to phylogenetic signal, it is more likely to show overall group behavior with emphasis on covariance of all the non-metric traits. Multivariate tests such as a Multiple Correspondence Analysis help to illuminate complex relationships between taxa and multiple non-metric dental trait expression, rather than the distribution of a specific trait in different populations.

A principal components analysis (PCA) is frequently utilized to reduce dimensions of complex data while preserving essential information. This multivariate tool is utilized often in analyses of fossil data. A typical PCA, while not wholly excluding non-parametric data, relies upon the variance structure of continuous variables and does not accurately assess the variance displayed in categorical variables. A Multiple Correspondence Analysis (MCA) is able to perform dimension reduction upon a dataset with two or more categorical variables, such as the seven scored traits utilized for this study. An MCA thereby assigns two vector axes based on highest eigenvalues and proportion of variances retained for each dimension. Like a PCA, an MCA illustrates behavior and clustering of individuals in relation to variables, but treats each score category as a variable, rather than using central tendency for each dental feature.

Limitations to a Multiple Correspondence Analysis are shared with other factor analysis methods in that there is no tolerance for missing data points as well as an exclusion of values of “0”. Given the limitations of working with incomplete fossil material, several steps had to be taken to prepare the data set for factor analysis. None of the *Papio ursinus* individuals represented by casts in this study had fully observable lingual and buccal margins with which a score for the lingual and buccal cingula could be assigned. This resulted in a minimum of two MCA’s to be performed: one which excluded *Papio ursinus* and assessed all traits in the remaining taxa and another which excluded the buccal and lingual cingulum but included all taxa. For all MCA’s performed, individuals containing missing values for any singular variable had to be excluded by means of the “na.omit” function in R.

All traits included in this study had a possible score of zero, which would indicate absence of the respective dental feature. The default setting of the MCA procedure in the *FactoMineR* package is to exclude values of zero for assessments of variance. Due to the high prevalence of the value “0” in this dataset, a dummy dataset had to be created which treated the integer “0” as a non-number value represented by the symbol “0”. This transformation allowed for the value of zero to be retained in the dataset, as absence of dental traits was a measure intended to be analyzed in this study as it pertains to phylogenetic signal.

2.2.3 Regression Analysis

Given that ideal applications for this scoring procedure would be predictive, a regression model which predicts taxonomic category on the basis of score for a respective trait would be a useful application. Given the non-parametric nominal values obtained from a scoring system, a typical linear regression model is not applicable. Logistic regression, however, is a means to identify predictive regression models from such data. With significant variation in sample sizes, and some taxon being represented by only a few individuals, the central tendency of the dataset used in the logistic regression must be checked via a resampling method.

2.2.4 Computerized Resampling

The process of bootstrapping a data set essentially resamples a population multiple times in order to mimic different populations that could have been sampled. Bootstrapping is typically employed when the distribution of data is non-parametric, and is especially useful when assessing fossil material, where sampling is non-random. The computerized resampling procedure provides confidence intervals and parameter estimates through which a range of plausible values can be assessed (DiCiccio and Efron 1996). Bootstrapping has also been employed in analysis of fossil material to estimate values where data points are missing. The use of bootstrapping here helps to not only buffer against the inherently limited samples presented in the fossil record, but also to assess central tendencies of non-normally distributed data with specified intervals of confidence. For the purpose of assessing phylogenetic signal, overlapping confidence interval values used in tandem with results from pairwise comparison could possibly invalidate significant differences between taxa, while non-overlapping intervals would support significantly different expression of the traits between taxa.

Bootstrapping is thereby a means to assess accuracy and distribution of central tendency for each taxon and provides a test of regression model fit. If the mean score of each taxon for the tested traits falls within the 95% confidence interval for resampled mean score, then the results of the logistic regression are likely representative of the overall population. Bootstrapping, however, still cannot accommodate entirely missing data, so no population estimates for the buccal and lingual cingulum could be given for *Papio ursinus*.

3 RESULTS

3.1 Univariate Tests

3.1.1 Mesiolingual Accessory Feature

3.1.1.1 Kruskal-Wallis H test and Pairwise Comparison

Independent-Samples Kruskal-Wallis Test Summary

Total N	215
Test Statistic	105.503[a]
Degree Of Freedom	7
Asymptotic Sig.(2-sided test)	<.001

a. The test statistic is adjusted for ties.

Table 1 Kruskal-Wallis mesiolingual accessory feature

Pairwise Comparisons of Species

Sample 1-Sample 2	Test Statistic	Std. Error	Std. Test Statistic	Sig.	Adj. Sig.[a]
Pp. white-P. ursinu	1.023	21.999	.046	.963	1.000
Pp. white-Pp. broom	3.005	22.800	.132	.895	1.000
Pp. white-Pp. jones	10.500	25.403	.413	.679	1.000
Pp. white-P. kindae	20.602	21.692	.950	.342	1.000
Pp. white-P. cynoce	38.105	20.038	1.902	.057	1.000
Pp. white-P. robins	92.727	28.804	3.219	.001	.036
Pp. white-P. anubis	100.630	19.203	5.240	<.001	.000
P. ursinu-Pp. broom	-1.982	18.934	-.105	.917	1.000
P. ursinu-Pp. jones	-9.477	21.999	-.431	.667	1.000
P. ursinu-P. kindae	19.580	17.584	1.113	.266	1.000
P. ursinu-P. cynoce	37.082	15.498	2.393	.017	.468
P. ursinu-P. robins	91.705	25.852	3.547	<.001	.011
P. ursinu-P. anubis	99.607	14.402	6.916	<.001	.000
Pp. broom-Pp. jones	-7.495	22.800	-.329	.742	1.000
Pp. broom-P. kindae	17.597	18.576	.947	.343	1.000
Pp. broom-P. cynoce	35.100	16.615	2.113	.035	.970
Pp. broom-P. robins	89.722	26.537	3.381	<.001	.020
Pp. broom-P. anubis	97.625	15.597	6.259	<.001	.000
Pp. jones-P. kindae	10.102	21.692	.466	.641	1.000
Pp. jones-P. cynoce	27.605	20.038	1.378	.168	1.000
Pp. jones-P. robins	82.227	28.804	2.855	.004	.121
Pp. jones-P. anubis	90.130	19.203	4.694	<.001	.000
P. kindae-P. cynoce	17.503	15.058	1.162	.245	1.000
P. kindae-P. robins	-72.125	25.591	-2.818	.005	.135
P. kindae-P. anubis	80.028	13.927	5.746	<.001	.000
P. cynoce-P. robins	-54.622	24.205	-2.257	.024	.673
P. cynoce-P. anubis	62.525	11.179	5.593	<.001	.000
P. robins-P. anubis	7.903	23.518	.336	.737	1.000

Each row tests the null hypothesis that the Sample 1 and Sample 2 distributions are the same.

Table 2 Pairwise Comparison mesiolingual accessory feature

A Kruskal-Wallis H test was performed for each variable in order to assess the significance of pairwise comparison between taxa. The results of the Kruskal-Wallis H test for the mesiolingual accessory feature indicate a significant difference between taxa ($p > 0.001$). Resulting pairwise comparisons show that in the extant taxa, *Papio anubis* is significantly different from *Papio ursinus* ($p = 0.000$), *Papio cynocephalus* ($p = 0.000$) and *Papio kindae* ($p = 0.000$). *Papio cynocephalus, Papio kindae,* and *Papio ursinus* are not significantly different from each other. The extinct taxa show *Papio robinsoni* as significantly different in expression from two other fossil taxa: *Parapapio whitei* ($p = 0.036$) and *Parapapio broomi* ($p = 0.020$). None of the three *Parapapio* species in this study were significantly different from each other. When comparing extinct to extant taxa, *Papio robinsoni* is not significantly different in expression of the mesiolingual trait from any extant taxa except *Papio ursinus* ($p = 0.011$). All three *Parapapio* taxa in this study, *Parapapio whitei* ($p = 0.000$), *Parapapio jonesi* ($p = 0.000$) and *Parapapio broomi* ($p = 0.000$) are significantly different from *Papio anubis*.

3.1.1.2 Chi-Square test of Independence

Chi-Square Tests

	Value	df	Asymptotic Significance (2-sided)
Pearson Chi-Square	139.980[a]	28	<.001
Likelihood Ratio	161.369	28	<.001
N of Valid Cases	215		

a. 26 cells (65.0%) have expected count less than 5. The minimum expected count is .65.

Table 3 Chi-Square Mesiolingual Accessory

The Chi-Square test of independence is used here to test the null hypothesis: there is no significant association between frequency of different dental scores and taxonomic assignment, as defined in this study. This dataset for the scores of the mesiolingual trait inherently violates the assumption of 20% or fewer cells having an expected count less than 5. While the significant ($p < 0.001$) Pearson Chi-Square value is invalidated, the significant likelihood ratio ($p < 0.001$) indicates that there is a significant association between species and expression of the mesiolingual accessory feature. Given the results of this test, the null hypothesis would be rejected.

3.1.2 Interconulus

3.1.2.1 Kruskal-Wallis H Test and Pairwise Comparison

Independent-Samples Kruskal-Wallis Test Summary

Total N	210
Test Statistic	96.823[a]
Degree Of Freedom	7
Asymptotic Sig.(2-sided test)	<.001

a. The test statistic is adjusted for ties.

Table 5 Kruskal Wallis Interconulus

Pairwise Comparisons of Species

Sample 1-Sample 2	Test Statistic	Std. Error	Std. Test Statistic	Sig.	Adj. Sig.[a]
P. ursinu-P. cynoce	42.463	15.029	2.825	.005	.132
P. ursinu-P. kindae	71.619	17.769	4.031	<.001	.002
P. ursinu-Pp. white	-73.911	20.580	-3.591	<.001	.009
P. ursinu-Pp. broom	-88.591	18.267	-4.850	<.001	.000
P. ursinu-P. robins	89.190	24.820	3.593	<.001	.009
P. ursinu-Pp. jones	-104.892	21.167	-4.955	<.001	.000
P. ursinu-P. anubis	117.198	14.020	8.359	<.001	.000
P. cynoce-P. kindae	-29.156	15.284	-1.908	.056	1.000
P. cynoce-Pp. white	-31.447	18.477	-1.702	.089	1.000
P. cynoce-Pp. broom	-46.128	15.860	-2.908	.004	.102
P. cynoce-P. robins	-46.727	23.106	-2.022	.043	1.000
P. cynoce-Pp. jones	-62.428	19.128	-3.264	.001	.031
P. cynoce-P. anubis	74.735	10.697	6.986	<.001	.000
P. kindae-Pp. white	-2.292	20.766	-.110	.912	1.000
P. kindae-Pp. broom	-16.972	18.477	-.919	.358	1.000
P. kindae-P. robins	-17.571	24.975	-.704	.482	1.000
P. kindae-Pp. jones	-33.273	21.348	-1.559	.119	1.000
P. kindae-P. anubis	45.579	14.292	3.189	.001	.040
Pp. white-Pp. broom	14.681	21.194	.693	.489	1.000
Pp. white-P. robins	15.280	27.047	.565	.572	1.000
Pp. white-Pp. jones	30.981	23.739	1.305	.192	1.000
Pp. white-P. anubis	43.287	17.666	2.450	.014	.400
Pp. broom-P. robins	.599	25.332	.024	.981	1.000
Pp. broom-Pp. jones	-16.301	21.765	-.749	.454	1.000
Pp. broom-P. anubis	28.607	14.908	1.919	.055	1.000
P. robins-Pp. jones	-15.701	27.497	-.571	.568	1.000
P. robins-P. anubis	28.008	22.463	1.247	.212	1.000
Pp. jones-P. anubis	12.306	18.346	.671	.502	1.000

Each row tests the null hypothesis that the Sample 1 and Sample 2 distributions are the same.
Asymptotic significances (2-sided tests) are displayed. The significance level is .050.

Table 4 Pairwise Comparison Interconulus

In the case of the interconulus, *Papio ursinus* was significantly different from all extant taxa (excluding *Papio cynocephalus)*: *Papio kindae* (p = 0.002) and *Papio anubis* (p = 0.000). *Papio anubis* and *Papio kindae* were also significantly different from each other (p = 0.005). The expression of the interconulus in extant taxa shows a clinal variation wherein absence and presence of lower scores tend to be highest in southernmost residing taxa, and presence of the highest scores most frequent in northernmost taxa. In the extinct taxa, there was no significant difference in expression of the interconulus between species. Comparisons of extinct to extant samples showed a significant difference between all extinct species in this study and *Papio ursinus* (*Parapapio whitei* [p = 0.009], *Parapapio broomi* [p = 0.000], *Pp jonesi* [p = 0.000] and *Papio robinsoni* [p = 0.000]). This difference is based on *Papio ursinus* having the lowest mean rank score for the interconulus of all taxa in this study. *Parapapio jonesi* was also significantly different from *Papio cynocephalus* (p = 0.031).

3.1.2.2 Chi-Square Test of Independence

Chi-Square Tests

	Value	df	Asymptotic Significance (2-sided)
Pearson Chi-Square	170.417[a]	28	<.001
Likelihood Ratio	180.260	28	<.001
N of Valid Cases	210		

a. 27 cells (67.5%) have expected count less than 5. The minimum expected count is .10.

Table 6 Chi-Square Interconulus

The chi-square test of independence is testing the null hypothesis that there is no association between interconulus score and designation of species categories. The results of this test show that the likelihood ratio (p < .001) is significant. This indicates that there is significant difference for the ratio of the observed to expected frequencies of interconulus score between taxa and therefore the null hypothesis would be rejected. Frequencies of interconulus scores therefore are associated with the taxonomic categories used in this study.

3.1.3 Mesial Fovea, Distal Fovea, and Split Hypocone

3.1.3.1 Kruskal-Wallis H tests and Pairwise Comparisons

Independent-Samples Kruskal-Wallis Test Summary

Total N	215
Test Statistic	17.517[a]
Degree Of Freedom	7
Asymptotic Sig.(2-sided test)	.014

a. The test statistic is adjusted for ties.

Independent-Samples Kruskal-Wallis Test Summary

Total N	211
Test Statistic	40.216[a]
Degree Of Freedom	7
Asymptotic Sig.(2-sided test)	<.001

a. The test statistic is adjusted for ties.

Independent-Samples Kruskal-Wallis Test Summary

Total N	213
Test Statistic	10.953[a]
Degree Of Freedom	7
Asymptotic Sig.(2-sided test)	.141

a. The test statistic is adjusted for ties.

Table 7 Kruskal-Wallis for (from left to right) Mesial Fovea, Distal Fovea, and Split Hypocone

Pairwise Comparisons of Species

Sample 1-Sample 2	Test Statistic	Std. Error	Std. Test Statistic	Sig.	Adj. Sig.[a]
P. robins-P. cynoce	9.556	18.986	.503	.615	1.000
P. robins-Pp. jones	-19.545	22.593	-.865	.387	1.000
P. robins-Pp. broom	-23.889	20.815	-1.148	.251	1.000
P. robins-P. ursinu	-24.432	20.278	-1.205	.228	1.000
P. robins-P. anubis	33.506	18.447	1.816	.069	1.000
P. robins-P. kindae	40.313	20.073	2.008	.045	1.000
P. robins-Pp. white	-58.636	22.593	-2.595	.009	.265
P. cynoce-Pp. jones	-9.990	15.718	-.636	.525	1.000
P. cynoce-Pp. broom	-14.333	13.032	-1.100	.271	1.000
P. cynoce-P. ursinu	-14.876	12.157	-1.224	.221	1.000
P. cynoce-P. anubis	23.951	8.768	2.732	.006	.177
P. cynoce-P. kindae	-30.757	11.811	-2.604	.009	.258
P. cynoce-Pp. white	-49.081	15.718	-3.123	.002	.050
Pp. jones-Pp. broom	4.343	17.884	.243	.808	1.000
Pp. jones-P. ursinu	4.886	17.256	.283	.777	1.000
Pp. jones-P. anubis	13.961	15.062	.927	.354	1.000
Pp. jones-P. kindae	20.767	17.015	1.221	.222	1.000
Pp. jones-Pp. white	-39.091	19.926	-1.962	.050	1.000
Pp. broom-P. ursinu	.543	14.852	.037	.971	1.000
Pp. broom-P. anubis	9.618	12.234	.786	.432	1.000
Pp. broom-P. kindae	16.424	14.571	1.127	.260	1.000
Pp. broom-Pp. white	-34.747	17.884	-1.943	.052	1.000
P. ursinu-P. anubis	9.075	11.297	.803	.422	1.000
P. ursinu-P. kindae	15.881	13.793	1.151	.250	1.000
P. ursinu-Pp. white	-34.205	17.256	-1.982	.047	1.000
P. anubis-P. kindae	-6.806	10.925	-.623	.533	1.000
P. anubis-Pp. white	-25.130	15.062	-1.668	.095	1.000
P. kindae-Pp. white	-18.324	17.015	-1.077	.282	1.000

Each row tests the null hypothesis that the Sample 1 and Sample 2 distributions are the same.
Asymptotic significances (2-sided tests) are displayed. The significance level is .050.

a. Significance values have been adjusted by the Bonferroni correction for multiple tests.

Pairwise Comparisons of Species

Sample 1-Sample 2	Test Statistic	Std. Error	Std. Test Statistic	Sig.	Adj. Sig.[a]
P. cynoce-P. ursinu	-5.115	13.542	-.378	.706	1.000
P. cynoce-Pp. broom	-10.757	14.820	-.726	.468	1.000
P. cynoce-Pp. jones	-24.297	17.509	-1.388	.165	1.000
P. cynoce-Pp. white	-33.888	17.509	-1.935	.053	1.000
P. cynoce-P. kindae	-38.683	13.542	-2.856	.004	.120
P. cynoce-P. robins	-38.683	22.624	-1.710	.087	1.000
P. cynoce-P. anubis	54.440	9.768	5.573	<.001	.000
P. ursinu-Pp. broom	-5.642	16.810	-.336	.737	1.000
P. ursinu-Pp. jones	-19.182	19.223	-.998	.318	1.000
P. ursinu-Pp. white	-28.773	19.223	-1.497	.134	1.000
P. ursinu-P. kindae	33.568	15.696	2.139	.032	.909
P. ursinu-P. robins	33.568	23.975	1.400	.161	1.000
P. ursinu-P. anubis	49.325	12.584	3.920	<.001	.002
Pp. broom-Pp. jones	-13.540	20.143	-.672	.501	1.000
Pp. broom-Pp. white	-23.131	20.143	-1.148	.251	1.000
Pp. broom-P. kindae	27.926	16.810	1.661	.097	1.000
Pp. broom-P. robins	27.926	24.719	1.130	.259	1.000
Pp. broom-P. anubis	43.683	13.950	3.131	.002	.049
Pp. jones-Pp. white	-9.591	22.197	-.432	.666	1.000
Pp. jones-P. kindae	14.386	19.223	.748	.454	1.000
Pp. jones-P. robins	14.386	26.419	.545	.586	1.000
Pp. jones-P. anubis	30.143	16.779	1.796	.072	1.000
Pp. white-P. kindae	4.795	19.223	.249	.803	1.000
Pp. white-P. robins	4.795	26.419	.182	.856	1.000
Pp. white-P. anubis	20.552	16.779	1.225	.221	1.000
P. kindae-P. anubis	15.756	12.584	1.252	.211	1.000
P. robins-P. anubis	15.756	22.064	.714	.475	1.000
P. kindae-P. robins	.000	23.975	.000	1.000	1.000

Each row tests the null hypothesis that the Sample 1 and Sample 2 distributions are the same.
Asymptotic significances (2-sided tests) are displayed. The significance level is .050.

a. Significance values have been adjusted by the Bonferroni correction for multiple tests.

Table 8 Pairwise Comparison for Mesial Fovea (Right) and Distal Fovea (Left)

A Kruskal-Wallis test of the mesial fovea showed a significant difference (p = 0.014) across taxa. Pairwise comparison illustrated that only two taxa, *Papio cynocephalus* and *Parapapio whitei* differed significantly (p = 0.050). Results of a Kruskal-Wallis H test for the distal fovea also showed a significant difference among taxa (p < 0.001). Pairwise comparisons revealed, however, that the only significant differences existed between *Papio anubis* and three taxa: *Papio ursinus* (p = 0.002), *Papio cynocephalus* (p = 0.000) and *Parapapio broomi* (p = 0.028). This difference is on the basis of *Papio anubis* having higher instance of a score of 2, while *Papio ursinus, Papio cynocephalus* and *Parapapio broomi* had a higher frequency of a score of 1.

A Kruskal-Wallis H test revealed that there was also no significant difference among taxa for expression of a split hypocone (p = 0.141). Typical expression for all the taxa sampled was a score of 0, or absence of the feature, with only a few statistical outliers showing presence of a split hypocone. *Papio anubis* had the overall highest frequency of presence of this trait, though the majority of individuals in this taxon expressed absence.

3.1.3.2 Chi-Square Test of Independence

Chi-Square Tests

	Value	df	Asymptotic Significance (2-sided)
Pearson Chi-Square	17.598[a]	7	.014
Likelihood Ratio	19.811	7	.006
N of Valid Cases	215		

a. 4 cells (25.0%) have expected count less than 5. The minimum expected count is 1.76.

Chi-Square Tests

	Value	df	Asymptotic Significance (2-sided)
Pearson Chi-Square	40.407[a]	7	<.001
Likelihood Ratio	43.070	7	<.001
N of Valid Cases	211		

a. 4 cells (25.0%) have expected count less than 5. The minimum expected count is 2.47.

Chi-Square Tests

	Value	df	Asymptotic Significance (2-sided)
Pearson Chi-Square	11.005[a]	7	.138
Likelihood Ratio	13.074	7	.070
N of Valid Cases	213		

a. 8 cells (50.0%) have expected count less than 5. The minimum expected count is .43.

Table 9 Chi-Square (from left to right) for Mesial Fovea, Distal Fovea, and Split Hypocone

The likelihood ratio significance value for the chi-square test of independence for mesial fovea score is significant (p = 0.006). This indicates that there is a significant association between lingual cingulum score and species. The likelihood ratio for the distal fovea is also significant ($p < 0.001$). With this value, the null hypothesis is rejected, supporting a significant association between distal fovea score and species category. A chi-square test of independence for split hypocone score resulted in an insignificant p-value for likelihood ratio ($p = 0.070$). This result supports a failure to reject the null hypothesis that split hypocone score is not associated with species category.

3.1.4 Lingual and Buccal Cingulum

3.1.4.1 Kruskal-Wallis H test and Pairwise Comparison

Independent-Samples Kruskal-Wallis Test Summary

Total N	181
Test Statistic	50.762[a]
Degree Of Freedom	6
Asymptotic Sig.(2-sided test)	<.001

a. The test statistic is adjusted for ties.

