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Identification of a Derived Dental Trait in the Papionini Relative to Other Old World Monkeys

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ABSTRACT Variation in the shape of teeth provides an immense amount of information about the evolutionary history and adaptive strategy of a mammalian lineage. Here, we explore variation in the expression of a purported molar lingual remnant (the interconulus) across the Old World Monkeys (Primates: Cercopithecidae) with the aim of elucidating a component of the adaptive radiation of this family. This radiation is characterized by a wide geographic range (Asia and Africa) as well as diverse dietary niches. While all of the cercopithecids are distinguished by their derived bilophodont molars, the colobines have evolved taller and more pointed cusps compared with the cercopithecines. We investigate whether the interconulus also correlates with phylogenetic affinity and/or dietary adaptation. We assess the frequency and range of interconulus expression in 522 specimens representing seven species of Old World Monkeys (*Cercopithecus mitis*, $n = 78$; *Macaca fascicularis*, $n = 85$; *Macaca mulatta*, $n = 70$; *Papio hamadryas*, $n = 55$; *Colobus guereza*, $n = 76$; *Presbytis melalophos*, $n = 82$; *Presbytis rubicunda*, $n = 76$). Results show that the interconulus has a significantly higher frequency and degree of expression in Tribe Papionini and exhibits ordered metameric variation with greatest expression in the third molars. Given the rarity of the interconulus in other closely related taxa, and its morphological distinction from the purportedly homologous features in other primates, we interpret the high degree of expression of the interconulus to be a trait derived in papionins that originated in the Miocene baboon/macaque ancestor. Am J Phys Anthropol 155:422–429, 2014. © 2014 Wiley Periodicals, Inc.

The Old World Monkeys (OWM) represent one of the best examples of an adaptive radiation within living primates. Molecular phylogenies suggest that Family Cercopithecidae diverged into Subfamily Cercopithecinae and Colobinae lineages ~19.4 Ma (e.g., Meyer et al., 2011) in the early Miocene of Africa. Within the cercopithecines, Tribe Papionini (*Papio* and *Macaca*) is hypothesized to have diverged from Tribe Cercopithecini (*Cercopithecus*) ~12 Ma (Meyer et al., 2011). The OWM have the broadest geographic range of any primate family, not considering humans, and are distributed across Africa and Asia, with African and Asian colobines dividing into clades, often considered subtribes (Nowak, 1991; Perelman et al., 2011). The OWM also inhabit a wide-range of ecological niches. While the colobines are predominately arboreal, subsisting on a diet comprised primarily of leaves, fruits and flowers, the cercopithecines range from arboreal to terrestrial and have more varied diets that can include dense grasses, intertidal invertebrates, fruits, eggs, and small vertebrates (Table 1; Nowak, 1991).

The morphology of primate molars is often interpreted as a dietary adaption. The pattern in which cusps are arranged on primate molars evolved from the ancestral mammalian trigone shape which included a lingual cingulum at the base of the crown. From this primitive molar shape, the anthropoids evolved maxillary molars with four cusps: the paracone, metacone, protocone, and hypocone (Simpson, 1936). The cercopithecids are further characterized by a reduction of the lingual cingulum and the evolution of bilophodont molars (Swindler, 1976; Lucas, 2004). The occlusal contact between the cusps of bilophodont maxillary and mandibular molars, with the lophs guiding the movement, allows for efficient grinding and crushing motion which is presumed to be a dietary adaptation in response to increased seed consumption and folivory (Delson, 1975; Maier, 1977; Happel, 1988; Ungar, 2010).

The interconulus is a variable feature seen on the lingual aspect of the maxillary molars of some cercopithecid species (Saheki, 1966; Hlusko, 2002). Noted in descriptive analysis as early as the 19th century (Batujeff, 1896), the interconulus (Remane, 1960; Hlusko, 2002) has gone by many different names including: lingual cingulum (e.g., Osborn, 1897), lingual conule (e.g., Chang et al., 2010), median lingual accessory groove cusp (e.g., Saheki, 1966), and groove cusp (e.g., Batujeff, 1896; de Terra, 1905). Morphologically, the interconulus lies between the protocone and hypocone with expression ranging from a pit in the groove between the lophs to a

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TABLE 1. Species sampled and basic ecology summary