Independent-Samples Kruskal-Wallis Test Summary

Total N	182
Test Statistic	28.896[a]
Degree Of Freedom	6
Asymptotic Sig.(2-sided test)	<.001

a. The test statistic is adjusted for ties.

Table 10 Kruskal-Wallis (left to right) Lingual Cingulum and Buccal Cingulum

Pairwise Comparisons of Species

Sample 1-Sample 2	Test Statistic	Std. Error	Std. Test Statistic	Sig.	Adj. Sig.[a]
Pp. white-Pp. broom	21.399	19.265	1.111	.267	1.000
Pp. white-P. kindae	27.797	19.072	1.457	.145	1.000
Pp. white-P. cynoce	40.077	16.932	2.367	.018	.377
Pp. white-Pp. jones	59.909	21.465	2.791	.005	.110
Pp. white-P. anubis	79.590	16.327	4.875	<.001	.000
Pp. white-P. robins	91.097	24.339	3.743	<.001	.004
Pp. broom-P. kindae	6.398	16.558	.386	.699	1.000
Pp. broom-P. cynoce	18.678	14.039	1.330	.183	1.000
Pp. broom-Pp. jones	-38.510	19.265	-1.999	.046	.958
Pp. broom-P. anubis	58.191	13.304	4.374	<.001	.000
Pp. broom-P. robins	69.698	22.423	3.108	.002	.040
P. kindae-P. cynoce	12.280	13.773	.892	.373	1.000
P. kindae-Pp. jones	-32.112	19.072	-1.684	.092	1.000
P. kindae-P. anubis	51.794	13.022	3.977	<.001	.001
P. kindae-P. robins	-63.301	22.257	-2.844	.004	.094
P. cynoce-Pp. jones	-19.832	16.932	-1.171	.241	1.000
P. cynoce-P. anubis	39.513	9.618	4.108	<.001	.001
P. cynoce-P. robins	-51.021	20.453	-2.495	.013	.265
Pp. jones-P. anubis	19.681	16.327	1.205	.228	1.000
Pp. jones-P. robins	31.188	24.339	1.281	.200	1.000
P. anubis-P. robins	-11.507	19.955	-.577	.564	1.000

Each row tests the null hypothesis that the Sample 1 and Sample 2 distributions are the same.
Asymptotic significances (2-sided tests) are displayed. The significance level is .050.

a. Significance values have been adjusted by the Bonferroni correction for multiple tests.

Table 11 Pairwise Comparison Lingual Cingulum

Pairwise Comparisons of Species

Sample 1-Sample 2	Test Statistic	Std. Error	Std. Test Statistic	Sig.	Adj. Sig.[a]
Pp. white-P. kindae	7.619	16.743	.455	.649	1.000
Pp. white-Pp. broom	14.118	17.445	.809	.418	1.000
Pp. white-Pp. jones	44.600	19.811	2.251	.024	.512
Pp. white-P. robins	46.143	22.005	2.097	.036	.756
Pp. white-P. anubis	48.086	14.456	3.326	<.001	.018
Pp. white-P. cynoce	50.889	15.032	3.385	<.001	.015
P. kindae-Pp. broom	-6.499	15.095	-.431	.667	1.000
P. kindae-Pp. jones	-36.981	17.777	-2.080	.037	.787
P. kindae-P. robins	-38.524	20.193	-1.908	.056	1.000
P. kindae-P. anubis	40.467	11.512	3.515	<.001	.009
P. kindae-P. cynoce	43.270	12.227	3.539	<.001	.008
Pp. broom-Pp. jones	-30.482	18.439	-1.653	.098	1.000
Pp. broom-P. robins	32.025	20.778	1.541	.123	1.000
Pp. broom-P. anubis	33.968	12.510	2.715	.007	.139
Pp. broom-P. cynoce	36.771	13.172	2.792	.005	.110
Pp. jones-P. robins	1.543	22.801	.068	.946	1.000
Pp. jones-P. anubis	3.486	15.641	.223	.824	1.000
Pp. jones-P. cynoce	6.289	16.175	.389	.697	1.000
P. robins-P. anubis	1.943	18.341	.106	.916	1.000
P. robins-P. cynoce	4.746	18.799	.252	.801	1.000
P. anubis-P. cynoce	-2.803	8.840	-.317	.751	1.000

Each row tests the null hypothesis that the Sample 1 and Sample 2 distributions are the same.
Asymptotic significances (2-sided tests) are displayed. The significance level is .050.

a. Significance values have been adjusted by the Bonferroni correction for multiple tests.

Table 12 Pairwise Comparison Buccal Cingulum

Expression of the lingual cingulum did show a significant difference across taxa ($p < 0.001$). In the extant taxa, *Papio anubis* was significantly different from *Papio kindae* ($p = 0.001$) and *Papio cynocephalus* ($p = 0.001$). *Papio ursinus* was excluded from measure of this trait as well as the buccal cingulum, as none of the casted individuals utilized in this study had this feature observable. In the extinct taxa, *Papio robinsoni* was significantly different from *Parapapio whitei* ($p = 0.004$) and *Parapapio broomi* ($p = 0.040$). *Parapapio jonesi* was different from *Parapapio whitei* ($p = 0.072$), though not significantly, when implementing an alpha value of 0.05. Comparing extinct to extant taxa, *Papio anubis* was significantly different in lingual cingulum expression from *Parapapio whitei* ($p = 0.000$) and *Parapapio broomi* ($p = 0.000$).

The degree of expression of the buccal cingulum also showed significant difference across species (p < 0.001). Pairwise comparison in the extant taxa showed only significant difference between *Papio kindae* and two other species: *Papio anubis* (p = 0.009) and *Papio cynocephalus* (p = 0.008). The other significant differences in buccal cingulum expression existed only between extinct and extant comparisons. *Parapapio whitei* was significantly different from *Papio anubis* (p = 0.018) and *Papio cynocephalus* (p = 0.015).

3.1.4.2 Chi-Square Test of Independence

Chi-Square Tests

	Value	df	Asymptotic Significance (2-sided)
Pearson Chi-Square	69.672[a]	24	<.001
Likelihood Ratio	80.591	24	<.001
N of Valid Cases	181		

a. 23 cells (65.7%) have expected count less than 5. The minimum expected count is .27.

Chi-Square Tests

	Value	df	Asymptotic Significance (2-sided)
Pearson Chi-Square	74.725[a]	24	<.001
Likelihood Ratio	57.363	24	<.001
N of Valid Cases	182		

a. 25 cells (71.4%) have expected count less than 5. The minimum expected count is .04.

Table 13 Chi-Square (left to right) Lingual Cingulum and Buccal Cingulum

Both the buccal and lingual cingula had significant likelihood ratios (p < 0.001) indicating a significant association between cingula scores and taxonomic classification.

3.2 Multivariate Tests

3.2.1 Multiple Correspondence Analysis (MCA 1) Excluding Papio ursinus

Eigenvalues

	Dim.1	Dim.2	Dim.3
Variance	0.353	0.269	0.241
% of var.	12.995	9.908	8.892
Cumulative % of var.	12.995	22.903	31.794

Categorical variables (eta2)

	Dim.1	Dim.2	Dim.3
Mesiolingual	0.686	0.214	0.544
Interconulus	0.434	0.352	0.377
MesialFovea	0.001	0.039	0.282
DistalFovea	0.051	0.149	0.125
SplitHypocone	0.123	0.115	0.003
LingualCingulum	0.772	0.568	0.321
BuccalCingulum	0.401	0.446	0.036

Table 14 Eigenvalues and Dimensional Component Matrix

This Multiple Correspondence Analysis excludes all *Papio ursinus* individuals and represents the remaining seven species with respect to all seven dental traits. The first two dimensions extracted capture the highest percentage of variance (Table 14) with a total percentage of 22.903%. The traits found to be not statistically significant from the univariate analysis were included to ascertain if there were any notable instances of covariance.

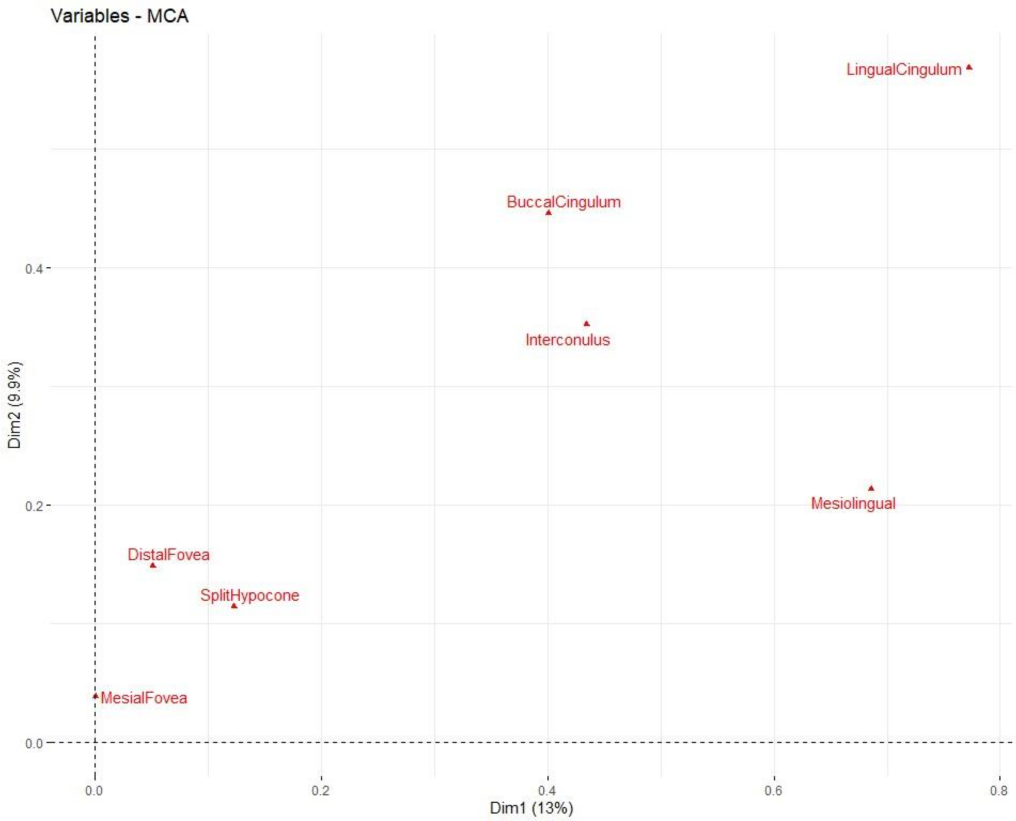

Figure 8 Variable Correlations to Principal Dimensions

The MCA results for variables and their association to principal dimensions (Figure 8) illustrate a graphical expression of the component loadings (Table 14). On axis 1, scores for the buccal cingulum, interconulus, mesiolingual element, and lingual cingulum were highly correlated with the first dimension. On axis 2, the buccal and lingual cingulum were highly correlated with the second dimension, while the interconulus, mesiolingual accessory, and distal fovea were only slightly associated. Scores for the split hypocone and mesial fovea were poorly correlated with both axes. While this assessment of the overall variable categories is pertinent to interpretation of individual behavior, it does not show how individual categories within each variable group affect the skew of plotted individuals.

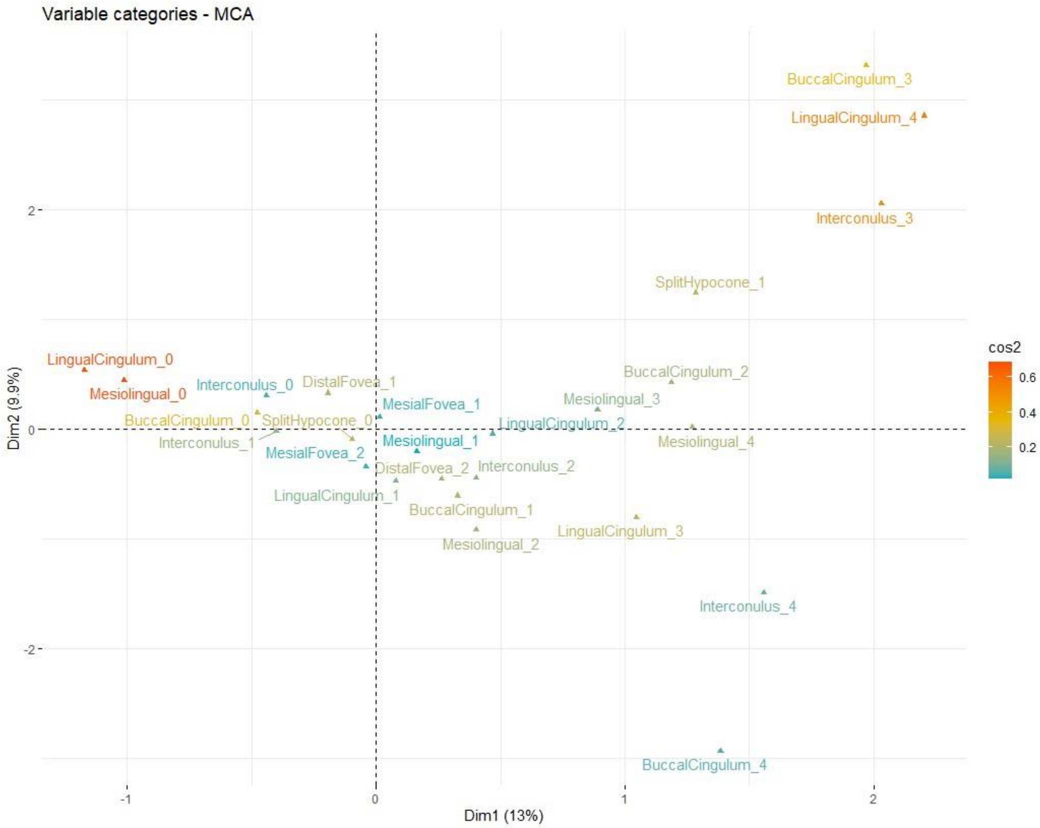

Figure 9 Variable Category Plot

In order to assess how scores for each category affected individual skew, the coordinates of variable categories had to be plotted in R using the *fviz_mca_var* function (Figure 9). This analysis revealed that lower scores and absence for the majority of traits resulted in individuals resting near zero on the second axis. On axis 1, however, absence of traits resulted in individual skew to the negative end, while higher, more intensive scores resulted in a positive skew.

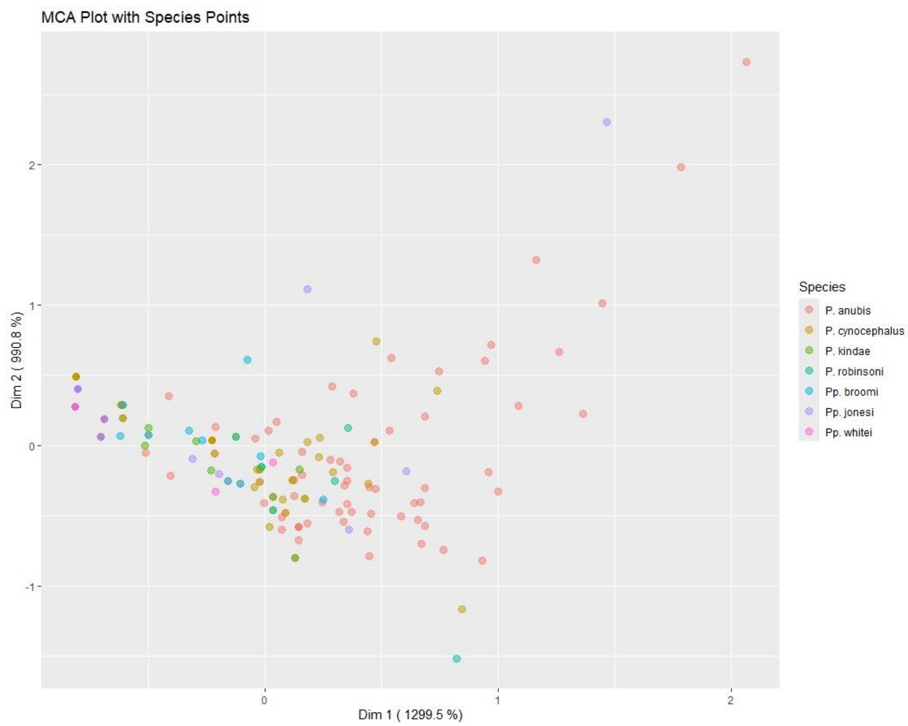

Figure 10 MCA Plot of Species

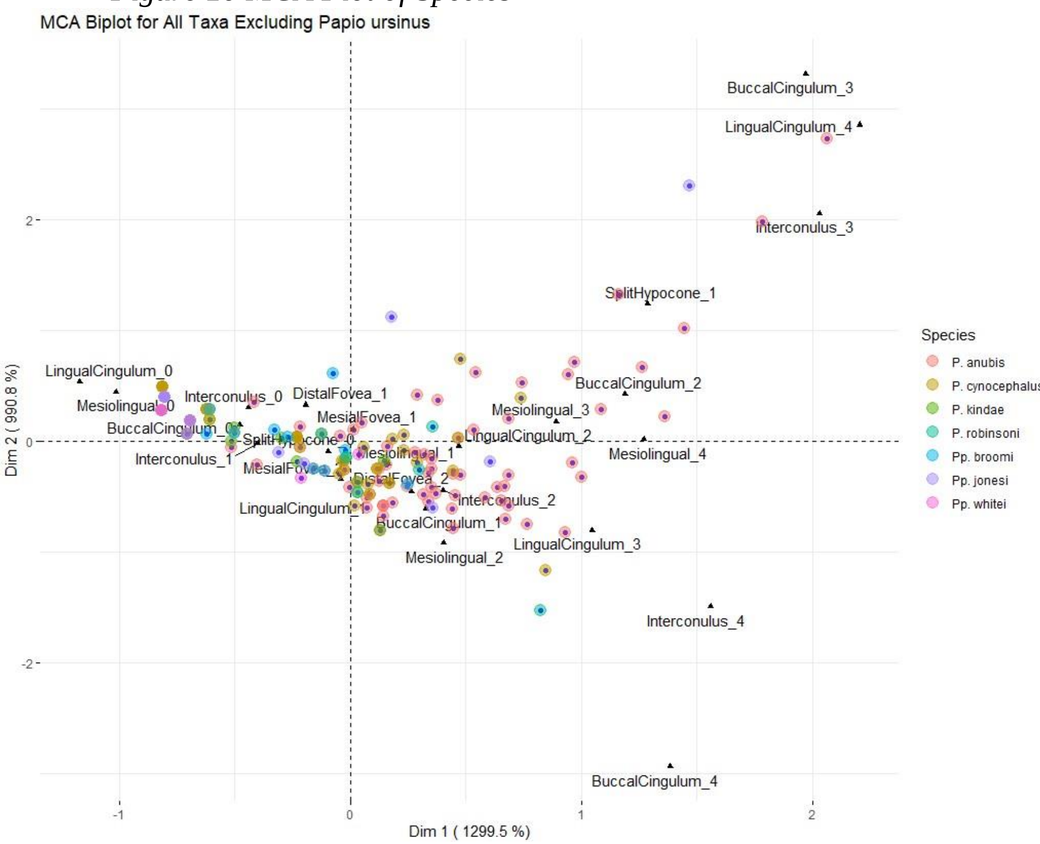

Figure 11 MCA Biplot of Species and Variable Categories

With this insight and ability to plot individuals along with weighted variable scores, certain patterns in taxa emerge. Axis 1 (Figures 10 & 11) illustrates a measure of intensity of the lingual cingulum and the subsequent accessory features, the mesiolingual accessory and interconulus, and its expression in taxa. The extant *Papio anubis* expresses primarily positive on this axis, illustrating high prevalence of the highest scores for these traits. *Papio kindae* and *Papio cynocephalus* skew closer to zero or primarily negative, illustrating reduced expression of these traits. In the extinct taxa, the signal is more difficult to assess as there is a high degree of overlap. Several *Papio robinsoni* individuals occupy both negative and positive spaces on this axis, indicating a high degree of individual variation in regard to expression of the lingual cingulum and lingual accessory features. *Parapapio broomi* individuals express either slightly positive or slightly negative, showing a net behavior near zero. This indicates that *Parapapio broomi* individuals typically have a milder expression of these traits and some absence. *Parapapio jonesi* shows some of the highest degree of variation among the fossil taxa, partially due to one outlier (SK551) having a lingual cingulum score of 4, skewing that individual highly positive on both axes. While *Parapapio jonesi* has some of the most negatively skewed individuals on axis 1, there are some individuals that skew slightly positive. *Parapapio whitei* primarily scored negative on this axis, indicating lack or reduced expression of these lingual traits.

Axis 2 primarily appears to identify outliers based on the most extreme expression of both the lingual and buccal cingula and ignores the highest expression of the lingual accessory features. Scores of 4 for the mesiolingual accessory and interconulus were at or near zero on this axis. This portrays the possibility that length of the cingulum does not necessarily correspond to intensity of the accessory features on that cingulum. While the extreme expressions of the buccal and lingual cingula represent the most negative and positive variables respectively, there is a general trend that as each axis approaches zero, these traits reduce in intensity. Individuals residing closer to zero on this axis therefore are expected to have a lower degree of expression of these cingula. *Papio anubis* shows the highest degree of variation on this axis, with the majority of individuals being slightly negative, though a sizable amount skewing slightly positive. The most positive individual on this axis belongs to *Papio anubis*. This illustrates that moderate expression of these cingula is the most common state of this species, though individuals can frequently express extreme variants of this trait. *Papio cynocephalus* is shown at essentially zero, indicating a low degree of expression or overall absence of the traits. *Papio kindae* also has a large number of individuals located near zero, with a few slightly negatively skewed. This indicates a low degree of expression and more commonly a score of zero than neighboring *Papio cynocephalus*. *Papio robinsoni* shows a degree of variation in the expression of these traits, with one highly negatively skewed individual, but with most falling at or near zero. Similarly*,* *Parapapio broomi* had a few individuals that were slightly negative, but most fell near zero. *Parapapio jonesi* was the most variable extinct taxon on this axis with an individual scoring highly positive and some scoring moderately negative. This indicates that *Parapapio jonesi* primarily shows a lower degree of expression of these traits, but individuals did show some tendency for a more extreme expression of the cingula. *Parapapio whitei* generally showed the highest degree of absence of these cingula out of all the fossil taxa.

Assessing the behavior of individuals and variables on these reduced dimensional axes supports the univariate analyses that traits such as the presence or absence of a split hypocone, as well as the shape of the mesial and distal fovea are poor indicators for taxonomic assignment. These features also illustrate poor covariance with the heritable lingual features, indicating a general lack of relatedness between expressions of these traits. This analysis does, however, illuminate that a higher score of the lingual cingulum does not necessarily indicate a higher score for lingual accessory features. While absence of any lingual cingulum concurs with absence of lingual accessory features, as evidenced by taxa that skew negatively on axis 1 and near zero on axis 2, slight presence of the cingula is all that is required to have high scores for the mesiolingual accessory feature and interconulus.

3.2.2 Multiple Correspondence Analysis (MCA 2) Excluding the Lingual and Buccal Cingula

Eigenvalues

	Dim.1	Dim.2	Dim.3
Variance	0.347	0.263	0.258
% of var.	15.771	11.948	11.710
Cumulative % of var.	15.771	27.719	39.428

Categorical variables (eta2)

	Dim.1	Dim.2	Dim.3
Mesiolingual	0.614	0.382	0.262
Interconulus	0.612	0.496	0.511
MesialFovea	0.081	0.319	0.000
DistalFovea	0.322	0.001	0.260
SplitHypocone	0.107	0.116	0.256

Table 15 Eigenvalues and Dimension Component Matrix

This analysis includes all taxa present in this study and excludes the lingual and buccal cingulum to assess *Papio ursinus* in relation to all taxa sampled. The eigenvalues from this MCA illustrate that 27.719% of variance in this data set is represented by the first two dimensions. The overall component loadings of categorical variables (Table 15) and plotted correlations between the variables and principal dimensions (Figure 12) illustrate that the mesiolingual accessory and interconulus are highly correlated with the first and second dimensions. The split hypocone and distal fovea are slightly correlated to axis 1 and the mesial fovea is slightly correlated with axis 2.

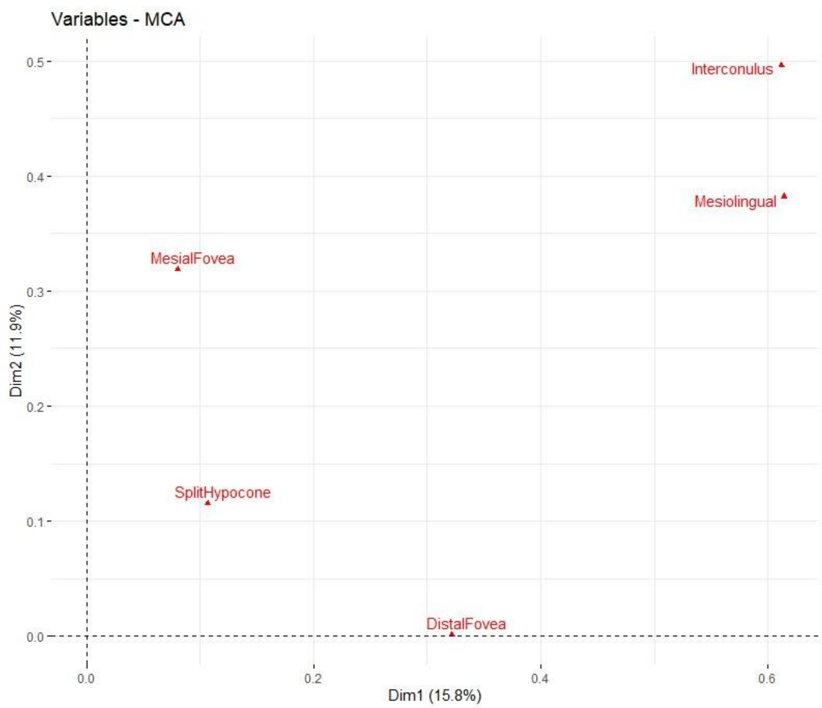

Figure 12 Variable Correlations to Principal Dimensions

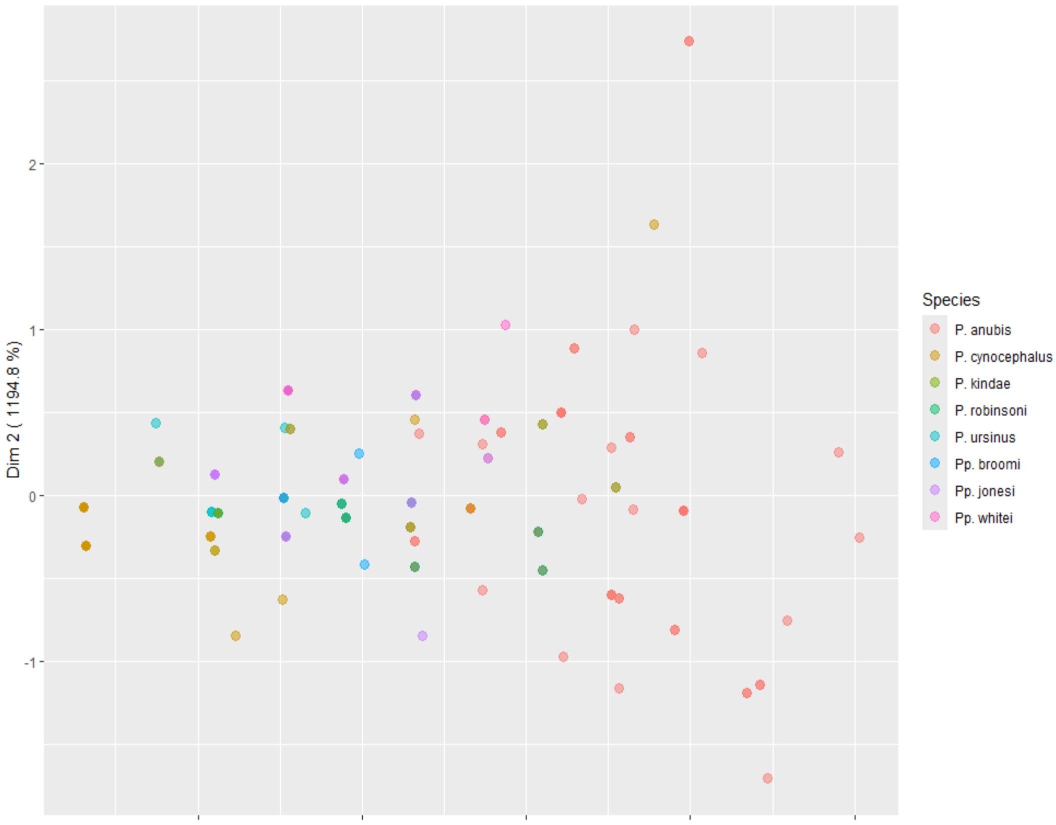

Figure 13 MCA Plot of Species

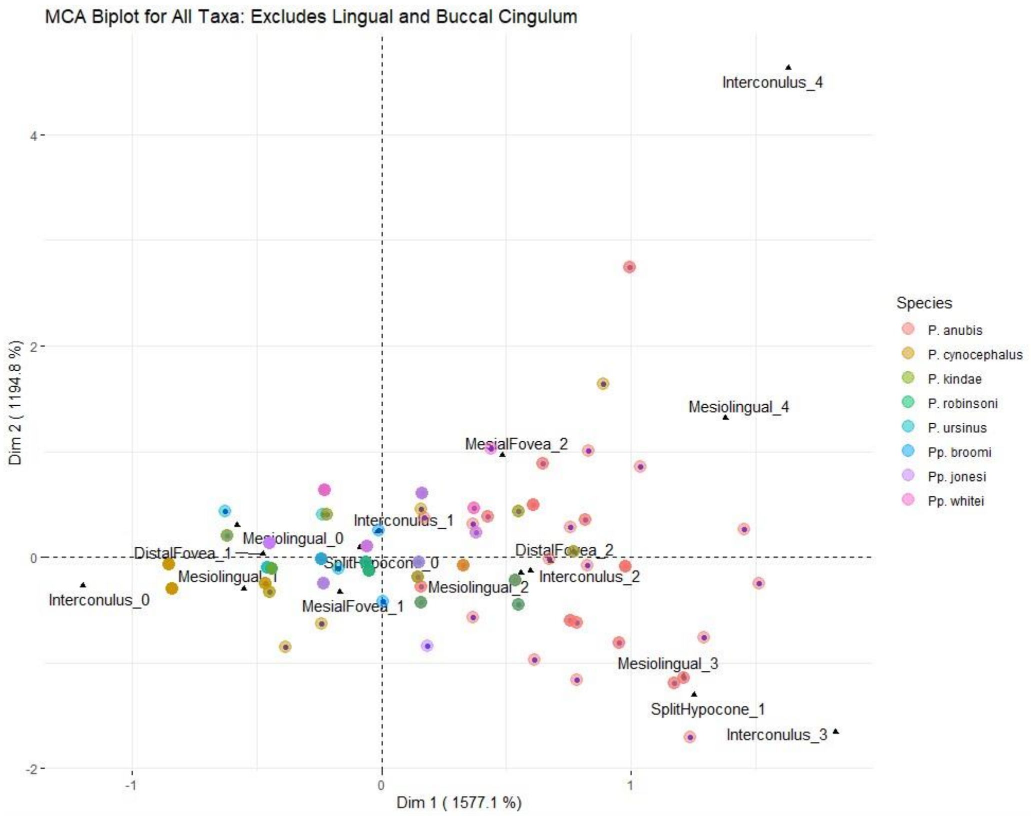

Figure 14 MCA Biplot of Species and Variable Categories

The biplot of individuals and variables show that, similar to the previous MCA result, axis 1 distributes individuals on the basis of intensity of score for the mesiolingual accessory and interconulus. Now with the inclusion of *Papio ursinus*, a full picture of variation of these lingual traits can be ascertained in the extant taxa. *Papio anubis* skews exclusively positive, indicating that few or no individuals lack the lingual traits and there is a typical condition for more extreme expression. *Papio cynocephalus* skews primarily negative with few individuals being slightly positive on this axis. Many of these values overlap with *Papio kindae*, indicating similar scores for these traits with only a few *Papio kindae* individuals expressing slightly more positive. *Papio ursinus* is the most negatively skewed extant species on this axis with no individuals being positive. *Papio robinsoni* is represented primarily near zero indicating mild to moderate expression of these traits with only a few individuals indicating probable absence of the lingual accessory features. *Parapapio broomi* resides mostly negative or near zero on this axis with only one individual expressing slightly positive and is the most negatively skewed of the *Parapapio* taxa. *Parapapio jonesi* resides near zero with some slight spread across the negative and positive axes. *Parapapio whitei* has substantial overlap with *Parapapio jonesi* and similarly exists slightly across both axes, averaging near zero. This indicates that all the *Parapapio* taxa behave similarly in regard to higher frequencies of moderate to low scores for these lingual accessory features.

Axis 2 of this MCA illustrates high positive skew for the most extreme expression of nearly all traits and a slight negative skew for more moderate scores. Scores of zero for the interconulus and mesiolingual accessory reside near zero on this axis. This axis primarily separates individuals on the basis of most extreme value and moderate to high expression. While the impact and correlation of the mesial fovea is smaller compared to the lingual accessory features, there appears to be some influence on the basis of a score of 1 causing negative skew while a score of 2 causes slight positive skew. All categories for the split hypocone and distal fovea are at or near zero for this axis, indicating little to no influence on individual behavior. On this axis, *Papio anubis* is primarily distinct from other taxa given a higher prevalence of extreme scores for these features. It is difficult to assess patterning for the other taxa in this study given the compression of this axis. While not all individuals at or near zero on this axis have little to no presence of these features, there is a possible estimation application when considering *Papio ursinus*. Given that *Papio ursinus* scores negatively on axis 1 and near zero on axis 2, it indicates a probable score of zero or near zero for the buccal and lingual cingulum in the context of the previous MCA.

3.2.3 Multiple Correspondence Analysis (MCA 3) of Extinct Taxa

Eigenvalues

	Dim.1	Dim.2	Dim.3
Variance	0.403	0.339	0.273
% of var.	16.585	13.965	11.238
Cumulative % of var.	16.585	30.551	41.788
	Dim.10	Dim.11	Dim.12
Variance	0.097	0.079	0.068
% of var.	3.999	3.239	2.795
Cumulative % of var.	88.494	91.734	94.528

Categorical variables (eta2)

	Dim.1	Dim.2	Dim.3
Mesiolingual	0.255	0.613	0.341
Interconulus	0.885	0.246	0.257
MesialFovea	0.030	0.055	0.214
DistalFovea	0.026	0.085	0.016
SplitHypocone	0.000	0.017	0.006
LingualCingulum	0.932	0.679	0.517
BuccalCingulum	0.691	0.679	0.559

Table 16 Eigenvalues and Principal Dimension Matrix

Given the substantial influence of *Papio anubis* in previous MCAs, the extinct taxa were separated to better understand individual behavior. Eigenvalue tables (Table 16) similarly indicate that 30.551% of total variance is captured in the first two dimensions. The component loadings and variable correlation plot (Figure 15) illustrate that, compared to previous MCA's, the interconulus score is less correlated to both axes in the fossil taxa. Dimensions 1 and 2 are most correlated to the buccal cingulum, lingual cingulum, and mesiolingual accessory scores.

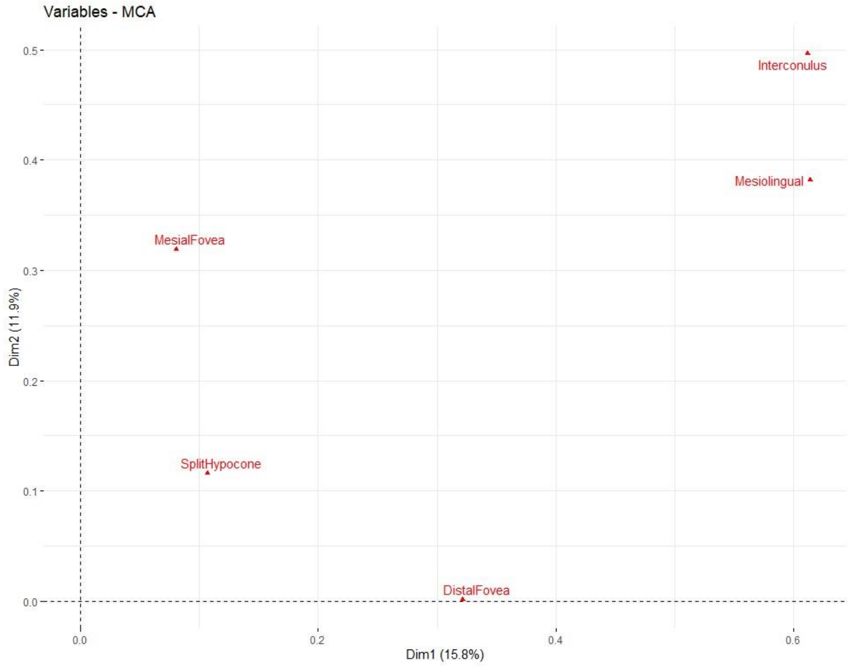

Figure 16 Variable Correlations to Principal Dimensions

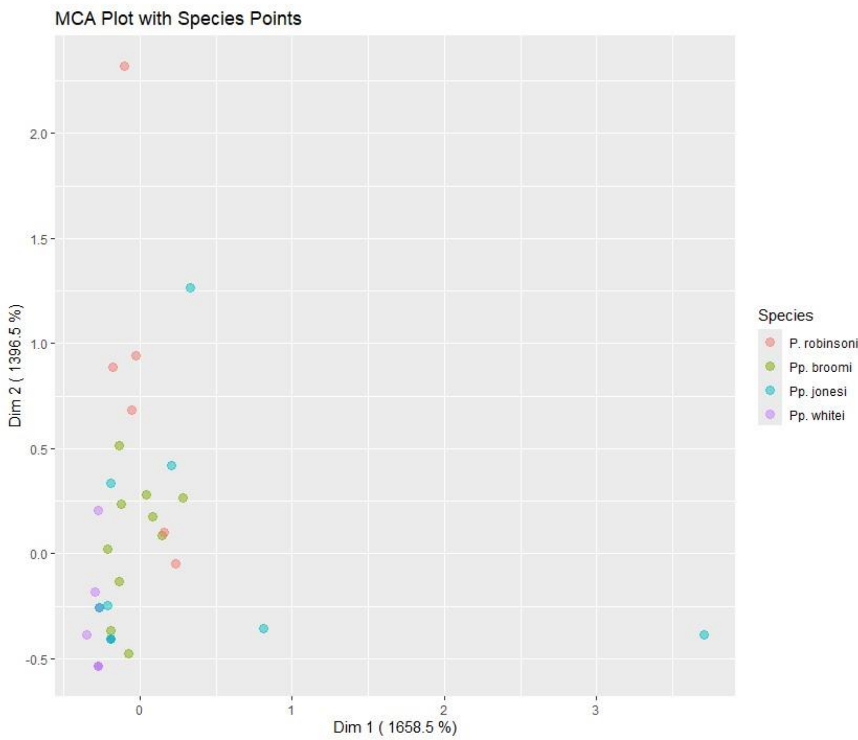

Figure 15 MCA Plot of Species

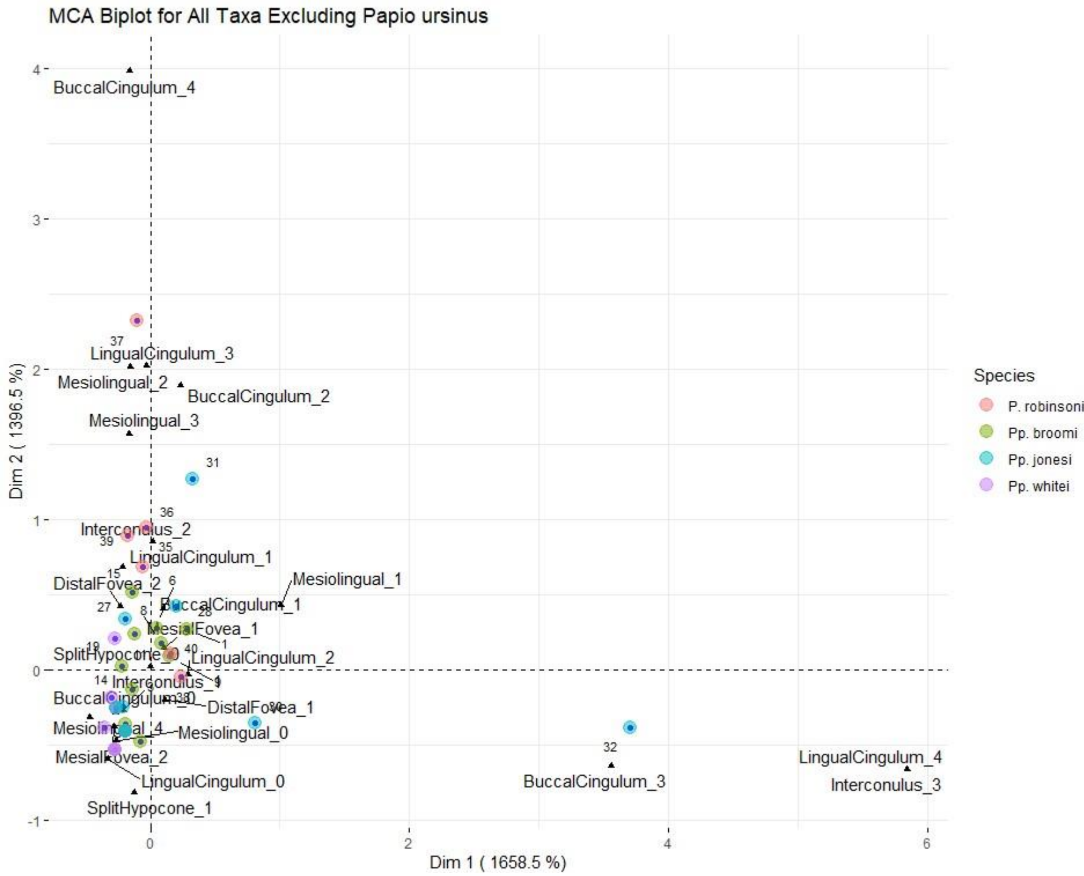

Figure 17 MCA Biplot of Species and Variables

The biplot of extinct taxa and variable categories (Figure 17) illustrates that on axis 1, most species are relatively condensed near zero, with some outliers but showing an overall pattern of absence skewing negative while presence skews positively. There are scores such as a buccal cingulum score of 3 and mesiolingual score of 4 which skew negatively, though, which confuses the interpretation of the results. Due to this discrepancy, a test of quality of representation was run on the variable category contributions. This test assesses the cos2 value for each variable category to determine how each scored value affects individual behavior on the axes. The results of this test were plotted (Figure 18) and the cos2 values of each category are ascribed a color denotation, as represented by the text for each category.

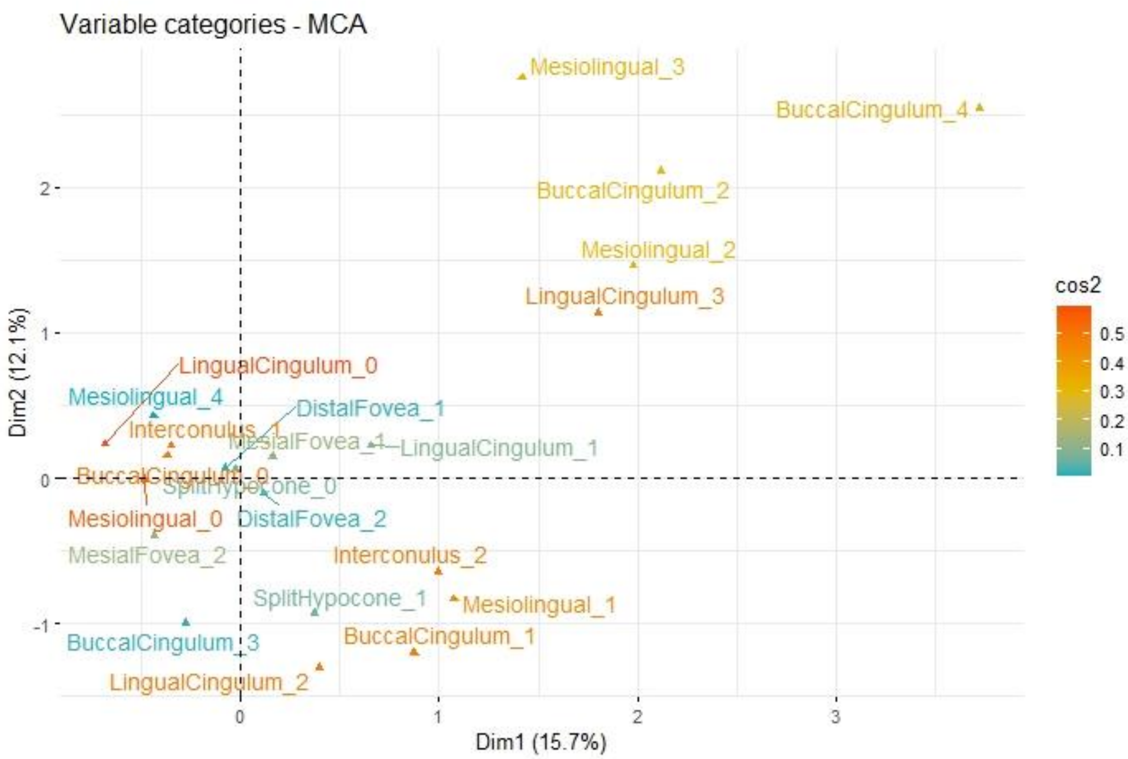

Figure 18 MCA Variable Category Cos2 Values

These results indicate that the categories of a mesiolingual score of 4 and buccal cingulum score of 3 were poorly represented in these dimensions and have less effect on the skew of individuals. A lingual cingulum and mesiolingual accessory score of 0, however, heavily affect negative data skew. Individuals that skew negatively are much more likely to therefore be represented by a score of zero in this data set for these traits. While there is significant overlap across all taxa in the biplot, there is some variation. *Papio robinsoni* exists almost exclusively on the positive end of axis 2, illustrating a higher frequency of presence for all traits with less evidence of absence. *Parapapio broomi* primarily exists on the positive end of the axis, with a few individuals slightly negative. The distribution of *Parapapio jonesi* is similar to *Parapapio broomi,* though there is more spread between highly positive and fairly negative individuals. *Parapapio whitei* is represented by the most negative individual on this axis with only one individual skewing slightly positive. There is still, however, substantial overlap between *Parapapio whitei* and the two other *Parapapio* taxa, indicating poor phylogenetic signal being ascertained from the covariance of these traits.