Family	Subfamily	Tribe	Genus	Species	Range[a]	Locomotor habitus[a]	Diet[a]	Sample size	Museums sampled
Cercopithecidae	Cercopithecinae	Cercopithecini	*Cercopithecus*	*mitis*	Africa	Arboreal	Diverse: roots, birds, eggs, small reptiles and insects	$N = 75$	AMNH MVZ NMNH
		Papionini	*Papio*	*hamadryas*	Africa	Terrestrial	Diverse: grasses, seeds, intertidal invertebrates	$N = 53$	MVZ NMNH
			Macaca	*fascicularis*	Asia	Arboreal	Diverse: invertebrates, fruits, leaves, eggs, vertebrates	$N = 85$	AMNH
			Macaca	*mulatta*	Asia	Arboreal	Diverse: invertebrates, fruits, leaves, eggs, vertebrates	$N = 69$	MVZ NMNH
	Colobinae	Colobini	*Colobus*	*guereza*	Africa	Arboreal	Leaves, fruits, flowers	$N = 75$	AMNH NMNH
			Presbytis	*melalophos*	Asia	Arboreal	Leaves, fruits, flowers	$N = 81$	AMNH NMNH
			Presbytis	*rubicunda*	Asia	Arboreal	Leaves, fruits, flowers	$N = 75$	AMNH NMNH

[a] Reported from Nowak (1991).

pronounced cingulum. Most researchers interpret the interconulus as a remnant of the lingual cingulum that characterizes primitive mammalian morphology (e.g., Saheki, 1966; Swindler, 1976).

Theories on the adaptive functions of lingual traits like the interconulus are speculative. There has been some suggestion that the derivation of lingual traits on the maxillary molars can protect the gums during mastication (e.g., James, 1960; Slaughter, 1970) and provide biomechanical advantage by adding intercuspal structural reinforcement (Delson, 1975; Happel, 1988; Macho and Spears, 1999). Alternately, the high, lingually smooth cusps of colobines are hypothesized to be important in shearing mechanics (e.g., Sirianni, 1974; Delson, 1975; Walker and Murray, 1975). Broadly speaking, dental morphology is an essential component of an animal's dietary adaptive suite, and herbivory is highly correlated with surface area in multicuspate mammalian molars (e.g., Hatley and Kappelman, 1980; Butler, 1981; Kay, 1984; Hunter and Jernvall, 1995). As such, it is not unreasonable to hypothesize that dietary preferences of cercopithecids may potentially be correlated causally with the presence of lingual traits in the molars, although the specific role these features may play in that adaptation remain to be determined.

Although the interconulus was originally described over a century ago (Batujeff, 1895; de Terra, 1905), Saheki (1966) was the first to undertake a detailed assessment of variation in interconulus presence. Saheki showed ordered distribution of the interconulus with most frequent presence in the third molars in a sample of *Macaca fascicularis* and *Macaca fuscata* (Saheki, 1966; *Macaca fascicularis* noted as *Macaca irus* in cited text). Interconulus expression has also been widely recognized and described in *Papio hamadryas* (de Terra, 1905; Saheki, 1966; Swindler, 1976; Hlusko, 2002; Hlusko and Mahaney, 2003), and there have been reports of other OWM also expressing the trait (e.g. Batujeff, 1895; Eck, 1977).

Hlusko (2002) formally characterized expression of the interconulus in *Papio*, developing a typology for scoring the trait. Hlusko reported expression of the interconulus in ~40% of a sample of 329 captive baboons, with expression increasing distally along the molar tooth row. Further study of the interconulus has resulted in high heritability estimates for the trait (Hlusko and Mahaney, 2003) consistent with studies that have demonstrated the heritability of other similar dental traits in humans (Biggerstaff, 1973; Berry, 1976; Scott and Turner II, 1997).

These previous morphological and genetic studies suggest that variation in the interconulus may be taxonomically diagnostic, and as such, we undertook a broad taxonomic investigation in order to better understand the evolutionary relevance of this phenotype. We also described metameric variation in expression of the trait, defined as the statistical distribution of the trait within the maxillary molar tooth row. Characterizing the pattern of variation for heritable dental traits can expound the genetic mechanisms underlying the evolutionary history of mammalian dentition (e.g., Weiss et al., 1998; Rizk et al., 2008) and improve our understanding of the evolutionary forces that shaped the variation we see across primates today, and more specifically within cercopithecids.