Axis 2, especially with considerations for cos2 values, shows more extreme scores for nearly all traits skewing positively and moderate scores skewing negatively. Scores of zero (absence) are represented essentially at zero for this axis. On this axis, *Papio robinsoni* represents the most positive values, indicating higher scores for the mesiolingual accessory, buccal cingulum, and lingual cingulum. The majority of *Papio robinsoni* individuals, however, are scored negatively with only one individual near zero. This illustrates primarily moderate scores for these traits, with capacity for more extreme values. *Parapapio broomi* and *Parapapio jonesi* show a wide range of scores across both the negative and positive ends of the axis with several individuals populating near zero. *Parapapio whitei* are projected primarily near zero with only slight encroachments into the negative and positive axes.

3.3 Predictive Modeling

3.3.1 Logistic Regression Analysis

Logistic Regression Analysis (LRA) was performed on only the traits deemed predictive for the majority of taxa based on statistically significant univariate values and multivariate cos2 indicators. Given the observed covariance from the MCA analyses and evolutionary relationships between these structures, the mesiolingual accessory feature, interconulus, and lingual cingulum were selected for creation of logistic regression models.

3.3.1.1 LRA for Mesiolingual Accessory Feature Score

```
Coefficients:
                 (Intercept) Mesiolingual
P. cynocephalus   1.3294098   -1.1863031
P. kindae         0.7554291   -1.5175995
P. robinsoni     -1.9313488   -0.2746985
P. ursinus        1.1497463   -2.6036576
Pp. broomi        0.8933373   -2.2188557
Pp. jonesi        0.2578369   -1.9143450
Pp. whitei        0.2578940   -1.9143110

Std. Errors:
                 (Intercept) Mesiolingual
P. cynocephalus   0.3685995    0.2168575
P. kindae         0.4267174    0.3320472
P. robinsoni      0.8154724    0.3420654
P. ursinus        0.4159437    0.5534906
Pp. broomi        0.4327494    0.4963323
Pp. jonesi        0.4981171    0.5348308
Pp. whitei        0.4981082    0.5348054

Residual Deviance: 596.5
AIC: 624.5
```

Table 17 Multinomial Regression Summary

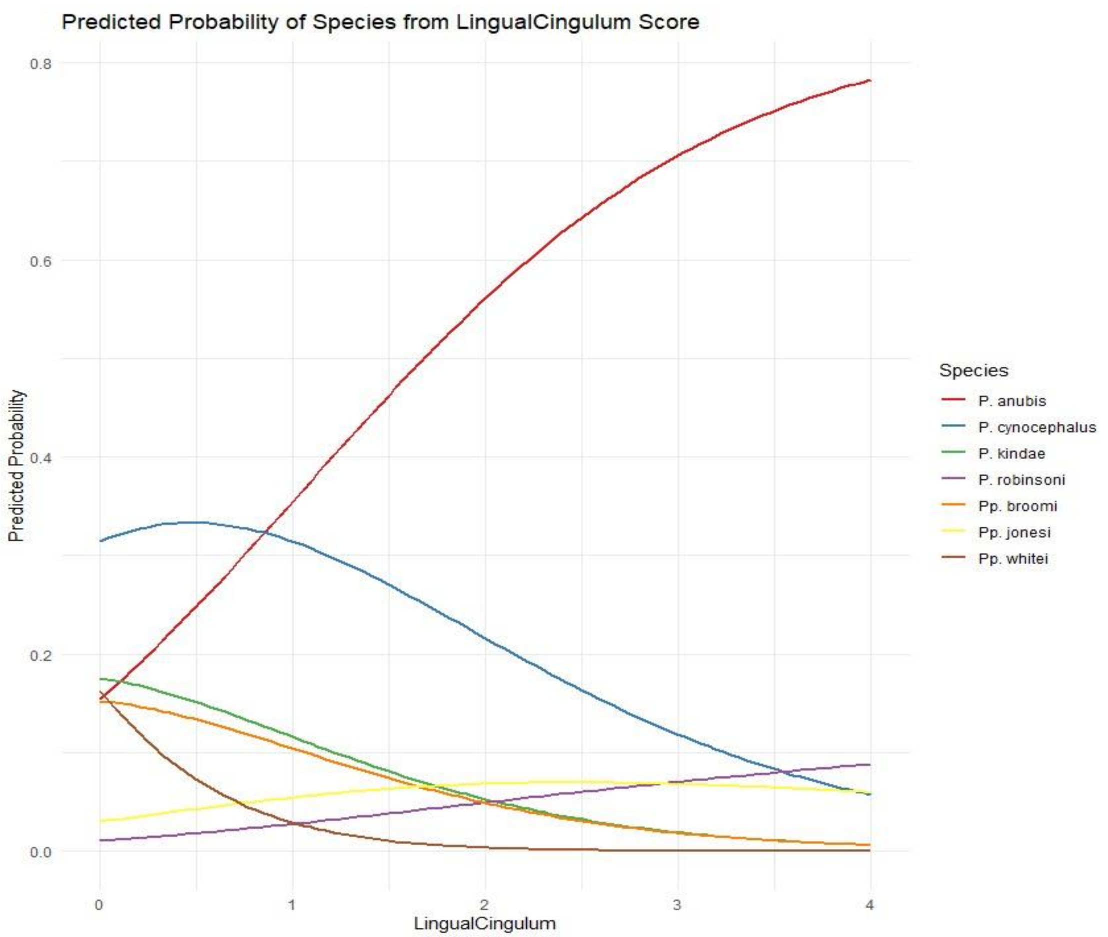

Figure 19 Predicted Probabilities of Species by Mesiolingual Score

The “multinom” function from the *nnet* package in R was utilized for this regression analysis for its ability to handle three or more nominal outcome and predictor variables that are neither continuous nor ordinal. The predicted probability for the outcome variable—species—is estimated based on a possible score of 0 – 5 for the mesiolingual accessory trait, or predictor variables. As a result, with proper model fit, species classification of papionins could be predicted from mesiolingual accessory score. The predicted probability lines for each species were simultaneously plotted (Figure 19) to show correlations between mesiolingual score and probability percentage of indicating a specific taxonomic category. The most independently behaving taxon is *Papio anubis*, which nears a predictive probability of 100% for a mesiolingual accessory score of 4. As evidenced by the MCA analyses, *Papio anubis* has the highest propensity of any papionin taxa sampled for extreme expression of this trait. While the predictive values for other taxa on the basis of mesiolingual accessory score are dwarfed in comparison, there are nuanced trends that can be observed. Two extant taxa, *Papio ursinus* and *Papio kindae* have their highest predictive values for a mesiolingual accessory score of 0. *Papio cynocephalus*, while also showing a low predictive probability for higher scores, has its highest predictive peak between 0.5 and 1, indicating the second highest score frequency of presence of all extant taxa. In the extinct taxa, all three *Parapapio* species have their highest predictive probabilities for a score of 0. *Papio robinsoni*, however, has a peak predictive probability between a score of 2 or 3. This indicates that in fossil sites bearing papionins, unidentified individual maxillary molars that lack presence of a mesiolingual accessory feature are more likely to belong to *Parapapio* than *Papio*.

3.3.1.2 LRA for Interconulus Score

Coefficients:

	(Intercept)	Interconulus
P. cynocephalus	2.3966878	-2.5279612
P. kindae	0.6756862	-1.4626438
P. robinsoni	-0.8530107	-1.1694296
P. ursinus	2.4765093	-5.8320753
Pp. broomi	-0.1767474	-0.8724711
Pp. jonesi	-1.5800996	-0.2667219
Pp. whitei	-0.1550535	-1.3346526

Std. Errors:

	(Intercept)	Interconulus
P. cynocephalus	0.4922644	0.4159108
P. kindae	0.5727413	0.4257679
P. robinsoni	0.9145447	0.6674965
P. ursinus	0.5160626	1.0982569
Pp. broomi	0.6178238	0.4039138
Pp. jonesi	0.7912802	0.4426388
Pp. whitei	0.7303039	0.5468629

Residual Deviance: 594.2863
AIC: 622.2863

Table 18 Multinomial Regression Summary

Figure 20 Predicted Probabilities of Species for Interconulus ScoreTable 19 Multinomial Regression Summary

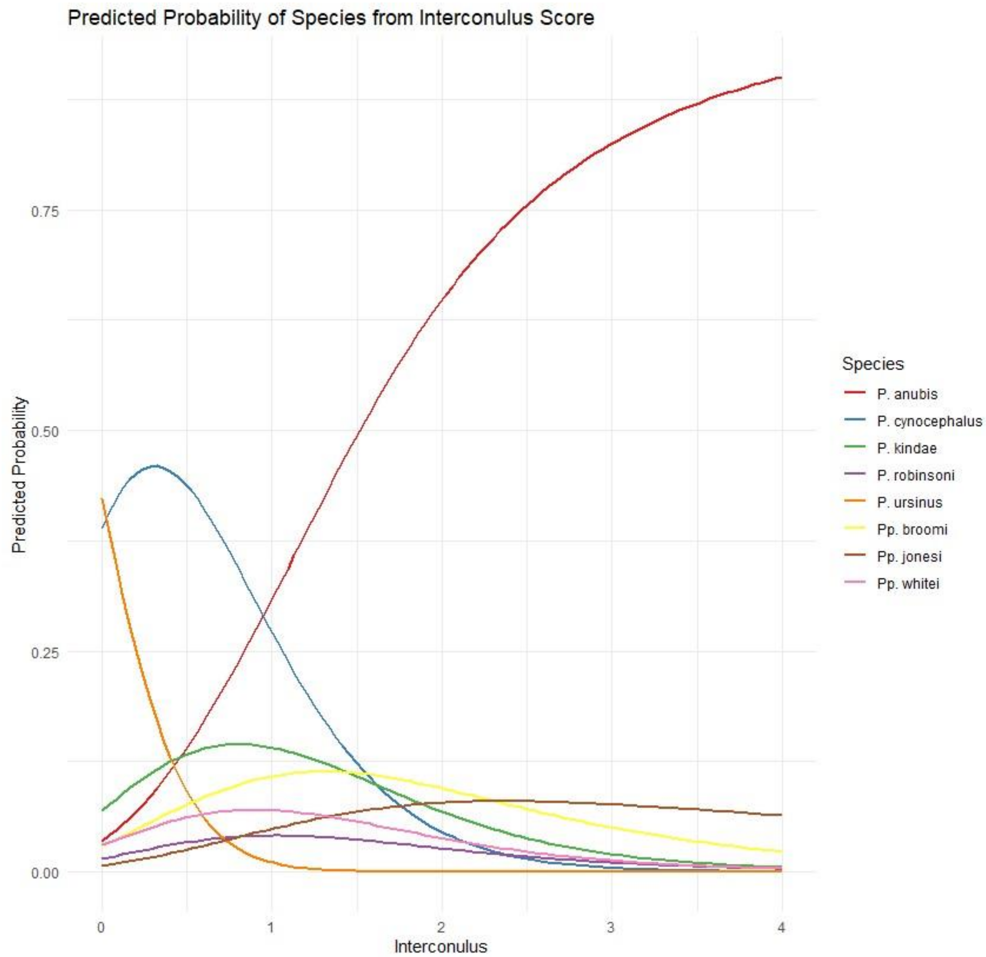

Figure 21 Predicted Probabilities of Species for Interconulus Score

The predicted probabilities of species from interconulus score presented more discernable patterns, especially in the extant taxa. *Papio ursinus* showed the highest predicted probability of any taxa for an interconulus score of 0. This illustrates that papionin teeth with the lowest expression of the interconulus would most likely belong to *Papio ursinus*. *Papio anubis*, similar to predicted probabilities for the mesiolingual accessory, had the highest degree of expression for scores between 2 and 4. The estimation line for *Papio cynocephalus* showed a peak in predicted probability nearing 45% for an interconulus score between 0 and 0.5. *Papio kindae* showed a discernable peak near the score "1", indicating a higher frequency of this degree of expression for the interconulus in this extant species. *Parapapio broomi, Parapapio whitei* and *Parapapio jonesi* had similar predictive curves which were highest between the scores of 1 and 2, but showed poor affinity for any particular score generally. *Papio robinsoni* had a similar predictive output to *Papio cynocephalus*, indicating the interconulus as a poor predictive measure for this taxon.

3.3.1.3 LRA for Lingual Cingulum Score

	(Intercept)	LingualCingulum
P. cynocephalus	0.70898061	-0.8321467
P. kindae	0.12532219	-1.2462369
P. robinsoni	-2.68201493	0.1248393
Pp. broomi	-0.01607636	-1.2113474
Pp. jonesi	-1.64206479	-0.2327474
Pp. whitei	0.05071612	-2.5612094

Std. Errors:

	(Intercept)	LingualCingulum
P. cynocephalus	0.3358354	0.2128817
P. kindae	0.4129235	0.3463259
P. robinsoni	0.8596705	0.3758186
Pp. broomi	0.4286506	0.3578468
Pp. jonesi	0.6282709	0.3263875
Pp. whitei	0.4514244	0.7614783

Table 21 Multinomial Regression Summary

Figure 23 Predicted Probabilities of Species for Lingual Cingulum ScoreTable 22 Multinomial Regression Summary

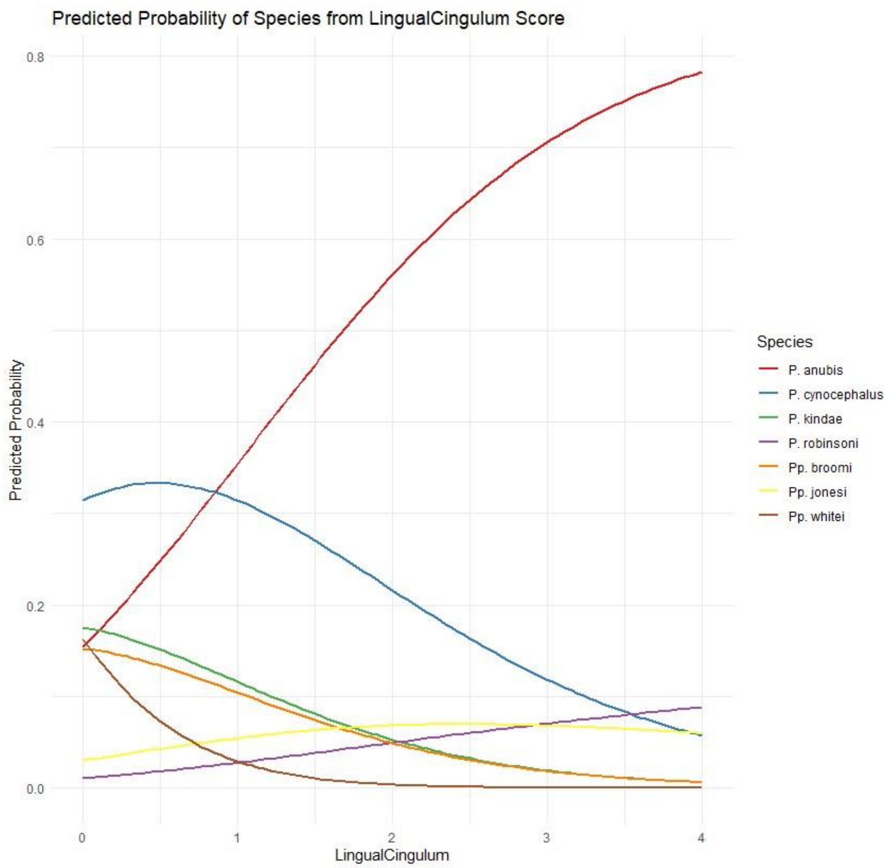

Figure 24 Predicted Probabilities of Species for Lingual Cingulum Score

This LRA, which assesses predicted probability of species from scores of the lingual cingulum illustrated similar trends to the LRA's from the mesiolingual accessory and interconulus, but with some marked differences. *Papio anubis*, again, had the highest predictive probabilities for the highest range of scores for this feature. *Papio cynocephalus* had its highest predictive value corresponding to a score of 0.5 – 1 with reduced probabilities of scores larger than 2. This indicates that, while *Papio cynocephalus* may not have the highest predictive value for a 0 score, its range of scores is fairly limited to moderate expression or absence of the lingual cingulum. *Papio kindae* exhibited a highest probability of 0 indicating an increased frequency of absence of the lingual cingulum compared to *Papio cynocephalus*. The *Parapapio* taxa in this study showed more distinctive predictive signals for this trait than any other taxon. *Parapapio broomi*, for example, had the highest overall predicted probability for a score of 0, but actually reached predictive peak closer to 0.25. While this indicates the high degree of absence in the fossil sample, there is still inclination for lower scores as well. *Parapapio jonesi* had the lowest predicted probability for absence between the *Parapapio* taxa and showed considerable variation in expression of this trait. *Parapapio whitei* had its highest predicted probability at a score of 0, and rapidly tapered to 0% predicted probability for scores larger than 2. *Papio robinsoni* was arguably the most unique of the fossil taxa with a near linear increase between higher score and predicted probability, with a top value of 10% predicted probability for a score of 4.

3.3.1.4 LRA for Lingual Cingulum and Mesiolingual Accessory Scores

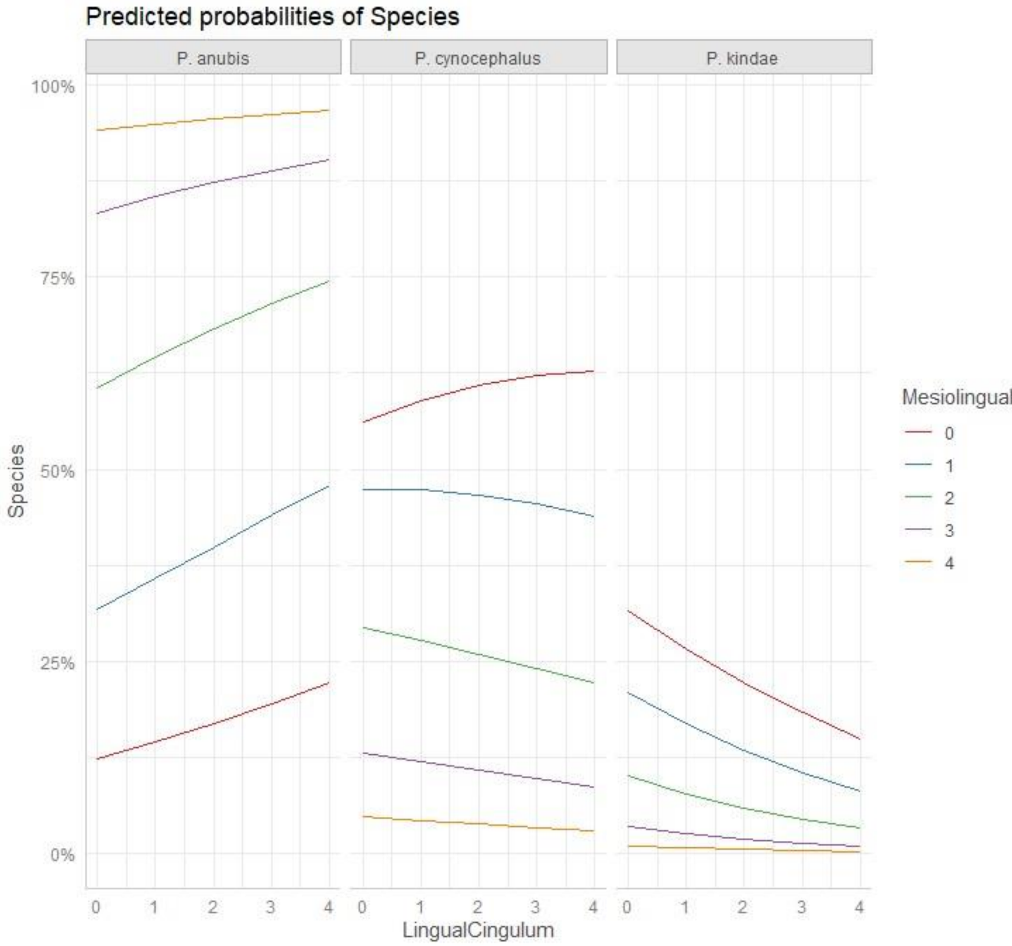

Figure 27 LRA for Extant Taxa (Lingual Cingulum / Mesiolingual Accessory Feature)

Logistic regression analysis is not only useful for assessing predicted probability of population groups by central tendency of a single trait, but also can be utilized to assess how multiple predictors interact with outcome probabilities. Figure 22 illustrates extant species predicted probabilities from mesiolingual accessory score, whilst holding lingual cingulum score as a constant by means of the “ggpredict” function plotted in R. This method expresses not only how predictor variables interact, but also poses an additional tool in the presence of missing data. Essentially, this method utilizes the covariation of traits in taxa to obtain higher predictive probabilities for taxonomic identification.

Figure 22 expresses the predicted probabilities (PP) for extant taxa on the basis of covariance for lingual cingulum (LC) and mesiolingual accessory (ML) scores. As will be repeatedly evident in subsequence LRA's of the three dental traits, *Papio anubis* has the highest PP values for all taxa across nearly all combinations of traits. This effect is likely due to the larger sample size of *Papio anubis* available as well as the high degree of individual variation observed in expression of the dental traits for this species. The high PP for a ML score of 4 and an LC score of 4 (~99%) is unsurprising given the results of the MCA. However, more nuanced analysis can be ascertained with this plotted representation of probabilities.

In the case of *Papio anubis*, an ML score of 0 produces the lowest PP in any combination with an LC score of 0-4. This indicates that, while ML scores of 0 are entirely possible in this taxon, it is not as strong of an indicator for this species as higher scores. A relatively sharp increase in PP between a score of 0 and 1 for LC score as well as a relatively high PP for an LC score of 4 and ML score of 0 support findings from the MCA, wherein ML and LC scores are not completely positively associated. Essentially, high scores for the lingual cingulum do not always correspond to high scores for the mesiolingual accessory feature. *Papio cynocephalus* illustrates a slightly negative relationship between LC score and PP. The highest PP value for *Papio cynocephalus* corresponds with an LC score of 4 and an ML score of 0 (~62%). This is the overall highest PP for this combination of scores in the extant taxa, indicating a decent probability for individuals with these scores belonging to *Papio cynocephalus*. *Papio* *cynocephalus* also illustrates a slight decline in PP for LC scores larger than 1 across all ML scores besides 0. *Papio kindae* has the highest PP for an LC score of 0 and an ML score of 0 (~35%). Similar to *Papio cynocephalus*, *Papio kindae* shows a decrease in PP for all ML scores in LC scores higher than 1. However, this effect is more severe in *Papio kindae*, indicating that probability of belonging to *Papio kindae* decreases as LC score increases beyond 1. In a predictive application, this suggests that an extant papionin maxillary molar with a lingual cingulum score larger than 1 is less likely to belong to *Papio cynocephalus* than *Papio kindae*.

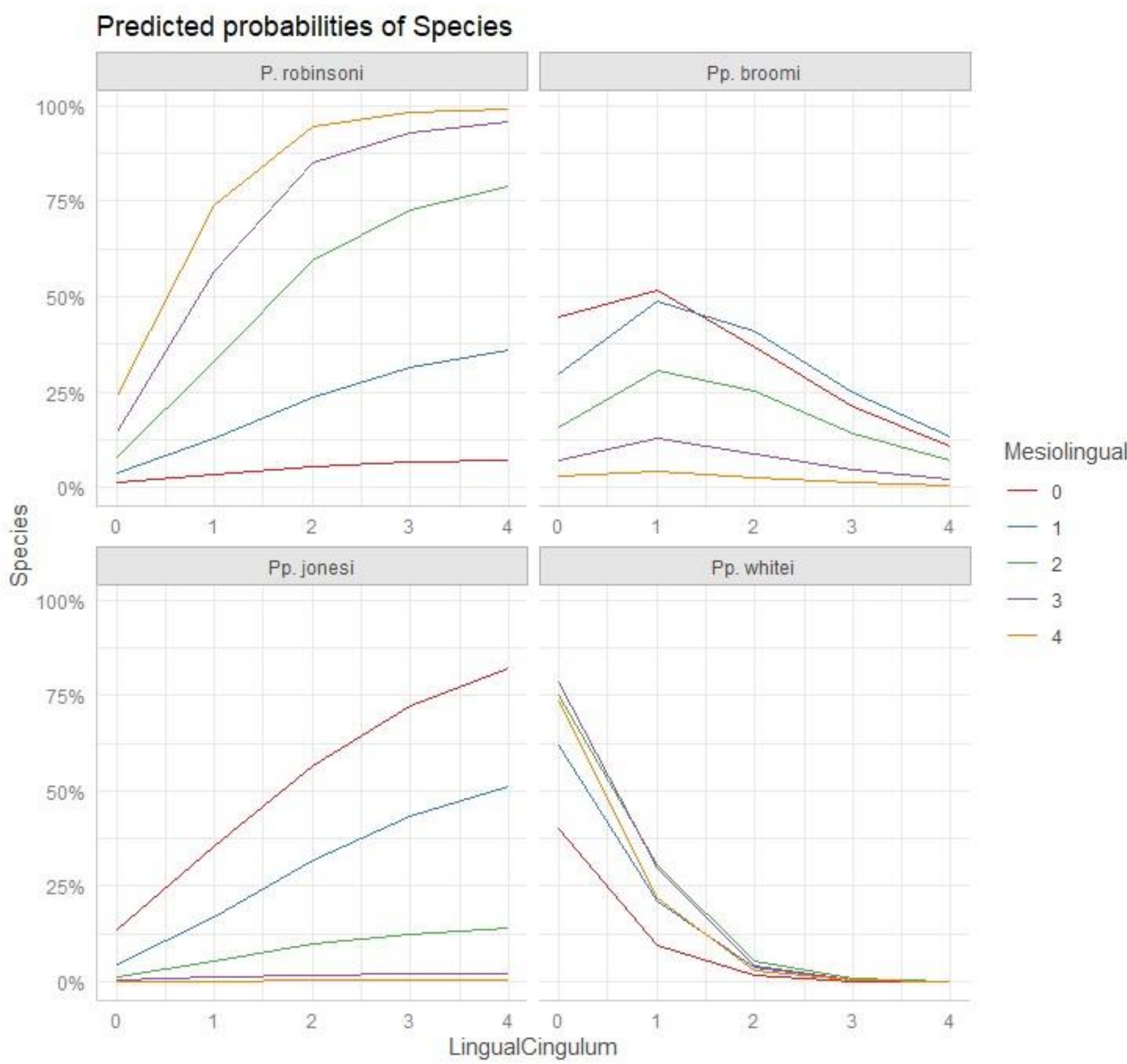

Figure 30 LRA for Extinct Taxa (Lingual Cingulum / Mesiolingual Accessory Feature)

In the fossil taxa (Figure 23), the exclusion of *Papio anubis* allows for a more discrete signal to be assessed between the covaried predictor variables and taxa. *Papio robinsoni* behaves somewhat similarly to the extant *Papio anubis* in that ML and LC scores of 4 produce the highest PP value for this taxon (~99%). Generally, high scores for the lingual cingulum (3,4) and the mesiolingual accessory feature (2,3,4) in *Papio robinsoni* produce the highest PP observed in all fossil taxa. A mesiolingual score of 0 has the lowest predictive probability, regardless of lingual cingulum score, for *Papio robinsoni*. *Parapapio broomi* has its highest PP value for an LC score of 1 and ML score of 0 (~55%). While not producing the highest PP (~48%) for *Parapapio broomi*, an LC and ML score of 1 are most highly predicted for *Parapapio broomi* out of all the fossil taxa. This indicates that either ML and LC scores of 0,0 or 1,1 would be reasonable grounds to estimate that a maxillary molar belongs to *Parapapio broomi*. *Parapapio jonesi* has the overall highest PP related to an ML score of 0, corresponding with an LC score of 3 (~77%) or 4 (~80%). ML scores of 2, 3 or 4 have poor PP values associated, regardless of LC score, indicating that any combinations of these scores in dentition are unlikely to be attributed to *Parapapio jonesi*.

Parapapio whitei is the most distinct of the *Parapapio* taxa in the case of covariation of mesiolingual accessory feature and lingual cingulum score. The highest PP values for *Parapapio whitei* correspond with an LC score of 0 and ML scores of 3 and 4 (75%). This is the highest PP value for all extinct taxa with respect to an LC score of 0, as well as the highest PP values for ML scores greater than 2 in the *Parapapio* taxa. While *Parapapio broomi* also shows a decrease in PP for LC scores greater than 1, this decrease is definitively less distinct than in *Parapapio whitei*. This indicates that maxillary molars from fossil contexts with LC scores larger than 1 are highly unlikely to belong to *Parapapio whitei*. These trends, which would typically be difficult to assess through other multivariate analysis tools, are made more apparent using this visualization method.

3.3.1.5 LRA for Lingual Cingulum and Interconulus Scores

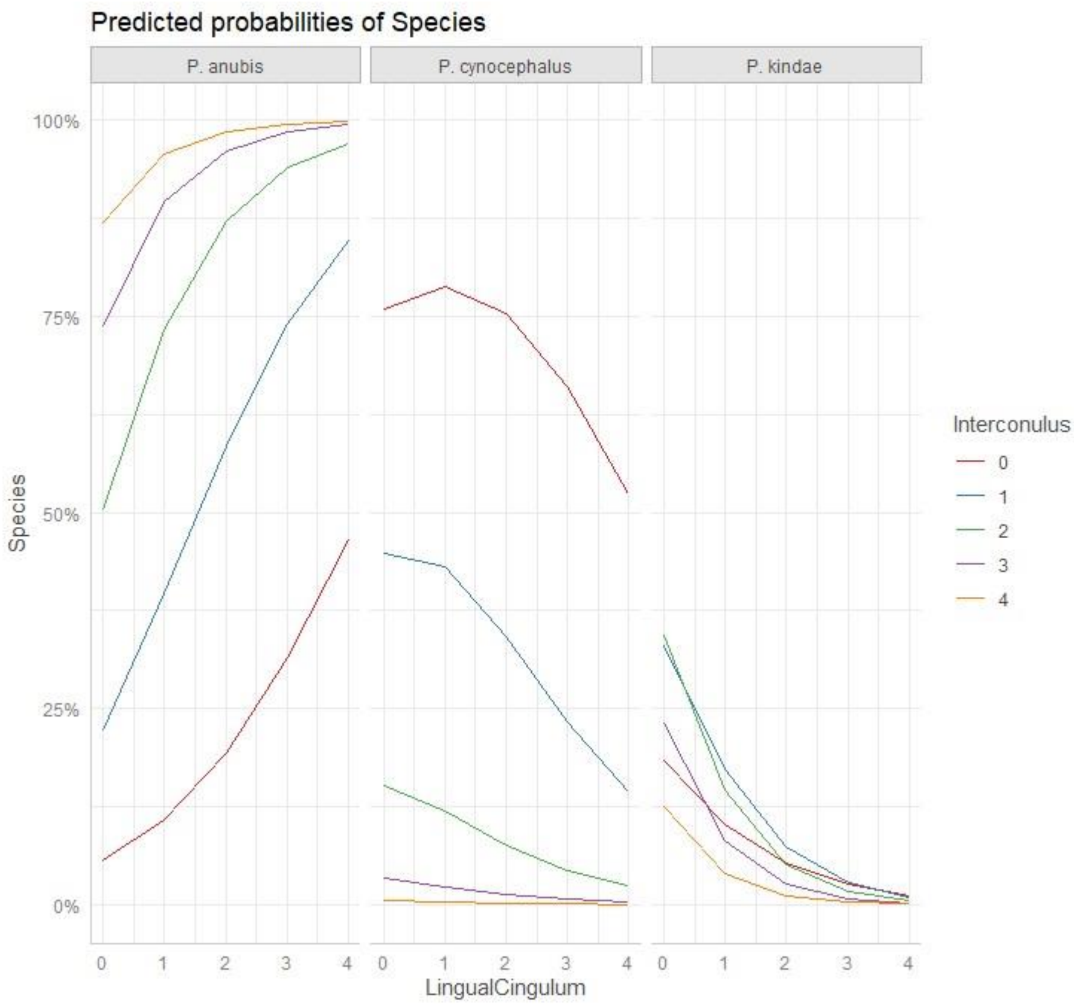

Figure 33 LRA for Extant Taxa (Lingual Cingulum / Interconulus)

A similar analysis was performed for the lingual cingulum and interconulus wherein the lingual cingulum is maintained as the constant. In this analysis, relationships between these two variables within defined species categories illustrate more specific predictors for taxon than previously accounted for in the factor analysis. In Figure 24, *Papio anubis* had the highest predictive probability (PP) overall for a lingual cingulum (LC) score of 3 or 4 and interconulus (IC) score of 4, indicating that individuals with these scores for these two traits would belong to *Papio anubis* over 99% of the time. While the predictive values for the other two extant taxa are dwarfed in comparison to *Papio anubis*, differences between them can still be informative. *Papio cynocephalus* has a highest predicted probability for a lingual cingulum score of 1, paired with an interconulus score of 0 (~77%). The highest PP for *Papio kindae* is an LC score of 0 and an IC score of 2 (~35%).

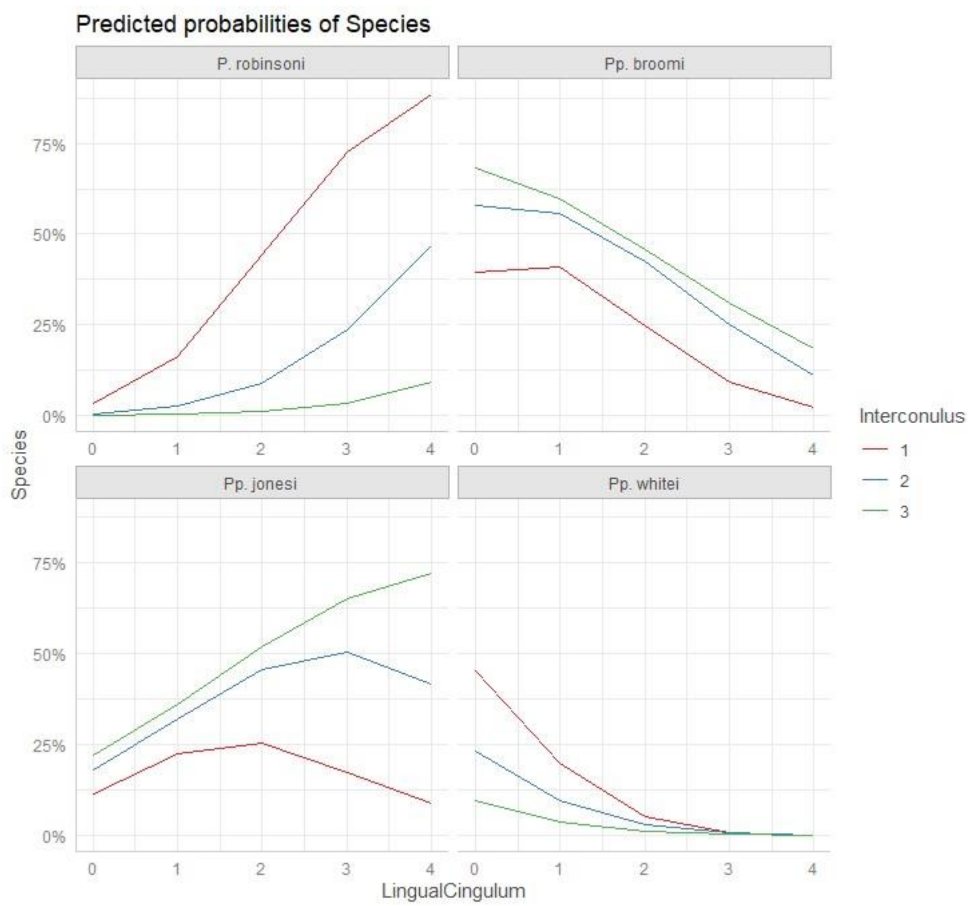

Figure 36 LRA for Extinct Taxa (Lingual Cingulum / Interconulus)

In the fossil taxa (Figure 25), *Papio robinsoni* had the highest predictive probabilities for an LC score of 4 and an IC score of 1 (~40%). *Parapapio broomi* illustrates a negative relationship between LC score and PP, with the highest predictive probability for an LC score of 0 and IC score of 3 (~75%). *Parapapio broomi* also had the overall highest PP from an IC score of 1 for all fossil taxa, which coincides with an LC score of 1 (~55%). *Parapapio jonesi* shows an inverse relationship to *Parapapio broomi* where PP increases with LC and IC score. The highest PP for *Parapapio jonesi,* and highest overall PP for fossil taxa, is for a LC score of 4 and an IC score of 3 (~82%). This is followed by the second highest PP for *Parapapio jonesi*: an LC score of 4 and an IC score of 2 (~75%). *Parapapio whitei* has the highest probability for an LC score of 0 and an IC score of 1 (~52%). *Parapapio whitei* has the lowest probability predictor values of all the *Parapapio* taxa, and its highest PP value (~52%) is only marginally higher than the same combination of scores in *Parapapio broomi* (~38%).

3.3.1.6 LRA for Mesiolingual Accessory Feature and Interconulus Scores

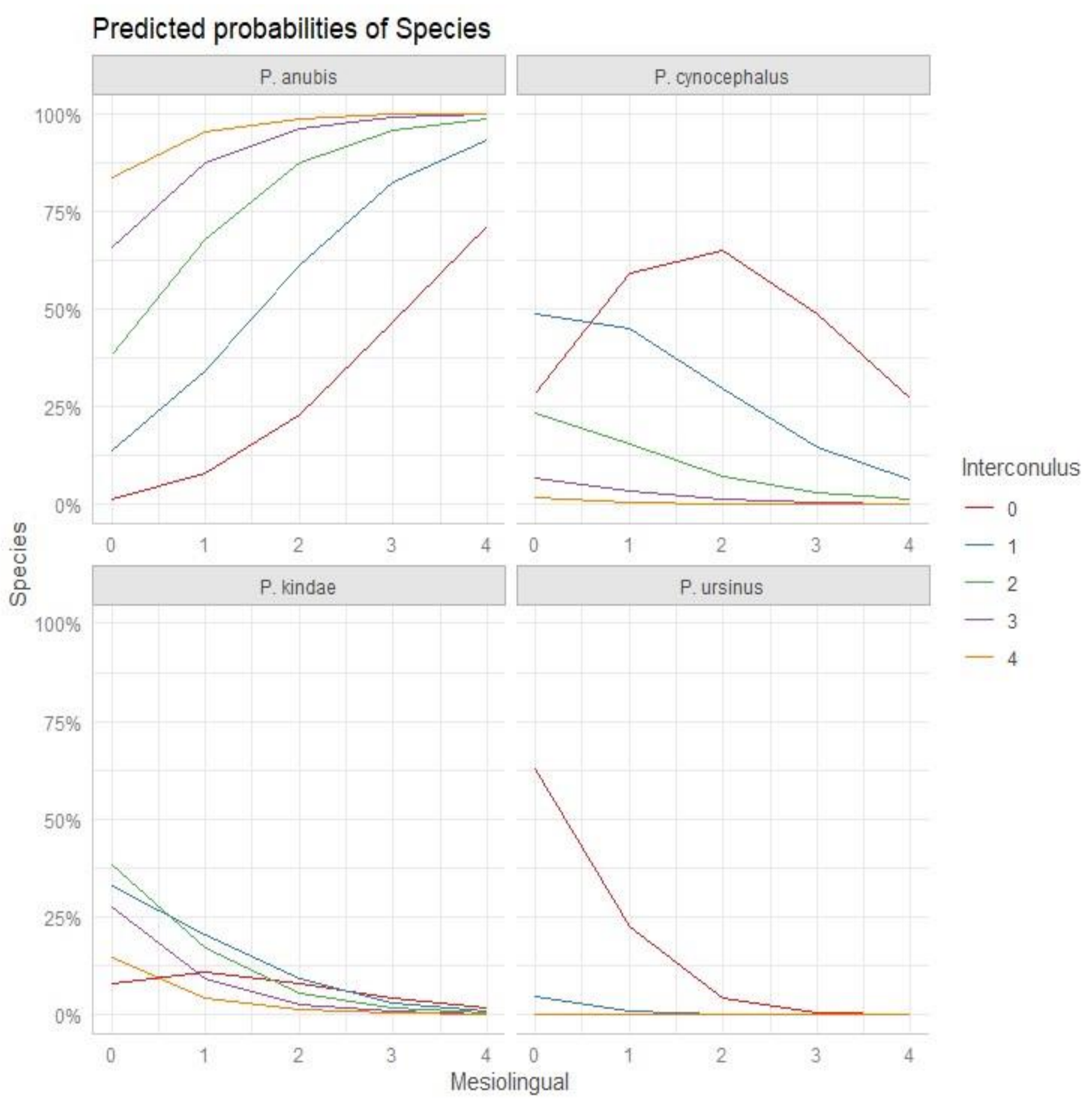

Figure 39 LRA for Extant Taxa (Mesiolingual Accessory Feature / Interconulus)

This analysis was performed to assess the impact of covariance between mesiolingual accessory and interconulus score on prediction probabilities for taxa. Due to extreme predictive probabilities for both *Papio anubis* and *Papio ursinus* compared to all other taxa, this dataset was most coherently displayed when the extant taxa were separated from the extinct. The LRA for extant taxa (Figure 26) also included *Papio ursinus*, as both traits were observable for this taxon. This regression analysis revealed that a mesiolingual accessory (ML) score of 4 and an interconulus (IC) score of either 2, 3 or 4 were the highest probability predictors for *Papio anubis* (~99%). While an ML score of 4 and IC score of 0 were still the highest for *Papio anubis* out of any taxa, this combination was not the highest possible predictor within the species. *Papio cynocephalus* had the highest predictive probability (PP) for an ML score of 2 and IC score of 0 (~55%). The covaried regression for *Papio kindae* showed a somewhat unusual structure. The highest PP value for *Papio kindae* was for an ML score of 2 and IC score of 0 (~65%). There is, however, a secondary peak showing an ML score of 1 and IC score of 0 as also predictive for an extant individual belonging to *Papio cynocephalus* (~60%). This is the highest PP for this combination of scores across all extant taxa. *Papio ursinus* had the overall highest PP for a ML score of 0 and an IC score of 0. A combination of these scores predicts individuals as belonging to *Papio ursinus* ~65% of the time, respectively. Predictive probabilities of essentially any other combination of scores for *Papio ursinus* are nearly 0%, indicating that an individual with a ML score higher than 1 and IC score higher than 0 are very unlikely to be attributed to *Papio ursinus*.