MATERIALS

The interconulus was scored from the maxillary molars of 522 cercopithecid skulls housed in the collections of the University of California's Museum of Vertebrate Zoology (MVZ), the American Museum of Natural History (AMNH), and the National Museum of Natural History (NMNH). Our sample includes seven species (*Cercopithecus mitis*, $n = 78$; *Macaca fascicularis*, $n = 85$; *Macaca mulatta*, $n = 70$; *Papio hamadryas*, $n = 55$; *Colobus guereza*, $n = 76$; *Presbytis melalophos*, $n = 82$; *Presbytis rubicunda*, $n = 76$) from two extant subfamilies of OWM, the Cercopithecinae and the Colobinae. The species sampled span both cercopithecid tribes, Asian and African papionins and both subtribes of colobine (Perelman et al., 2011). Our sample also includes species ranging in size, diet and locomotor habitus (Table 1). Interconulus expression was assessed in a subsample of *Chlorocebus aethiops* ($n = 6$) and *Theropithecus gelada* ($n = 9$), but small sample sizes prohibited us from including these species in statistical analyses.

METHODS

Data collection

The interconulus is a quantitatively variable trait. However, its unusual shape and position on the crown makes it difficult to measure through the use of calipers. Standardized scoring systems have proven to be a useful way by which to quantify such traits (e.g., the ASUDAS plaques; Scott and Turner II, 1997). We followed the scoring system established by Hlusko (2002) for use on baboons. In this expression scale, variation ranges from a score of 1, in which no evidence of an interconulus is present, to 5, in which there are multiple lingual projections extending towards the cusps. Although a considerable amount of the variation is lost when continuously variable traits are quantified as discrete, quantitative genetic analyses of interconulus variation in baboons yielded high heritability estimates (Hlusko and Mahaney, 2003), demonstrating that these discrete categories still capture a significant amount of the underlying biology.

The mesiodistal lengths and buccolingual breadths were also recorded for each of the teeth for which the interconulus was scored, the protocol for which follows standard practice and is described in detail elsewhere (Grieco et al., 2013). Maxillary molars are abbreviated as "M", followed by a number that indicates tooth position. The second maxillary molar, for example, is abbreviated as M2.

Analyses

We conducted statistical analyses using JMP 10.0.0 (SAS Institute, Inc., San Francisco, CA). In order to assess sexual dimorphism in expression of the trait (e.g., Garn and Lewis, 1966; Townsend et al., 1990), a preliminary subsample analysis was performed using the Wilcoxon rank sums test to compare mean interconulus expression by sex, at each molar position, within each species. Results of the Wilcoxon rank sums test were not significant at any tooth position for any species, indicating that mean interconulus scores are not dependent on sex. This is consistent with quantitative genetic analyses that have shown the interconulus to have high heritability estimates with no significant variance attributable to sex (Hlusko and Mahaney, 2003). Since we found no significant sex-based differences in mean interconulus scores, male and female specimens, as well as specimens of unknown sex, were lumped into a single category in the statistical analyses.

Studies have shown that the left and right sides of the dental arcade exhibit a high degree of symmetry (Baume and Crawford, 1980; Townsend et al., 1990), and the symmetry of interconulus expression has been previously reported (Hlusko and Mahaney, 2003). To determine that the samples used in our study follow expectations of symmetry, we performed a preliminary assessment of score symmetry using a Pearson's likelihood test. The mean interconulus scores were compared across the dental arcade for each species. With the exception of the M2 in *Presbytis rubicunda*, all molars had significance scores of $<P = 0.0001$ for symmetry, indicating the sides are significantly dependent. After noting significant symmetry, with no preference all subsequent statistical analyses were performed on the data recorded from the left molars.

We used a series of nonparametric statistics to compare presence and expression of the interconulus across species and within the molar tooth row. We analyzed presence of the interconulus using general frequency statistics and compared mean interconulus expression across species at each molar position using nonparametric Wilcoxon pairwise statistics with a Bonferroni adjusted value of $P = 0.0024$ (seven species and three molars for 21 comparisons). Finally, we compared mean interconulus expression across molar position within each species using nonparametric Wilcoxon pairwise statistics with a Bonferroni adjusted value of $P = 0.017$ (three molars for three comparisons).