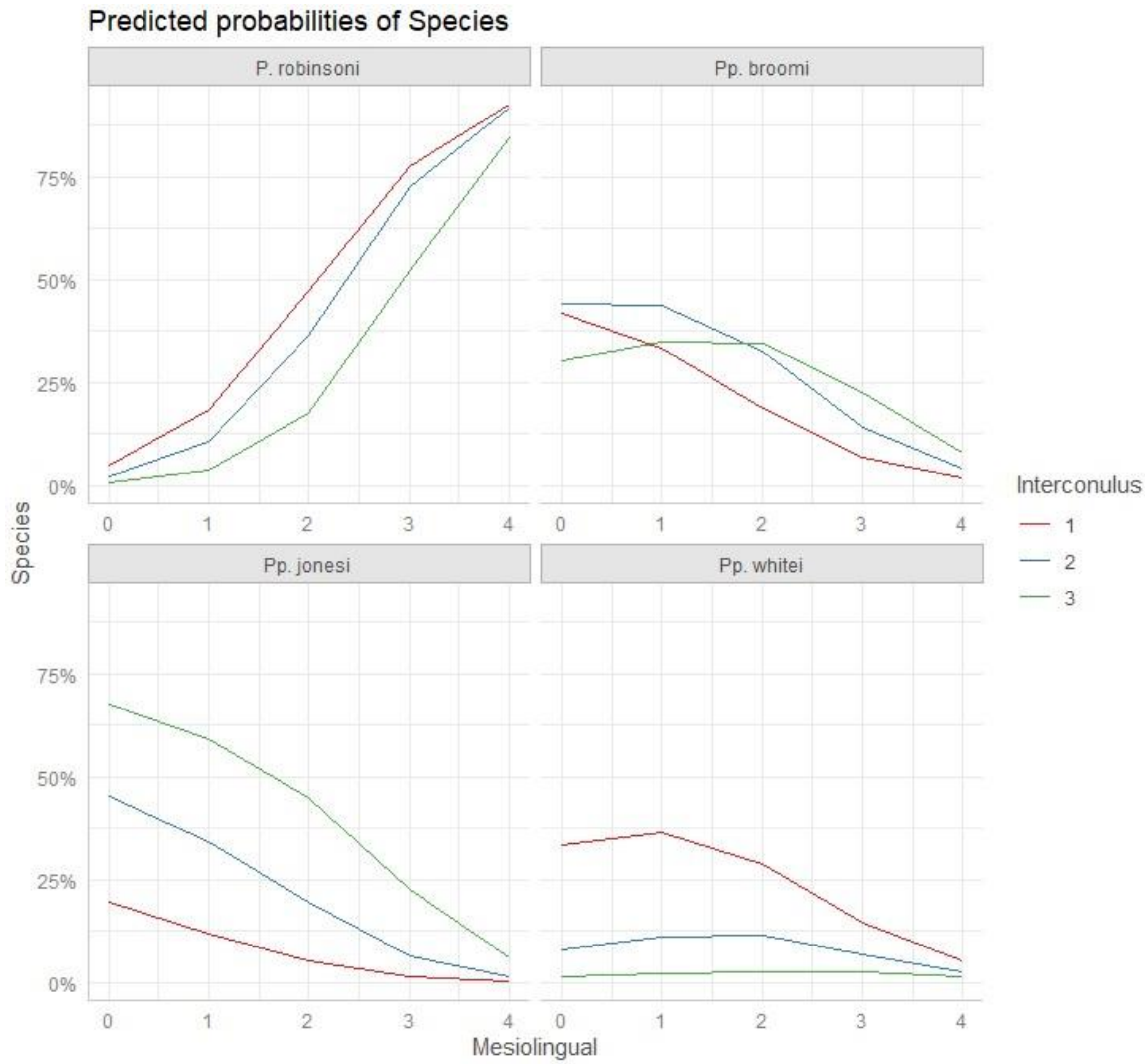

Figure 42 LRA of Extinct Taxa (Mesiolingual / Interconulus)

In the LRA for extinct taxa (Figure 27), *Papio robinsoni* has the highest PP for an ML score of 4 and IC score of 1 (~90%). *Papio robinsoni* generally had the highest PP for an IC score of 1, 2 or 3 in any combination with a ML score of 3 or 4. Any interconulus score combined with a ML score of 4 has a minimum PP of ~85% for belonging to *Papio robinsoni*. Predictive probabilities for *Parapapio broomi* and *Parapapio jonesi* had relatively similar distributions. The combination of an ML score of

1 and IC score of 2 was the highest PP for *Parapapio broomi* (~50%), followed by a secondary peak: an ML score of 2 and IC score of 3 (~48%). Of the *Parapapio* taxa, *Parapapio broomi* had the highest PP for a ML score of 4, combined with an IC score of 3 (~17%), though the difference is relatively small. *Parapapio jonesi* had the overall highest PP for an ML score of 0 and IC score of 3 (~68%) in all fossil taxa. *Parapapio jonesi* also had the lowest PP for nearly any ML score combined with an IC score of 1. *Parapapio whitei* had the overall lowest predictive power for any combination of scores across all taxa. Its respective highest PP was for an ML score of 1 and IC score of 1 (~30%), which is lower than the PP for that combination of scores in *Parapapio broomi* (~38%). While presence of high predictive probability is inarguably informative when using these scores to predict taxonomic classification, absence or reduction of these probabilities can be equally informative. For example, fossil papionin maxillary molars with a mesiolingual score of 0 combined with any nonzero interconulus score are less likely to belong to *Papio robinsoni* than any of the *Parapapio* taxa included in this study. Within *Parapapio*, individuals with an IC score of 1 and any combination of ML score between 1-4 are more likely to belong to *Parapapio broomi* than *Parapapio jonesi*.

3.4 Bootstrapping With Replacement for Predictor Variables

3.4.1 Mesiolingual Accessory Feature

Bootstrap Statistics :

	original	bias	std. error
t1*	2.4210526	-0.0022088623	0.14442265
t2*	0.8444444	0.0027863278	0.11522541
t3*	0.6000000	0.0009984032	0.18595138
t4*	2.0000000	-0.0006578701	0.37112455
t5*	0.2000000	-0.0007027951	0.09281205
t6*	0.2941176	0.0078245998	0.14649736
t7*	0.4000000	0.0068308603	0.15972873
t8*	0.4000000	0.0311529785	0.41694707

	[,1]	[,2]	[,3]	[,4]	[,5]
[1,]	0.95	22.87	973.72	2.12286416	2.6943514
[2,]	0.95	24.95	975.90	0.62500000	1.0831563
[3,]	0.95	37.79	986.42	0.29166667	1.0000000
[4,]	0.95	4.17	902.40	1.00000000	2.5000000
[5,]	0.95	45.04	990.01	0.05263158	0.4375923
[6,]	0.95	50.23	992.35	0.07839641	0.7087372
[7,]	0.95	17.50	964.90	0.10000000	0.7142857
[8,]	0.95	56.94	996.36	0.00000000	1.7915302

Table 24 Summary of Bootstrap Statistics (left) and Original Sample Standard Deviations (right)

Given varied sample sizes for each species and non-normal distribution of the original dataset, mean values had to be assessed as the central tendency with which the bootstrapping procedure was performed. The “original” column in Table 20 represents the mean score of the mesiolingual accessory for each species in the original dataset. The “bias” column describes in what direction bootstrapped values estimated central tendency for each species. Positive values indicate over-estimation while negative values indicate under-estimation. Bias values near zero indicate that the resampled population statistics neither over- nor under-estimated the original population central tendency. The “standard error” column measures the standard deviation across all bootstrapped samples to indicate degree of variability. In the case of the mesiolingual accessory, the majority of bias values are near zero, indicating that the bootstrapped samples neither over- nor under-estimate mean score for each species. To assess the quality of the bootstrapped estimates, the standard error is compared to the standard deviation for each species. The standard error being lower than the standard deviation for each taxa indicates a more accurate sampling procedure, as evidenced in Table 20.

Table 20 also shows confidence intervals for mean values of the resampled data. The original mean scores of the original sample are included in the upper and lower estimates of the bootstrapped sample. This indicates that, upon resampling 1,000 times, there is a range through which 95% of all means will lie. The fact that all species mean scores from the original population fall within this 95% confidence interval indicates that the mean for each species is likely an accurate assessment of population mean score.

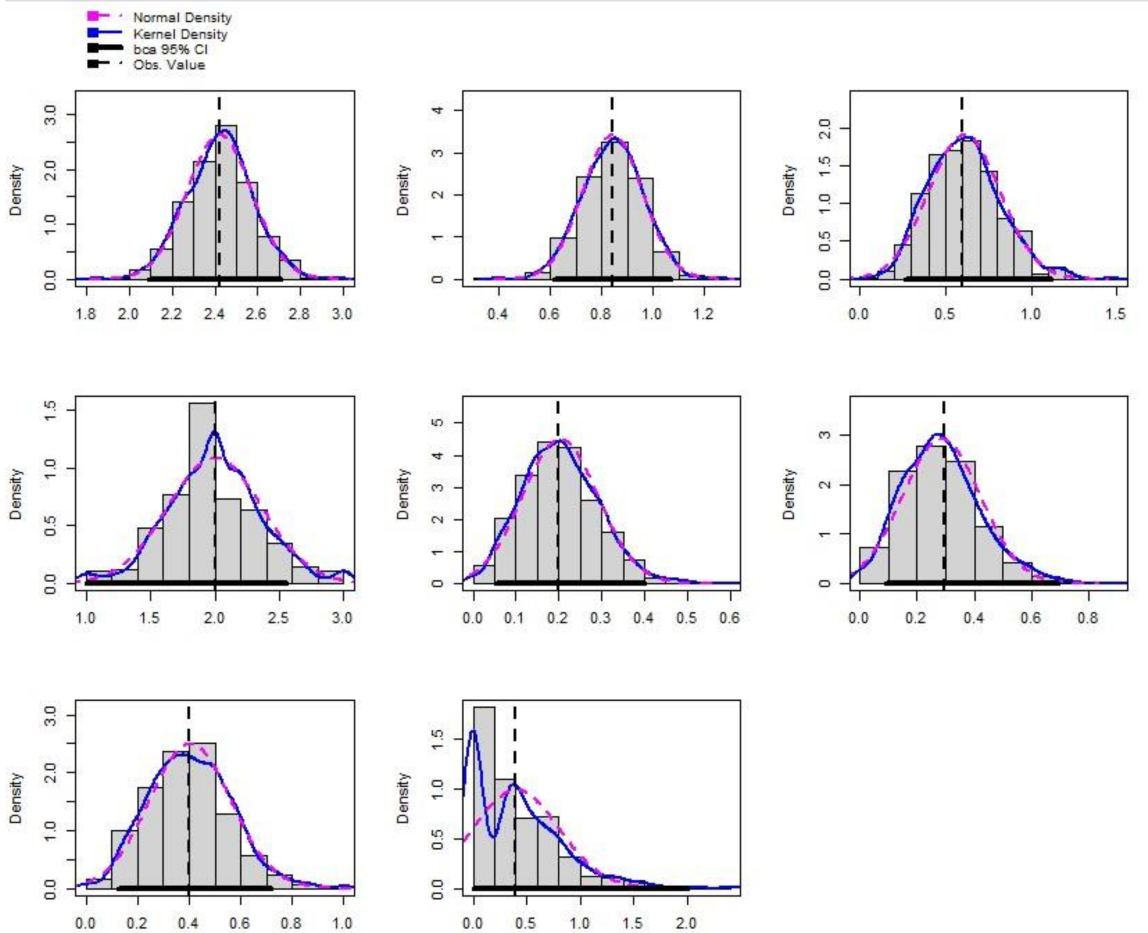

Figure 45 Probability Histograms of Bootstrapped Means for (from left to right) P. anubis, P. cynocephalus, P. kindae, P. robinsoni, P. ursinus, Parapapio broomi, Parapapio jonesi, and Parapapio whitei.

Probability histograms (Figure 28) better illustrate distribution of mean score for each species as well as which species show a more normal distribution of mean score than others. *Papio anubis*, for example, is relatively normal in mean score distribution, with the highest frequency of mean scores aligning with the original population mean. The shape of the kernel density line and normal distribution line mostly overlap with only relatively small tails on both sides falling outside of the 95% confidence interval. The majority of species in this study showed normal distribution for mean mesiolingual accessory score. *Parapapio whitei* is less normally distributed as the original mean is lower than the majority of bootstrapped mean frequencies and the kernel density does not emulate a normal distribution curve. This is expected *Parapapio whitei*, as this taxon is comprised of relatively small sample size.

This non-normal distribution is also a result of this taxon having high instances of a score of 0 for the mesiolingual accessory feature and no continuous negative values, based on the nominal variables used. It is highly statistically likely that resampled mean values for these species would be closer to 0 than the true population mean, therefore skewing the majority of mean values nearer to 0. While bootstrapping is frequently used to assess whether parametric tests can be performed on a data set, all statistical tests used in this study are non-parametric and make no inferences regarding a normal Gaussian distribution. The non-normal distribution of mean values in this bootstrap, therefore, does not invalidate any previous analyses.

3.4.2 Interconulus

Bootstrap Statistics :

	original	bias	std. error
t1*	1.7631579	-1.014500e-03	0.08824183
t2*	0.6666667	6.234247e-03	0.13423924
t3*	1.0500000	7.767302e-05	0.08823381
t4*	1.1666667	6.817903e-03	0.18425152
t5*	0.0500000	7.700970e-05	0.04957386
t6*	1.2941176	4.624279e-03	0.10853367
t7*	1.6000000	9.968794e-04	0.22040817
t8*	1.1000000	-2.905530e-03	0.10016475

	[,1]	[,2]	[,3]	[,4]	[,5]
[1,]	0.95	33.93	983.19	1.6032128	1.9423294
[2,]	0.95	23.38	973.97	0.4166667	0.9353616
[3,]	0.95	24.96	975.91	0.8823529	1.2307692
[4,]	0.95	55.34	993.71	1.0000000	2.0000000
[5,]	0.95	75.70	999.32	0.0000000	0.2818798
[6,]	0.95	26.92	978.01	1.0833333	1.5294118
[7,]	0.95	30.71	981.28	1.2000000	2.0934271
[8,]	0.95	77.22	999.08	1.0000000	1.5095515

Table 27 Summary of Bootstrap Statistics (left) and Original Sample Standard Deviations (right)

The non-parametric resampling procedure for the interconulus showed similar results as the bootstrap returned bias values near zero for all taxa as well as standard error values lower than overall standard deviation values for the population. Mean values of interconulus score for the original sample were between 1.04-1.75 with the exception of *Papio ursinus* ($\bar{x}$ = .045). All original sample mean values were included within the respective resampled 95% confidence intervals, corroborating the sample mean falls within 95% of all 1,000 resampled means.

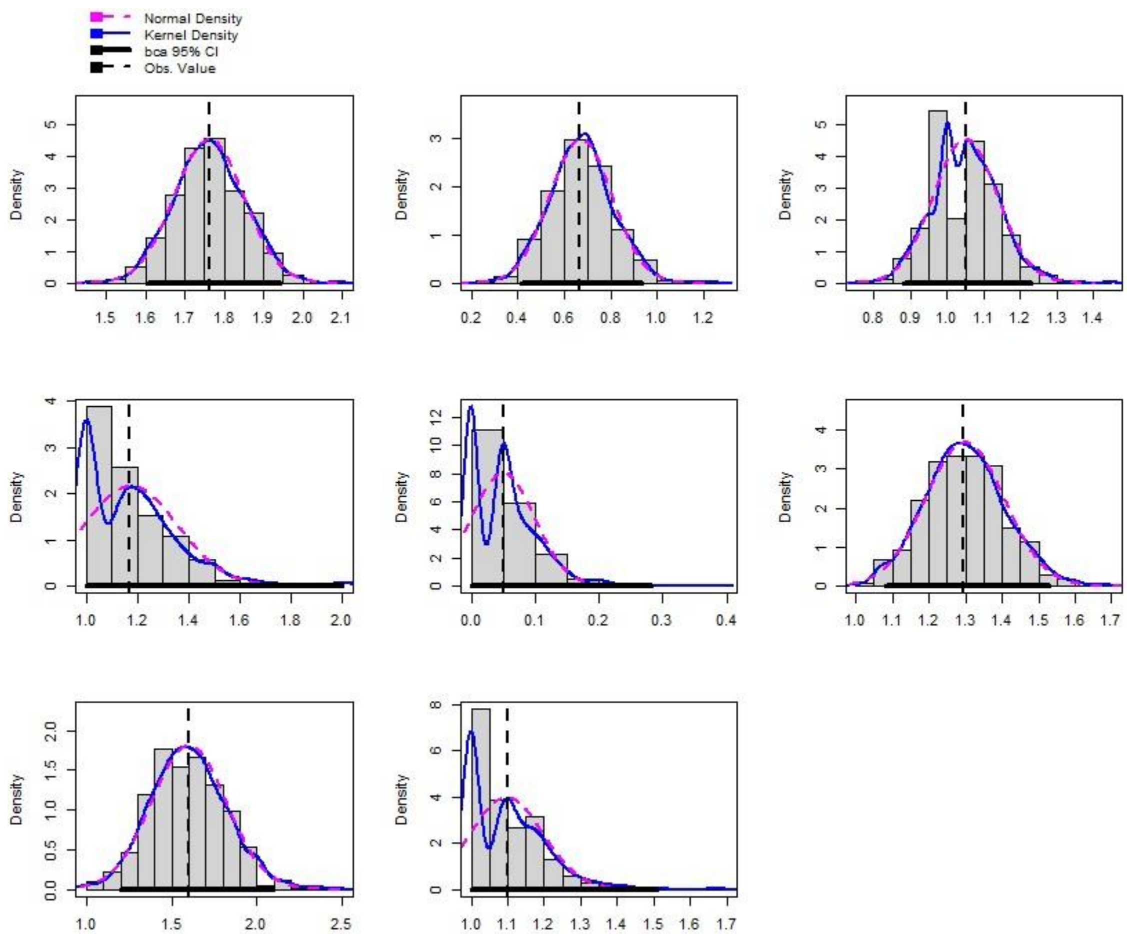

Figure 48 Probability Histograms of Bootstrapped Means for (from left to right) P. anubis, P. cynocephalus, P. kindae, P. robinsoni, P. ursinus, Parapapio broomi, Parapapio jonesi, and Parapapio whitei.

Table 29 Summary of Bootstrap Statistics (left) and Original Sample Standard Deviations (right)Figure 49 Probability Histograms of Bootstrapped Means for (from left to right) P. anubis, P. cynocephalus, P. kindae, P. robinsoni, P. ursinus, Parapapio broomi, Parapapio jonesi, and Parapapio whitei.

The probability histograms of possible sample means for interconulus score (Figure 29) show more taxa deviating from the normal distribution. Resampled means for *Papio anubis*, *Parapapio broomi*, and *Parapapio jonesi* were the most normally distributed. The resampled mean distribution for *Papio robinsoni, Papio ursinus,* and *Parapapio whitei* are expressed as a non-normal distribution likely due to high instances of the lowest score category observed in the respective species. The probability histogram of resampled means for *Papio kindae*, however, is non-normal and the high prevalence of the lowest occurring score is not the cause. While the bootstrap results did not report a highly negative bias, it appears that the original sample mean is higher than the highest frequency mean value, which is between 0.95 and 1.00 compared to the original $\bar{x} = 1.04$. While not falling outside of the 95% confidence interval, this could still indicate that, if a different sample had been chosen to represent the population of *Papio kindae*, mean interconulus score could be lower.

3.4.3 Lingual Cingulum

Bootstrap Statistics :

	original	bias	std. error
t1*	1.8405797	0.006757193	0.1271528
t2*	0.9555556	-0.001120119	0.1413908
t3*	0.6666667	0.004734604	0.1779500
t4*	2.0000000	-0.007256752	0.3651793
t5*	0.6875000	0.015827483	0.2550489
t6*	1.5555556	-0.013749679	0.4967328
t7*	0.2000000	0.004749175	0.1330912

	[,1]	[,2]	[,3]	[,4]	[,5]
[1,]	0.95	22.68	973.35	1.6085090	2.1000000
[2,]	0.95	33.77	983.34	0.6953737	1.2587593
[3,]	0.95	21.48	971.52	0.3394979	1.0000000
[4,]	0.95	7.13	926.06	1.0000000	2.5000000
[5,]	0.95	32.13	982.53	0.2631579	1.2666667
[6,]	0.95	28.84	979.61	0.5689699	2.5555556
[7,]	0.95	41.46	989.13	0.0000000	0.5466822

Table 30 Summary of Bootstrap Statistics (left) and Original Sample Standard Deviations (right)

Figure 50 Probability Histograms of Bootstrapped Means for (from left to right) P. anubis, P. cynocephalus, P. kindae, P. robinsoni, Parapapio broomi, Parapapio jonesi, and Parapapio whitei.Table 31 Summary of Bootstrap Statistics (left) and Original Sample Standard Deviations (right)

Bootstrap statistics for the lingual cingulum score means show minimal bias from the central tendency of the resampled data and a relatively low standard error compared to the standard deviation. The original mean scores showed more variation between taxa than present for the mesiolingual accessory feature and interconulus. There are also fewer instances of overlap for the confidence interval values indicating that, for normally distributed taxa, parametric tests could be conducted. However, inconsistencies in the normal distribution of resampled mean scores indicate that this would only be applicable for 5 of the 7 taxa present and would likely add little additional inference to this analysis.

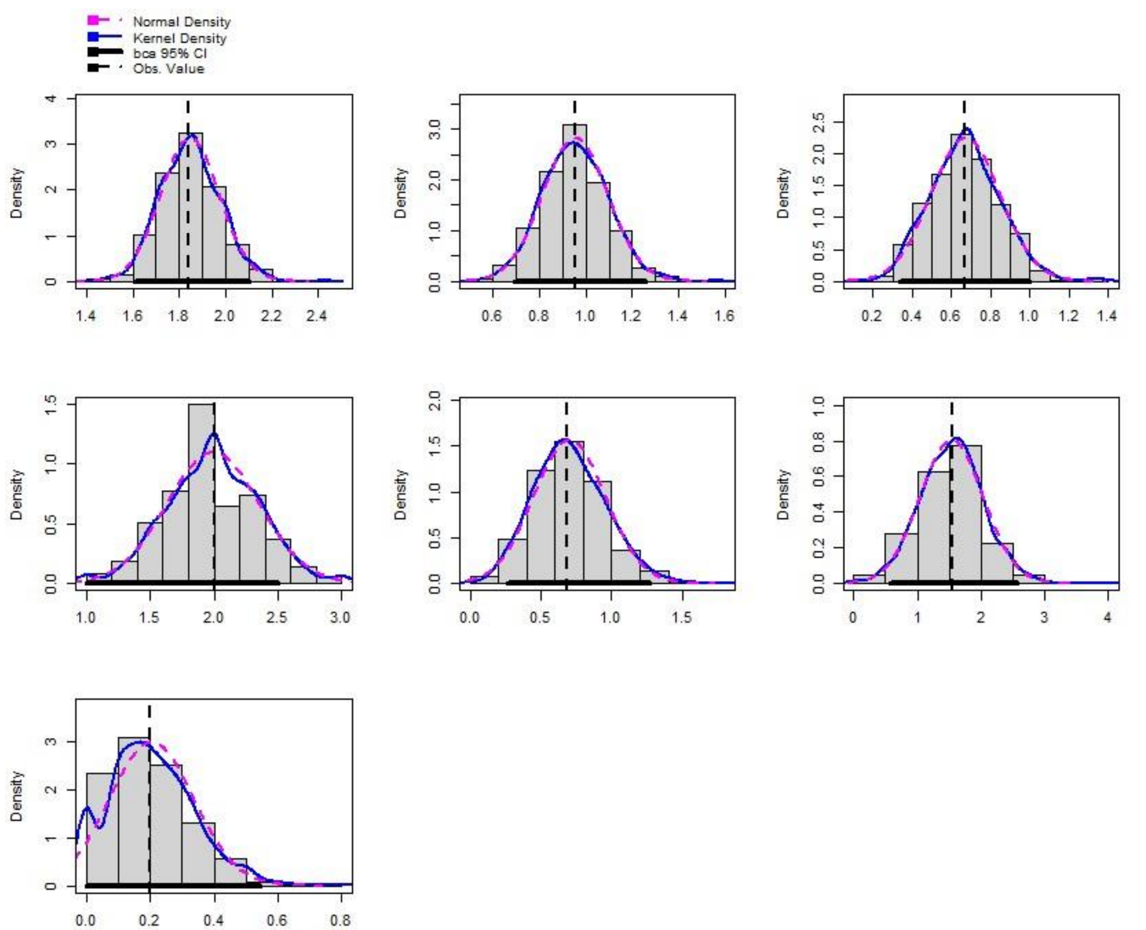

Figure 51 Probability Histograms of Bootstrapped Means for (from left to right) P. anubis, P. cynocephalus, P. kindae, P. robinsoni, Parapapio broomi, Parapapio jonesi, and Parapapio whitei.