RESULTS

Frequency of interconulus expression

All seven species showed at least some level of interconulus expression within their respective samples (Table SI, Supporting Information). However, the frequency of interconulus presence was significantly higher in papionins, ranging from 6–40% in the three species sampled (Table II). *Papio hamadryas* had the highest frequency of interconulus presence at each tooth position, with presence ranging from 49–60%. In contrast, the interconulus was present in just 6–16% of cercopithecins sampled, and in only 0–14% of colobines.

Species means for degree of expression

While all species showed some degree of expression of the interconulus, *Papio hamadryas* had the highest average degree of expression at each tooth position with the exception of the M2 in *Macaca mulatta* (Fig. 1). Average expression of the interconulus was significantly different when comparing almost any molar of one species with any other molar of another species. This indicates significant interspecies variation in interconulus expression even when comparing the most extreme ranges of expression.

Metameric variation in expression

For six of the seven species, the third molar exhibited the most frequent presence of the interconulus, and the greatest degree of expression. *Cercopithecus mitis* differed from the other six species in having the M2 as the

TABLE II. Sample size, interconulus presence, average expression, and range for each species. X = upper, L = left, M = molar, # = tooth position.

Species	Statistics	XLM1	XLM2	XLM3
Cercopithecus mitis	*N*=	68	75	67
	Mean expression	1.06	1.29	1.13
	Presence frequency	0.06	0.16	0.09
	Range	1–2	1–4	1–5
Macaca fascicularis	*N*=	83	85	70
	Mean expression	1.17	1.73	1.86
	Presence frequency	0.16	0.46	0.51
	Range	1–3	1–4	1–5
Macaca mulatta	*N*=	68	69	65
	Mean expression	1.06	1.26	1.72
	Presence frequency	0.06	0.16	0.46
	Range	1–2	1–4	1–5
Papio hamadryas	*N*=	51	53	50
	Mean expression	1.67	1.70	2.06
	Presence frequency	0.49	0.47	0.60
	Range	1–4	1–4	1–5
Colobus guereza	*N*=	73	75	74
	Mean expression	1.00	1.04	1.18
	Presence frequency	0.00	0.03	0.14
	Range	1	1–3	1–4
Presbytis melalophos	*N*=	81	81	81
	Mean expression	1.00	1.01	1.09
	Presence frequency	0.00	0.01	0.07
	Range	1	1–2	1–3
Presbytis rubicunda	*N*=	75	75	69
	Mean expression	1.03	1.01	1.09
	Presence frequency	0.03	0.01	0.09
	Range	1–2	1–2	1–2

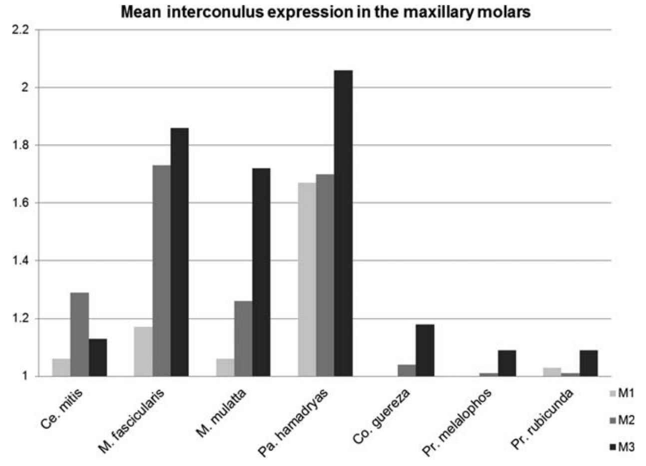

Fig. 1. Mean interconulus expression by species. Score of 1 indicates no expression. Score of 5 indicates greatest expression.

most variable tooth with the greatest degree of interconulus expression. In papionins, average expression of the interconulus varied metamerically, increasing from the first to the third molar. The first molar exhibited lowest mean expression of the interconulus in all species with the exception of *Presbytis rubicunda* in which the M1 and M2 were not significantly different. This variation, along with asymmetry in expression of the interconulus in *Presbytis rubicunda* and unexpected sexual dimorphism in *Presbytis rubicunda* postcanine dentition (Grieco et al., 2013), may suggest that the species differs in some odontogenic mechanisms, variation that Grieco et al. (2013) hypothesized could be related to dwarfism in the *Presbytis rubicunda* lineage.