Figure 52 Probability Histograms of Bootstrapped Means for (from left to right) P. anubis, P. cynocephalus, P. kindae, P. robinsoni, Parapapio broomi, Parapapio jonesi, and Parapapio whitei.

The probability histograms for resampled means of the lingual cingulum score (Figure 30) show primarily a normal distribution among taxa. *Papio cynocephalus* and *Parapapio whitei*, as in previous bootstraps, were the most non-normally distributed. This can likely be attributed to higher instance of the lowest possible score for the lingual cingulum being prevalent in these taxa, therefore skewing the data to the right, as 0 is the minimum value in this analysis. While this non-normal distribution, again, could be the result of small sample size, similarly sized sample populations like *Papio robinsoni* (n = 4) had a more normal distribution, and less proclivity for the lowest possible score.

4 DISCUSSION OF THE RESULTS

4.1 Extant Taxa

The Multiple Correspondence Analyses were performed to assess the effect of covariance of trait scores on the distribution of individuals. All three MCAs captured a relatively low percentage of overall variance (between 24-28%) and there was overlap between the majority of taxa. With the accepted caveat that overlap indicates relative similarity in trait frequencies, some distinctions were still discernable. In MCA 1, which included all traits but excluded *Papio ursinus,* a clinal variation was discernable for the extant taxa. The northernmost taxon, *Papio anubis,* had not only the highest frequency of presence for most mesial and buccal traits, but also had the highest scoring individuals. *Papio cynocephalus* and *Papio kindae,* which occupy territories bordering the southernmost expanses of *Papio anubis* distributions, ~~further south~~, were similarly distributed across both axes, illustrating a mixture of moderate scores and absence of features. While the majority of individuals attributed to *Papio anubis* expressed moderate scores for both cingula and the lingual accessory features (interconulus and mesiolingual accessory), this taxon presented the greatest frequency of the highest possible scores for each trait. This was additionally supported by MCA 2 as well as subsequent regression models. *Papio kindae* and *Papio cynocephalus* occupied similar locations on the biplot, indicating similar trait score frequencies. This location on both axes illustrates a higher prevalence of lower scores for the aforementioned features than in *Papio anubis*. While score frequencies were similar between *Papio kindae* and *Papio cynocephalus, Papio kindae* showed a stronger affinity for scores of 0, or absence.

MCA 2 illustrated distributions of trait frequencies but included *Papio ursinus.* Polarization on this biplot was primarily on the basis of interconulus and mesiolingual accessory score. In this MCA, *Papio ursinus* was polarized from *Papio anubis* on the basis of absence or presence of lingual accessory features. There was no overlap in the distribution of these taxa. *Papio cynocephalus* and *Papio kindae* occupied the space between these taxa and overlapped with upper and lower values for *Papio ursinus* and *Papio anubis*. This MCA further supports a clinal variation of lingual dental trait scores in the extant taxa where the southernmost taxon, *Papio ursinus*, has the highest prevalence of low score and absence, while the northernmost taxon, *Papio anubis*, has a higher proclivity for the highest scores. *Papio kindae* and *Papio cynocephalus* geographically occupy space between these taxa and show frequencies of trait scores that are moderate, with some overlap between the extremes.

Univariate assessment of regression in extant taxa was generally less informative than multivariate covariance regression models. This illustrated that score for a singular trait, even a trait observed to vary significantly among taxa, was insufficient for predicting taxonomic category. Predictive probabilities for extant taxa on the basis of the lingual cingulum and mesiolingual accessory score covariance showed that specific combinations of scores for these features were more probable to belong to certain species than others. An extant papionin maxillary molar with a mesiolingual accessory score of 4 and lingual cingulum score of 4 can be attributed to *Papio anubis* with roughly 99% accuracy. This combination of scores is 0% probable to appear in *Papio cynocephalus* and roughly 18% probable for *Papio kindae*. A mesiolingual accessory score of 0 and lingual cingulum score of 0 are most likely to be attributed to *Papio cynocephalus* (~39%).

An LRA for the covariance of interconulus and lingual cingulum score was less informative, with *Papio anubis* having the highest predictive probabilities for all combinations of scores. This indicates that the covariance of these two traits is a poor means to assign taxonomic category for extant species of papionins. An LRA for the covariance of the interconulus and mesiolingual accessory score showed the highest variation among extant species. Each taxon had one combination of scores that produced the highest predictive probability out of all other extant species. In *Papio anubis*, IC scores of 2, 3 or 4 combined with a ML score of 4 produced a PP of nearly 99%. These combinations of scores were essentially 0% for the three other extant species. In *P. cynocephalus*, an IC score of 4 and ML score of 0 had the highest PP of all taxa (~54%). This PP was rivaled only by *P. anubis*, which had a PP of ~46% for that score combination but showed a PP of ~0% in *P. kindae* and *P. ursinus*. *Papio kindae* had the highest PPs for an IC score of 0 and ML score of 2 (~72%) followed by an IC score of 1 and ML score of 0 (67.5%).

The predicted probabilities of *Papio ursinus*, which were not included in the previous LRA's due to poor representation of the lingual cingulum, further affirm the polarization from *P. anubis* in the factor analyses. The PP of *P. ursinus* was highest for an IC score of 0 and ML score of 0 (~99%). This is followed by the PP for an IC score of 0 and ML score of 1 (~85%). Both combinations of scores highest in *P. ursinus* are near 0 for not only *P. anubis,* but also in the other extant taxa (*P. cynocephalus* [PP = 0%]; *P. kindae* [PP = 18%]).

In the case of LRAs comparing covariance of the lingual cingulum score to either mesiolingual accessory or interconulus score, overlapping predictive probabilities with only subtle differences support findings from the multiple correspondence analyses. In these two LRAs for covariance, differences between taxa are subtle and could be interpreted as clinal. The LRA comparing covariance of interconulus and mesiolingual accessory score, however, supports more distinctive probabilities for species on the basis of multiple combinations of trait scores. Both *Papio anubis* and *Papio ursinus* have score combinations which near 100% predictive probability, implying a very strong correlation between these combinations and their respective taxon. These mutually exclusive score probabilities could be highly persuasive in an assignment of true species designation. *Papio cynocephalus* has two score combinations with predictive probabilities higher than 60%, which indicates a relatively good fit with slight overlap with *Papio anubis*. *Papio kindae* does have one predictive probability higher than 50%, but this combination overlaps heavily with *P. anubis*. Given the assessments of normality and smaller sample size of *P. kindae*, it is likely that a different sample of *P. kindae* individuals could produce more convincing PPs for a specific combination of trait scores.

In all MCAs, *P. kindae* and *P. cynocephalus* were difficult to distinguish from each other. These logistic regression analyses, most prominently in LRA for ML and IC score, visually illustrate a more evident difference in trait score frequencies between these two taxa. MCA results from this study could more readily support a clinal variation pattern with *P. ursinus* and *P. anubis* representing extremes followed by a gradient of variation between *P. kindae* and *P. cynocephalus*. If this were the case, Figure 19 would likely show *P. kindae* as fairly similar to *P. ursinus*. *Papio cynocephalus* would be more similar to *Papio anubis* given geographic proximity and observed hybridization.

While the score combination of IC 4 and ML 0 had similar PPs for *P. cynocephalus* and *P. anubis*, the general probability trends were quite different. In *P. anubis*, IC score, ML score, and PP had a positive relationship. The inverse was true for *P. cynocephalus*. *Papio cynocephalus* was also distinctive from *P. ursinus* on the basis of interconulus score. While both species showed a negative correlation between ML score and PP (near 0% for any ML value larger than 2), higher IC scores were distinctly more probable for *P. cynocephalus*. *Papio kindae* was arguably unique from both *P. ursinus* and *P. anubis* in predictive probabilities for species based on the covariance of the interconulus and mesiolingual accessory scores. For the majority of score combinations, predictive probabilities decreased as ML score increased, which was more similar to *P. ursinus*. High species predictive probability for an ML score of 2 and IC score of 0 with tapering probabilities for ML scores less than or greater than 2, however, was unique to this taxon. The second highest predictive value for an ML score of 0 and an IC score of 1 was more similar to *P. anubis*.

It is difficult to argue whether these differences in score covariance as predictive variables truly indicate differentiation on the taxonomic level of species or subspecies. If an alpha value of 0.05 was used to classify species, then on the basis of specific score combinations, *Papio anubis* and *Papio ursinus* would definitively be classified as separate species given PP values greater than 95% for at least one score combination. *Papio cynocephalus*, in this model, does not show a statistically significant difference when utilizing a 0.05 alpha value, but one could argue that the highest PP (~77%) is a high enough predictive value for that score combination to support true species designation. *Papio kindae* had the overall lowest predictive probabilities indicating it as the poorest candidate for demarcation of species. However, contextualizing these findings with the post-bootstrapped non-normal distribution for all traits as well as the small sample size, future studies could produce higher predictive values for specified score combinations that were not represented here.

4.2 Extinct Taxa

Factor analyses were used to assess covariance among all taxa to test whether *P. robinsoni* belongs to *P. hamadryas* or is distinctive as a species. The factor analyses also tested whether three distinctive *Parapapio* species truly exist within South African fossil contexts. MCA 1 illustrated a high amount of overlap between *P. robinsoni* and extant *P. kindae* and *P. cynocephalus* across both dimensions. While not entirely polarized from *P. anubis* on either axis, generally *P. robinsoni* was separated from the majority of *P. anubis* individuals. This illustrated that on the basis of the interconulus, mesiolingual accessory, lingual cingulum, and buccal cingulum score, *Papio robinsoni* appeared to be fairly similar to the two more moderately expressing extant taxa: *P. kindae* and *P. cynocephalus*.

MCA 2, which included *P. ursinus* and excluded the lingual and buccal cingula, illustrated a slightly more discernable signal. As in MCA 1, *P. robinsoni* individuals had overlapping ranges with *P. kindae* and *P. cynocephalus*. *Papio robinsoni*, in this MCA, did not have plotted values that overlapped with *P. ursinus* or *P. anubis*. Given that MCA 2 distinguished taxa on the basis of mesiolingual accessory and interconulus scores, *Papio robinsoni* appeared to have mostly moderate scores compared to *P. ursinus* in which there was a high prevalence of absence and in *P. anubis* which demonstrated a propensity for extreme lingual accessory scores. This outcome is somewhat unexpected given that previous hypotheses posit a Southern African origin for modern *Papio*, so dental scores between fossil South African *Papio robinsoni* should be most similar to the southern African chacma baboon (*P. ursinus*). While this factor analysis did illustrate that *P. robinsoni* was very similar in trait score expression to some extant taxa and dissimilar to others, it was difficult to assess which precise score combinations were most influential in accounting for these differences.

MCA 3 included all traits and excluded all extant taxa to assess covariance of trait scores for *Parapapio* and fossil *Papio*. In this factor analysis, *Papio robinsoni* was somewhat distinct from all *Parapapio* taxa on the basis of buccal and lingual cingula scores higher than 2 and higher mesiolingual accessory scores. While it is expected, given the observed morphological and temporal differences of fossil *Papio* from *Parapapio*, that *Papio robinsoni* would be distinct, higher scores for these traits indicated that they represented a more derived condition in fossil papionins. This opposes the proposed theory that the cingular remnant and related features like the lingual cingulum, mesiolingual accessory and interconulus (Hlusko 2018), represent the ancestral condition in papionins.

MCA 3 indicates that *P. robinsoni* is likely to be the least accurately classified as a distinctive species from all *Parapapio*. Given that *P. robinsoni* and all the *Parapapio* species supposedly are distinctive at the genus level, a higher degree of polarization would be expected. In the extant taxa, *Papio ursinus* and *Papio anubis*, members of the same genus, are more distinctively polarized than what is observed in the fossil genera.

There are several possible interpretations for this observed lack of polarization. The first being a limited sample size in the fossil taxa. Bootstrapped resampling (Figures 21, 22, & 23) illustrated that, for all resampled trait means, despite smaller sample sizes, there was a relatively normal distribution for *P. robinsoni* and all *Parapapio* taxa except *Parapapio whitei*. *Parapapio whitei*, however, is already the most polarized from *Papio robinsoni* with no overlap in individual distribution on MCA 3. The probabilities of bootstrapped means, in fact, indicate that the mean scores for the original sample are higher than those estimated by the resampling procedure. Upon utilizing a different sample of *Parapapio whitei*, it is likely that these significant trait scores would be lower, further polarizing *Parapapio whitei* from *P. robinsoni*.

Another possible explanation for this observed lack of polarization among genera is a matter of temporal distribution and microevolution. Of the individuals included in the MCA's all of the *Parapapio whitei* individuals utilized come from the fossil site of Makapansgat, estimated to be the oldest site included in this study. The *Parapapio jonesi* sample was comprised of individuals from Swartkrans. *Parapapio broomi* individuals sampled were from Sterkfontein. All *Papio robinsoni* individuals were from Swartkrans. The locality of individuals sampled is important for ruling out temporal differences as a confounding factor in interpretation of these results.

Given that Makapansgat is the oldest site followed chronologically by Sterkfontein Members 2 and 4 and Swartkrans Member 1, the distribution of individuals in this study across these dated sites is important to consider. *Parapapio whitei* is represented by individuals from the oldest and *Papio robinsoni* from the youngest sites, indicating that this polarization could be due to temporal differences. If this were the case, the lack of differentiation fossil *Papio* expresses between *Parapapio broomi* and *Parapapio jonesi* would be due to a higher instance of individuals sampled from later-dated sites. The *Parapapio jonesi* individuals are sampled from Swartkrans, indicating that prevalence of higher scores for the specified dental traits represents an evolutionary trajectory rather than a static feature within taxa. *Parapapio broomi*, however, is represented by individuals from Makapansgat. *Parapapio jonesi* is observed to be more negatively skewed on axis 1 of MCA 3 than *Parapapio broomi*, indicating that temporal distribution is at least not solely responsible for the lack of observed differences between *Parapapio* and *P. robinsoni*.

The third possible explanation for the lack of polarization between *Parapapio* and *P. robinsoni* is multifaceted. While spread across a notable temporal field, the fossil individuals in this study come from a similar geographic locality, southern Africa. The most notable and significant differences observed in the dental trait scores of extant taxa were from species that occupied different regions of the African continent: *Papio ursinus* in Southern Africa and *Papio anubis* in Northwest to Northeast Sub-Saharan Africa. This consideration could be used to interpret these findings in multiple ways.

The apparent lack of distinction in MCA 3 across the genus classification could indicate that this scoring system and categorical score frequencies are more applicable for assessing gene flow events across geographically overlapping populations. In this case, statistically significant differences are more likely to represent a lack of hybridization in extant and extinct taxa rather than identifying true taxonomic distinctions. This could be evidenced by the statistically significant differences in mean rank and mutually exclusive predicted probabilities observed in extant *P. ursinus* and *P. anubis*, which do not have overlapping territories in the wild (Jolly 1993; Jolly et al. 2011). *Papio kindae* and *Papio cynocephalus*, though individually possessing some relatively high predicted probabilities for covariance of specific score combinations, illustrated varying frequencies of gene flow and hybridization events, as supported by some genetic and behavioral studies (Harris 2000; Newman et al. 2004; Jolly et al. 2011).

Another possibility is that score frequencies and covariance of specific score combinations for the most influential dental traits are indeed effective identifiers for taxonomic category, meaning a re-classification of South African fossil papionins could be justified.

As in the extant taxa, Logistic Regression Analyses can help to provide more detail regarding covariance of specific trait scores than is discernable in the MCAs by reducing covariance to two predictor variables. Figure 23 shows that the only mutually exclusive predicted probabilities for mesiolingual accessory and lingual cingulum score are for ML scores of 3 or 4 and an LC score of 4 for *Papio robinsoni*. These combinations of scores have PPs greater than 98% for *Papio robinsoni* and are essentially 0% probable for any *Parapapio* taxa.

Regarding overall trends in LRA for covariance of ML and LC score, *P. robinsoni* appears more distinct based on a positive relationship between high ML and LC scores than is apparent in MCA 3. *Parapapio whitei*, as supported by the distribution of individuals in MCA 3, shows the inverse relationship to *P. robinsoni*, where an increased lingual cingulum score beyond 0 results in a rapidly decreased predicted probability. This affirms the polarization observed in MCA 3 and the possibility that temporal vectors have a positive correlation with the intensity of lingual accessory scores. *Parapapio jonesi*, represented by the highest number of individuals from the youngest dated sites out of all *Parapapio* taxa would be expected to have similar predicted probabilities for similar score combinations to *Papio robinsoni*. A high PP for the absence of the mesiolingual accessory and high scores for the lingual cingulum, however, is a combination relatively unique across all fossil taxa. Like in the more modern fossil *Papio*, there appears to be a positive relationship between LC score and PP, but only when combined with absence or a score of 1 for the mesiolingual accessory. This provides some clarification for the temporal hypothesis proposed to explain the lack of distinction between *P. robinsoni* and *Parapapio*. Essentially, lingual cingulum score could be more closely tied to temporal distribution than intensity of all lingual accessory traits. *Parapapio broomi* has the highest predicted probabilities for moderate ML and LC scores which are highest for ML scores of 1 or 0 and an LC score of 1. Absence of the lingual cingulum and scores higher than 1 steadily decrease predicted probabilities for *Parapapio broomi*. As a secondary pattern, it appears that mesiolingual accessory scores of 3 or 4 in fossil taxa are almost completely exclusive to *Papio*, regardless of lingual cingulum score. While these results could indicate a progression of mesiolingual accessory scores increasing over time, it is also possible that the presence of these extreme scores in *P. robinsoni* indicate a genus-specific expression not seen in *Parapapio*.

Figure 25 helps to explain the overlapping values in MCA 3 for fossil *Papio* and *Parapapio*. When the covariance of the lingual cingulum and interconulus scores were assessed in relation to predicted probabilities for species, the lack of a strong relationship between interconulus score and PP for *Papio robinsoni* compared to *Parapapio* became evident. While there is still a positive relationship between LC score and PP for *P. robinsoni*, interconulus score covaries poorly, indicating a more random relationship between IC score and LC score in *P. robinsoni*. *Parapapio broomi* and *Parapapio jonesi* showed much stronger correlations, negative and positive respectively, between LC score, IC score and PPs.

These regression trends contextualize discrepancies in MCA 3 by explaining the stronger positive skew of *Parapapio broomi* and *Parapapio jonesi* than expected. The more discernable covariance between interconulus and lingual cingulum score in *Parapapio broomi* and *Parapapio jonesi* likely skewed individuals further positive on axis 1, causing a closer alignment with *P. robinsoni* on the biplot.

Figure 27 most clearly differentiated between genera among the fossil taxa used in this study. When mesiolingual accessory score was held as the constant against interconulus score, a definitive difference between *P. robinsoni* and all *Parapapio* taxa was revealed. A positive relationship between ML score and PP for *P. robinsoni*, regardless of IC score, compared to the generally negative correlation between ML score and PPs for *Parapapio* further supports high scores for the mesiolingual accessory as the primary defining variable for separation of fossil genera. This LRA essentially removed the temporal variable, and trends were primarily affected by mesiolingual accessory score, while interconulus score had a minimal effect on predicted probabilities for fossil taxa.

5 INTERPRETIVE SIGNIFICANCE

The analyses utilized in this study were conducted to test the efficacy of using non-metric dental trait scores for assessing phylogenetic signal in fossil and extant papionins. Whether traits or the covariance of traits showed significant difference or predictive probabilities were then used to reassess taxonomic assignment of individuals. The univariate Kruskal-Wallis H test and Chi-square test of independence were performed initially to determine which dental traits varied significantly between species and therefore would be most suitable for predictive models. These tests illustrated that the mesiolingual accessory feature, interconulus, lingual cingulum, buccal cingulum, and, to a lesser extent, the distal fovea varied significantly between taxonomic categories. Several of these traits, however, were not suitable for regression analysis. While the goal of this study was to pursue traits that were informative for phylogenies, the excluded traits and why they were excluded also provided valuable insight.

5.1 Excluded Features and Interpretations

Features excluded from predictive modeling on the basis of insignificant values from univariate tests and low cos2 values in factor analyses included the split hypocone and mesial fovea. Frequencies of presence of a split hypocone in the taxa sampled were so minimal that individuals with presence of this feature were considered anomalous outliers. Given the highly symmetrical bilophodont nature of papionin maxillary dentition, presence of an asymmetrical crown feature such as the split hypocone was decidedly rare. The majority of individuals which expressed presence of this feature belonged to extant *Papio anubis*, which also possessed the highest degree of exaggerated lingual accessory features generally. While these lingual accessory features do not typically intersect with the occlusal plane, it is possible that the increased lingual asymmetry so profoundly present in *P. anubis* could be related to an increased degree of overall molar asymmetry, including features of the tooth crown.

The observed persistence of an anomalous feature in a single taxon that is not prevalent in other members of a sub-tribe could point to a dietary causation. When assessing variation in dentition generally, it is pertinent to consider diet as a factor. Modern baboons are described as dietary generalists with a frequent reliance on hard object feeding depending on seasonal variation and geographic distribution of food sources (Peters 1991). If the traits selected for this study were indeed reflective of dietary proclivity, one would expect a diet in *Papio anubis* that is different from the other extant taxa in this sample. This is not reflected in the majority of observational studies (Peters 1991; Nystrom 2004). Increased presence of the split hypocone in this taxon would thereby indicate either individual variation encapsulated in the larger sample size, or some form of sample bias which included a disproportionate number of individuals with this trait present that is not indicative of values for the overall species population.