DISCUSSION

While researchers have generally concluded that the interconulus represents a remnant of the primitive molar cingulum, a survey of the morphological diversity of lingual remnants highlights how distinctive the interconulus is from other purported primate cingular remnants (Fig. 2). The unique morphology of the cercopithecid interconulus, with the trait distinctly oriented between the mesial and distal lophs of the maxillary molars, appears to only occur in bilophodont molars, suggesting that this feature may share some of the developmental processes that result in bilophodonty. Tooth development is largely controlled by reiterative activation of a signaling cascade (e.g., Jernvall and Thesleff, 2000; Zhao et al., 2000), and current models of tooth morphogenesis identify spatial parameters, such as intercuspal distance, as playing an important role in cusp development and positioning (Salazar-Ciudad and Jernvall, 2002). These data suggest that accessory cusps can be influenced by upstream morphogenetic events. For example, Carabelli cusp expression in humans conforms to this model, as cusp expression varies with intercuspal spacing (Hunter et al., 2010). It is reasonable to hypothesize that morphogenesis of the interconulus utilizes the same developmental pathway as the lingual cusps, with expression being dependent on bilophodonty and the intercuspal spacing of the mesial and lingual lophs (note that for baboon maxillary molars, buccal cusp areas are genetically correlated but lingual cusps are not [Koh et al., 2010]). But while bilophodonty is a consistently diagnostic trait in extant cercopithecids, the distribution of the interconulus varies significantly

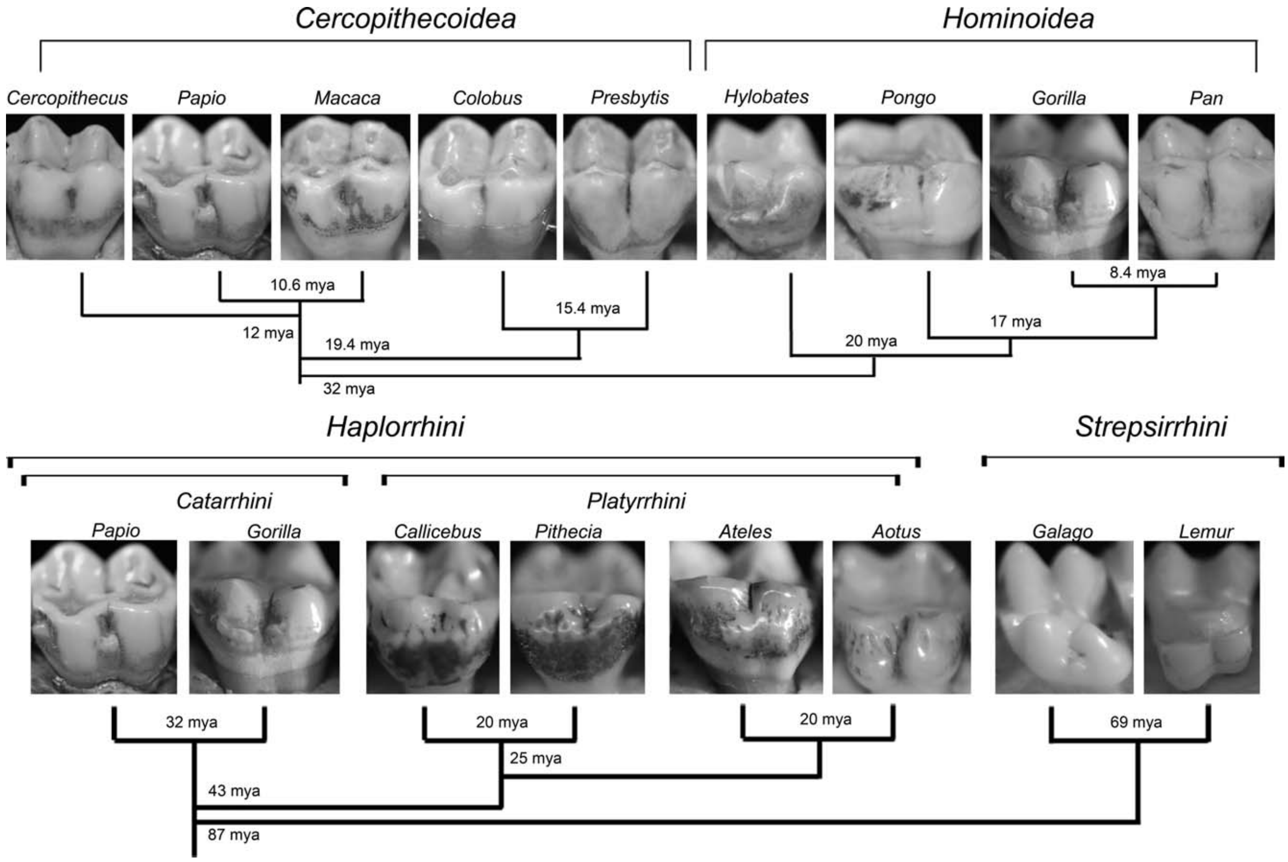

Fig. 2. Representatives of lingual variation in primate molars. Top: Cercopithecoidea and Hominoidea of the Catarrhines. Below: Haplorrhines and Strepsirrhines. All photographs show the lingual view of left M3's. Lineage divergence dates are from Xing et al. 2005, Meyer et al. 2011, and Perelman et al. 2011. The interconulus seen in Cercopithecoidea is morphologically distinct from other lingual traits in primates.

across tribes within the family. Given the lack of correlation between interconulus expression and tooth size (discussed in more detail below), we hypothesize that expression of this trait is influenced by a patterning mechanism rather than resulting from allometric effects.

Our results reveal significant expression of the interconulus in papionins and significantly less expression in cercopithecins and colobines. This pattern is seen in the frequency of interconulus presence as well as in the strength and range of overall expression (Fig. 3). Given this pattern of trait expression and frequency, we interpret these data as evidence that high frequency and degree of expression of the interconulus is a derived trait within the tribe that includes the genera *Papio* and *Macaca*, perhaps being the result of selection in its evolutionary history.

Based on molecular evidence, the papionins and cercopithecins diverged ~12 Ma (Meyer et al., 2011). Expression of the interconulus is not seen in basal cercopithecids, and fossil evidence suggests that the primitive lingual remnant was completely reduced before bilophodonty evolved in the family (Voruz, 1970).

Given that the interconulus is present in baboons and macaques, and that there is a general lack of expression in the cercopithecins and colobines, we hypothesize that significant interconulus expression evolved sometime after the Papionini-Cercopithecini split 12 Ma, and before the *Papio-Macaca* split ~10 Ma. This two million year window is within a period of climatic change characterized by the expansion of C4 grasslands in tropical and subtropical regions (e.g., Edwards et al., 2010; Strömberg, 2011). The plant fossil record, along with stable isotope data taken from deep-sea cores, soil samples, and other sources, provides evidence for an adaptive radiation of C4 grasses in Miocene Africa that is closely mirrored by a radiation of grazing mammals, likely influenced by the development of new ecological niches as grasslands replaced Paleogene forests (e.g., Zachos et al., 2001; Retallack et al., 2002; Jacobs, 2004; Strömberg, 2011). The evolution of significant interconulus expression may be related (but not necessarily causally so) to dietary adaptations during this environmental change, although it is seems unlikely to be correlated specifically with C4 grasses as a food source. There have been attempts to associate evolutionary changes in heritable dental phenotypes with dietary adaptation using isotope records, and carbon isotope analyses have shown a positive correlation between increase in postcanine occlusal surface and greater intake of C4 plants in the hominid fossil record (Sponheimer et al., 2013). However, enamel δ^{13}C isotope levels in other species demonstrate that dietary adaptation does not necessarily correlate with changes in dental morphology and feeding strategy (e.g., Boisserie and Merceron, 2011). For example, detailed analyses of isotope levels in suid and bovid lineages show significant