The mesial and distal foveae were also excluded from predictive regression modeling. Score frequencies for the mesial fovea varied insignificantly between taxa, and distal fovea expression was only significantly different between two extant taxa: *P. anubis* and *P. ursinus*. While the possible scores for these traits ranged between 0 and 2, the resulting expression in all taxa was dichotomous, i.e., only scores of 1 or 2 were present. There was little evidence of any covariance between these traits and those which varied significantly across many taxa. It is possible that the scoring criteria for the traits were adopted poorly from the hominoid scoring systems in applications to papionin maxillary molars. While neither a score of 1 or 2 for either fovea were indicative of molar crown asymmetries, the degree of visible variation observed for these traits likely does little to affect mastication. This visible variation, which was used to establish the scoring procedure for papionins, most likely reflects individual variation rather than any relationship to evolutionary lineages.

The buccal cingulum was also excluded from regression modeling since significant differences were only observed between *P. anubis* and *P. kindae* in the extant taxa, and no distinct differences among the extinct taxa. Factor analysis showed an overall high effect on the distribution of individuals, but the weights of individual score categories did not follow any distinguishable gradient pattern. The weighted effect of the two highest scores, 3 and 4, for this feature were entirely polarized while absence and moderate scores were near zero on both axes. This indicated that absence and low scores for this feature were common and varied with little patterning across the majority of taxa. The polarization of the higher scores would provide little insight into phylogenetic signal since individuals would be polarized on the basis of a relatively minute difference in score expression. It is unlikely that a single degree of expressed magnitude for this trait would correspond to meaningful taxonomic category designations. This polarization also caused an illogical covariance with the three lingual accessory traits.

These findings support the conclusion that buccal cingulum score is observed in relatively random frequencies in papionins, especially when compared to the lingual accessory traits. This could be due to the criteria of the scoring procedure itself. As in the ASUDAS, scores for this feature are dependent on how far distally this cingulum extends from the apex of the mesial marginal ridge. Essentially, scores for this feature are based on length rather than any measure of lateral extension or width. Unlike the lingual cingulum, there are no accessory features below the occlusal surface on the buccal edge of the molars featured in this study. The buccal margins of all the papionin molars sampled were devoid of any discernable accessory features. This could indicate, as in the other excluded traits, that individual variation is the main contributing factor in expression of the buccal cingulum.

It could be hypothesized that extreme scores for the buccal cingulum correspond with extreme lingual cingulum and lingual accessory scores as a means to maintain overall symmetry. While there appears to be some correlation between lingual accessory scores and buccal cingulum scores, high degrees of expression for these traits are not mutually inclusive. The majority of taxa with high lingual accessory scores have some presence of the buccal cingulum, but not to a symmetrical degree. Since this feature, as it presents in papionins, is a relatively thin ridge scored on the basis of distal extension, even the highest possible score does not create a symmetrical profile. Individuals with high scores for the lingual traits show an overall projection towards the midline of the palate. Individuals with the most extreme scores for the buccal cingulum have little lateral extension of the crown, indicating that symmetry is still not a factor.

Assessing the traits excluded from the regression modeling helped to identify that occlusal molar morphology is under a high degree of control due to the intensive masticatory demands of papionin diets. Humans and great apes as part of the hominoid radiation have dentition suited for the consumption of softer foods or are reflective of pre-masticatory processing techniques. Humans and apes are more likely to have selectively neutral persistence of accessory features on the molar crown that can be used to assess phylogenetic relationships. This study illustrates that such trends are not extended to papionins and therefore phylogenetic signal can only be assessed from features that do not comprise the occlusal surface.

5.2 Extant Taxa

The majority of theories regarding classification of extant *Papio* fall within two main camps. The first camp places all modern *Papio* groups within the species *Papio hamadryas* with distinction at the sub-species level on the basis of hybridization and clinal variation in craniofacial morphology (Frost et al. 2003; Gilbert et al. 2018). The second rejects reproductive isolation as a primary defining factor for taxonomy in baboons and acknowledges the presence of six distinct species in Africa (Groves 2014; Gilbert et al. 2018). These models will, henceforth, be mentioned as the single-species model and multi-species model.

Factor analyses utilized in this study did support a distribution of significant dental traits that align with a clinal variation pattern from south to north. Predicted probabilities ascertained from multinomial logistic regression analyses of covariance, however, illustrated that certain score combinations uniquely identified species. There is, however, no published literature regarding what predicted probability percentage is an acceptable baseline for defining taxonomic boundaries for logistic regressions that utilize solely nominal variables. Lynch (1991) does posit a reliable precedent for assessing “phylogenetic inertia” of fossil and extant primates using log odds procedures, which were utilized in this study to plot the S-curves in logistic regression models. Blomberg & Garland (2002) and Ives & Garland (2010) also utilized similar log-odds statistics to assess a phylogenetic signal of behavioral variables in various antelope clades. The aforementioned studies, however, utilized continuous predictor variables and subsequently relied upon parametric tests to gather significance values used to determine the strength of the phylogenetic signals.

Predicted probabilities were also assessed with the caveat that the values could only describe *patterns* in the phylogenetic signal and could not identify the *factors* contributing to such patterns (Lynch 1991; Ives and Garland 2010). These predictive values were therefore assessed under the assumptions posited by the two competing models of baboon taxonomic assignment as the primary factors to explain such patterns.

The single-species model could be supported by the combined inferences from factor and logistic regression analyses. The frequencies of higher scores for mesial accessory traits generally increase as taxa are distributed further north in the African continent. Covariance of the interconulus and mesiolingual accessory feature shows the highest degrees of species-specific variation, distinguishing these features as the most phylogenetically integrated of all features measured. The predicted probabilities of covariance of these traits do generally follow the clinal variation pattern observed.

South African *Papio ursinus* and northern central African *Papio anubis* are vastly different, as expected. Given the high instance of observed hybridization and largely overlapping territories between *P. anubis* and *P. cynocephalus*, the correlations between trait score covariance and predicted probabilities should be similarly positive between these groups. While proclivity for higher interconulus values is shared between the taxa, absence of the mesiolingual accessory feature is much more prevalent in *P. cynocephalus* and akin to patterns seen in *P. ursinus*. *Papio kindae*, which has a relatively limited overlap in territory with *P. anubis* and *P. ursinus*, shows a mosaic of trait score frequencies which align more readily with a clinal distribution.

Interpreting these same results with the assumptions implied by the multiple-species model could be used to support the existence of several distinct extant *Papio* species. The extreme polarization of *P. anubis* and *P. ursinus* could justify at least these groups as separate species. There is effectively no overlap in predicted probabilities of interconulus and mesiolingual accessory score covariance between these two groups. *Papio kindae*, while showing what could be interpreted as a mosaic of score frequencies, could also be argued as producing a relatively unique signal that follows neither a positive nor negative correlation. Observed hybridization between *Papio kindae* and *Papio ursinus* in multiple zones would likely correlate to trait frequencies more akin to *P. ursinus*, but the overall trends are relatively distinct.

5.3 Extinct Taxa

This study included three conspecific *Parapapio* species (*Parapapio broomi*, *Parapapio jonesi* and *Pp whitei*) and one member of extinct *Papio* (*Papio robinsoni*). The three *Parapapio* species are of specific interest due to ongoing controversy regarding whether a designation of species or subspecies is most appropriate. *Papio robinsoni*, while ultimately chosen due to representation of maxillary molar casts in the available materials, is also of particular interest given its proposed classification as a subspecies within *Papio hamadryas* (Gilbert et al. 2018). For *Parapapio*, the overall null hypothesis tested in this study would posit no significant difference between the proposed species, indicating likely a subspecies classification. A rejection of this null hypothesis would support that one or possibly all these groups belong to separate species. Whether *Papio robinsoni* varies significantly from the *Parapapio* taxa in this study is informative, though whether there is significant difference in dental trait scores from the overall extant population will help to assess if *Papio robinsoni* belongs to the extant species *Papio hamadryas*.

The null hypothesis first assessed for the fossil taxa states that there is no significant difference between the fossil *Papio* species included in this study and *Parapapio* individuals on the basis of scores for non-metric dental traits to discern a differentiation on the level of genera. Factor analysis alone did not capture a clear enough polarization to confidently assess how dental trait scores behave between fossil papionin genera. Overlapping individual ranges on the biplot (Figure 9) indicated either confounding factors affecting individual skew or poor association between dental trait scores and taxonomic categories. Logistic Regression Analyses illustrated that a combination of temporal distributions and poor covariance of the interconulus in *P. robinsoni* was responsible for the lack of polarization observed in MCA 3.

Lingual cingulum scores increased in taxa represented at younger fossil sites, indicating that expressed intensity of the lingual cingulum has increased in fossil papionins over time. The temporal variable rendered the lingual cingulum score a poor indicator for differentiation between genera, as a gradual increase was observed rather than punctuated equilibrium. Mesiolingual accessory score, however, proved to be the main defining variable between *Papio* and *Parapapio*. Scores of 3 or 4 for the mesiolingual accessory were non-existent in *Parapapio* and only observed in *Papio robinsoni*. The covariance of the mesiolingual accessory was assessed alongside the lingual cingulum and interconulus to determine predicted probabilities for the fossil taxa. With the inclusion of these covariance models, there were four combinations of scores that produced predicted probabilities for assignment to *Papio robinsoni* higher than 99% that were reciprocated with predicted probabilities of less than 1% in all *Parapapio* taxa. These results provide statistics to support the existence of two distinct papionin genera in South African fossil sites.

The genus *Parapapio* and the existence of four distinct species within this clade has undergone scrutiny. The historical basis for differentiating these species has been craniofacial and molar dimensions, but high degrees of inter-species variability for these measurements, which is larger than those tolerated for extant taxa, call into question the viability of more than one true *Parapapio* species in South African fossil sites. Factor analyses including both extinct and extant taxa showed a high degree of overlap and similar distributions of individuals across both axes much like extant *P. kindae* and *P. cynocephalus*. Even when an MCA was performed on only the extinct taxa, there was significant overlap between all *Parapapio* species.

Regression models showed a considerable amount of variation in trait score combinations between *Parapapio* taxa. However, since both models held the lingual cingulum score as the constant predictor variable, the majority of variation observed corresponded with site age estimates. Despite the high predicted probabilities and distinctive trends in these models, they do not support species designation of these *Parapapio* groups. Figure 27 presents the lowest difference in overall predictive trends between *Parapapio* taxa, and places *Papio robinsoni* as the most distinct fossil taxon.

The covariance of the interconulus and mesiolingual accessory feature scores, which removes the temporal variable, further illustrates this lack of difference in *Parapapio*.

5.4 Phylogenetic Assessment of All Sampled Taxa

The observed correlation between lingual cingulum expression and time in extinct taxa brings into question the variation observed in the extant taxa for this trait. Given that all extant species are from a single, modern temporal distribution, variation in score frequencies could be interpreted in several ways. The extinct taxa illustrated an evolutionary trajectory towards higher scores for the lingual cingulum regardless of taxonomic category. Reduction of the lingual cingulum could then be associated with the ancestral papionin condition and extension of this trait with a more derived condition. Given that *Papio robinsoni* likely represents the ancestral condition of *Papio*, extension of the lingual cingulum would be considered ancestral for the extant populations.

Geometric morphometric analysis of extant taxa shows *Papio anubis* as having the highest persistence of ancestral morphological features given similarities to *Papio robinsoni* (Gilbert et al. 2016). This aligns with similar predictive probability trends observed between *P. anubis* and *P. robinsoni* for dental trait score covariance. Factor analysis, however, showed *Papio robinsoni* aligning moreso with *P. kindae* and *P. cynocephalus.* This difference is on the basis of interconulus score expression being less exaggerated in *P. robinsoni*. This indicates that extreme expression of the interconulus is a more derived condition in *P. anubis* that is shared also with *P. cynocephalus*, though at a reduced frequency. Lingual cingulum scores, on the other hand, are most frequently 0 for *P. cynocephalus*, indicating a mixture of an ancestral interconulus expression and possibly a derived expression of the lingual cingulum. Since higher expressions of both the lingual cingulum and interconulus appear to be related to the ancestral *Papio* condition, it is worth noting that these scores appear at a very reduced frequency in *P. kindae* and are totally absent in *P. ursinus*.

Genetic estimates have placed *Papio ursinus* as the earliest diverging extant baboon taxon but is described as having highly derived craniodental morphologies that are dissimilar to both *P. robinsoni* and *P. anubis* (Gilbert et al. 2018; Santander et al. 2022). Results of this study corroborate a derived *Papio* condition for *P. ursinus* which, in terms of dental trait frequencies, is more similar to the ancestral papionin condition seen in *Parapapio*. If *P. ursinus* is accurately described as the first diverging extant lineage, the presence of such a derived dental condition is unexpected. This could suggest a relatively rapid deviation from the ancestral condition not observed in the other extant taxa. Alternatively, mtDNA and Y chromosomal analyses of genetic divergence estimates for *P. ursinus* could indicate a fossil lineage that is less related to *P. robinsoni* than the central and northern African clades (Newman et al. 2004; Santander et al. 2022). Higher degrees of expression of the lingual accessory traits could then be interpreted as the ancestral condition for north and central African baboons, while absence of these traits is the ancestral condition for southern African groups, like the chacma.

Zinner et al.'s mtDNA analysis (2009) proposed a binary split early in the extant baboon lineages consisting of a southern and northern clade. The southern clade encapsulated *P. ursinus*, *P. kindae*, and southern groups of *P. cynocephalus*. The northern grouping contained three geographically determined populations of *P. anubis*, *P. papio*, and an east African cluster (*P. hamadryas*, eastern *P. anubis* populations, and northern populations of *P. cynocephalus*). Santander et al.'s (2022) analysis produced the same general groupings, but with substantially older divergence dates for *Papio kindae* and southern *Papio ursinus*. Newman et al. (2004), however, posited a much closer relationship between *P. cynocephalus* and *P. anubis* than the other genetic analyses referenced, which would not align with the placement of *P. cynocephalus* primarily within the southern clade.

If absence of mesial accessory features corresponds to the ancestral condition of specifically the southern clade, then the progression of trait frequencies observed in this study aligns well with established genetic data. *Papio ursinus* would have been the first lineage to diverge from an ancestor with reduced lingual accessory features and thereby maintained expression of the ancestral condition. If presence of extreme scores for all lingual accessory traits is the ancestral condition for the northern clade, then the extreme scores observed in *Papio anubis* reflect a retention of that ancestral condition. *Papio papio* and *Papio hamadryas* were not included in this study, but future datasets which include these taxa would help to prove or disprove this trend.

The placement of *Papio cynocephalus* within the southern clade, but with notable admixture between northern taxa helps to contextualize the score frequencies observed for this taxon. Absence of the mesiolingual accessory and reduction of the lingual cingulum fits the ancestral diagnostics for the southern clade well. Persistence of a high interconulus score, however, indicates hybridization with members of the *Papio anubis* lineage. While not wholly disproving the findings from Newman et al. (2004), this affinity to more *P. ursinus*-like trait frequencies better aligns with the findings of both Zinner et al. (2009) and Santander et al. (2022).

Both Zinner et al. (2009) and Santander et al. (2022) describe *Papio kindae* as existing exclusively within the southern clade and as more distantly related to *P. ursinus* than *P. cynocephalus*. Santander et al. (2022) described *P. kindae* as a species formed from hybridization events between “proto-northern” groups and more northern reaching groups from the southern clade. High prevalence of absence and low scores for the interconulus and lingual cingulum in *P. kindae* reflects the southern influence on trait expression. A high prevalence of moderate mesiolingual accessory scores in *P. kindae* illustrate influence from northern populations.

5.5 Taxonomic Designations

Assuming the frequency of scored dental traits utilized in this study are indeed representative of phylogenetic signal and have been interpreted correctly alongside genetic and morphological data, there is an argument for the distinction of species in some extant papionin taxa. Most notably, the extensive differences in phylogenetic reconstruction between *Papio anubis* and *Papio ursinus* are persuasive grounds to differentiate them as separate species. Based on genetic dissimilarity to other taxa, Zinner et al. (2009) authoritatively places *Papio kindae* as a separate species. The results of this study could either confirm or deny this claim. The mosaic of dental trait frequencies observed in this taxon are distinct from all other taxa sampled, both extant and extinct. It is difficult, however, to determine if this unique signal is representative of a species or the result of a population perpetually affected by hybridization and gene flow events.

As evidenced from both phylogenetic analyses and low predicted probabilities from regression models, *Papio kindae* is the least convincing taxon for true species designation. With these results, three distinct taxonomic categories are supported: the Southern Clade, which includes *Papio ursinus* and *Papio [sp] cynocephalus* [*?Papio ursinus cynocephalus*], the Northern Clade (*Papio anubis*), and the ?Central African Hybrid Clade (*Papio kindae*)/[*?Papio sp. kindae*].

On the basis of trait score frequencies, *Papio robinsoni* most closely resembles extant *Papio anubis*. If future studies illustrate similar dental trait frequencies in all northern clade *Papio* species to *P. robinsoni* and *P. anubis,* an overall distinction of *Papio hamadryas* for members of this clade would be supported. This would result in the following nomenclature: *P. h. hamadryas, P. h. anubis, P. h. papio,* and *P. h. robinsoni*.

While this study affirmed *Papio robinsoni* as highly distinctive from *Parapapio,* there was little evidence to support the designation of three *Parapapio* species at the sampled sites. Variation between the named species groups was observed, but most measures could be explained by temporal distribution of taxa. In contrast to many studies, which find *Parapapio whitei* to be the least viable *Parapapio* taxon in southern African fossil sites, *Parapapio whitei* was the most distinctive grouping based on trait score frequencies.

6 CONCLUSIONS

In this study, frequencies of non-metric dental trait scores in fossil and extant papionins were used to assess phylogenetic signal and reassess taxonomy. For the extant taxa, this study generally aligns with a binary split between southern and northern taxa with hybridization accounting for trait frequencies that lie between extreme forms of expression. This study did support *Papio robinsoni* as being similar to northern taxa, but assignment specifically to *Papio hamadryas* cannot be assessed at this time without inclusion of an extant *Papio hamadryas* sample. This study also supports no discrete species designations between the three *Parapapio* taxa as variation in trait frequencies vary less significantly than in extant species.

Future studies would hope to include extant populations of *Papio cynocephalus* from both northern and southern populations within the observed territory. Inclusion of *Papio papio* and *Papio hamadryas* would also serve to either prove or disprove the ancestral conditions of northern clade taxa as well as provide better context for *Papio robinsoni*. For fossil contexts, *Papio izodi* and *Papio angusticeps* named samples could be assessed in comparison to *Papio robinsoni* to inform taxonomic assignment of these contested species.

Expressions of the lingual cingulum in extinct taxa appear to be heavily influenced by temporal distribution and are not definitively related to taxonomic assignment. To reassess *Parapapio* species more accurately on the basis of dental trait score frequency would require samples from similarly dated sites. As in all studies which utilize fossil materials, this study and the statistical analyses used did have results influenced by small sample sizes and non-normal distributions, as was especially evident for *Parapapio whitei*.

Applications for this systematic assessment of non-metric dental traits, however, could be especially profound in studies of fossils. Regression analyses from future robust samples could be used to create a scoring system that can predict taxon with varying degrees of certainty on the basis of dental trait scores. In cases where isolated papionin maxillary molars are found in fossil sites with no attributable skeletal elements, a taxonomic classification could be more readily assigned. Compared to previous methodologies which would primarily use dimensional measures, the use of non-metric dental scores obviate individual size and sex as confounding factors.

APPENDICES

List of Species and Individuals

Papio ursinus

ZM38324
ZM38341
ZM38315
ZM38356
ZM38372
ZM38320
ZM38321
ZM38319
ZM38330
ZM37387
ZM38353
ZM37677
ZM38344
ZM38328
ZM38365
ZM38363
ZM38342
ZM38380
ZM35917
ZM35947
ZM38361
NNMCatostG

Papio anubis

RG17738
RG2400
RG18471
RG11664
RG11153
RG10416
RG14450
RG17691
RG18472
RG18206
RG14695
RG9731
RG12441

RG6025
RG6229
RG6026
RG8311
MCZ21161
MCZ8304
MCZ23091
MCZ23085
MCZ21160
MCZ29786
MCZ26473
MCZ31619
MCZ17342
MCZ15378

Papio kindae

IRSNB7885
IRSNB10629
IRSNB10629B
IRSNB807E
IRSNB9102
IRSNB809B
IRSNB10619
IRSNB10627
IRSNB12863
IRSNB8531
IRSNB10624
IRSNB10642

Papio cynocephalus

MCZ44276
MCZ23083
NZP 367862
NZP384211
NZP384216
NZP384217
NZP384218
NZP384238
NZP384239
NZP396164
NZP396185
NZP396187
NZP396188
NZP452507

NZP452509

Parapapio broomi

STS251
STS325
STS332
STS368A
STS378A
STS530
STS544

Parapapio whitei

MP62
MP77
MP221
M3147

Parapapio jonesi

SK462
SK543
SK551

Papio robinsoni

SK458
SK461
SK564
SK565

Summary Table of Highest Predicted Probabilities from Score Combinations by Species

Taxon	Lingual Cingulum X Mesiolingual Accessory		Lingual Cingulum X Interconulus		Mesiolingual Accessory X Interconulus	
	Score Combinations	PP's	Score Combinations	PP's	Score Combinations	PP's
Papio anubis	4 , 4	100%	4 , 4	100%	4 , 4	100%
	3 , 4	99.50%	4 , 3	100%	4 , 3	100%
	4 , 3	99%	3 , 4	99%	4 , 2	100%
Papio cynocephalus	4 , 0	62%	1 , 0	77%	2 , 0	65%
	0 , 1	45%	0 , 0	76%	1 , 0	60%
	1 , 0	45%	2 , 0	75%	3 , 0	50%
Papio kindae	0 , 0	35%	0 , 1	30%	0 , 2	37%
	0 , 1	30%	0 , 2	28%	0 , 1	35%
	0 , 2	10%	0 , 3	23%	1 , 3	27%
Papio ursinus					0 , 0	65%
					1 , 0	24%
					0 , 1	10%
Papio robinsoni	4 , 4	100%	4 , 1	82%	4 , 1	88%
	3 , 4	99%	3 , 1	75%	4 , 2	87%
	4 , 3	98%	4 , 2	45%	4 , 3	80%
Parapapio broomi	1 , 0	68%	0 , 3	70%	0 , 2	45%
	1 , 1	52%	1 , 3	60%	1, 2	44%
	0 , 0	48%	0 , 2	58%	0 , 1	42%
Parapapio jonesi	4 , 0	80%	4 , 3	74%	0 , 3	65%
	3 , 0	75%	3 , 3	65%	1 , 3	60%
	2 , 0	65%	2 , 3	52%	0 , 2	45%
Parapapio whitei	0 , 3	77%	0 , 1	45%	1 , 1	37%
	0 , 4	75%	0 , 2	22%	0 , 1	35%
	0 , 2	75%	1 , 1	12%	2 , 1	27%

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