Measurement	*Ce. mitis*	*M. fascicularis*	*M. mulatta*	*Pa. hamadryas*	*Co. guereza*	*Pr. melalophos*	*Pr. rubicunda*
Interconulus	1 < 3 < 2	1 < 2 < 3	1 < 2 < 3	1 < 2 < 3	1 < 2 < 3	1 < 2 < 3	2 < 1 < 3
Molar length	3 < 1 < 2	1 < 3 < 2	1 < 3 < 2	1 < 2 < 3	3 < 1 < 2	3 < 1 < 2	3 < 1 < 2
Molar anterior width	1 < 3 < 2	1 < 3 < 2	1 < 3 < 2	1 < 2 < 3	3 < 1 < 2	3 < 1 < 2	3 < 1 < 2
Molar posterior	3 < 1 < 2	1 < 3 < 2	1 < 3 < 2	1 < 3 < 2	3 < 1 < 2	2 < 1 < 3	2 < 1 < 3
Presence frequency	1 < 3 < 2	1 < 2 < 3	1 < 2 < 3	2 < 1 < 3	1 < 2 < 3	1 < 2 < 3	2 < 1 < 3

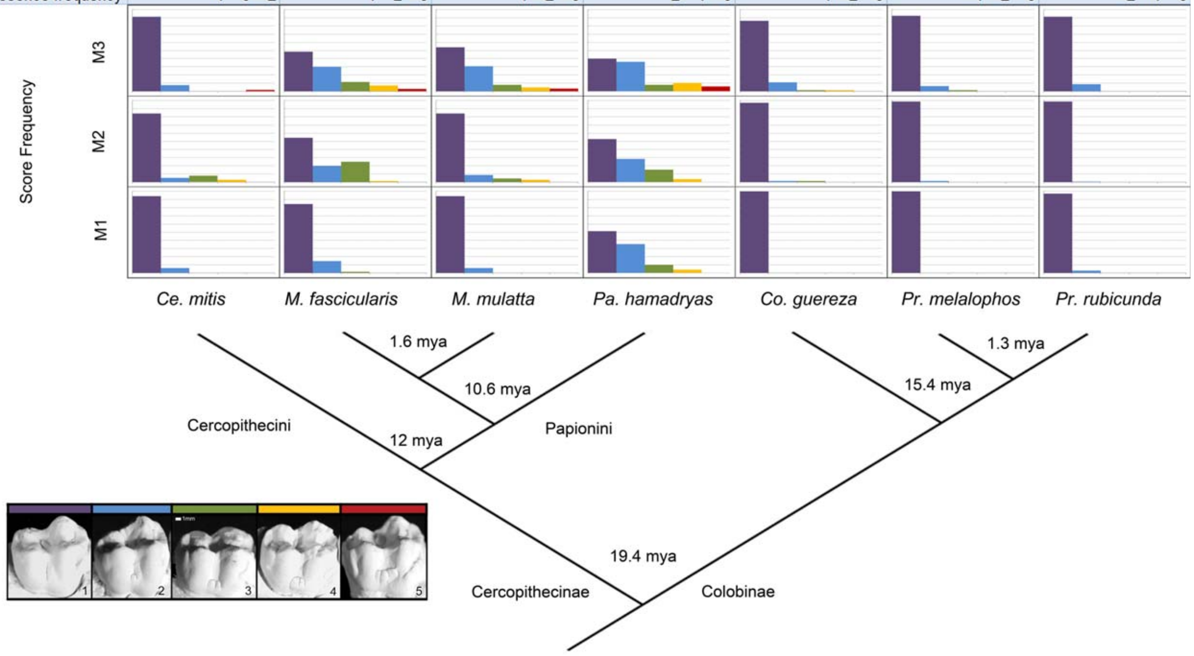

Fig. 3. This figure summarizes the results of this study superimposed on the clade's phylogeny. Top: Patterns of interconulus expression, metrics and interconulus presence frequency for each species. 1<2<3 refers to rank order of molar phenotype. Middle: Distribution of interconulus scores at each tooth position for each species. Legend is on the left. Score 1 indicates absence of the trait. Score 5 indicates greatest expression of the trait. Bottom: Phylogeny of species sampled, with molecular dates from Perelman et al. (2011). Panel of interconulus scores modified from Hlusko (2002). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

increase of enamel δ^{13}C at 2.8 Ma, suggesting major paleodietary change, without any corresponding changes in dental morphology (Bibi et al., 2013). As such, we are hesitant to assign any significance to the C4 grass expansion beyond noting a background of general climatic change.

Given the body size distribution of cercopithecids sampled, one could argue that significant interconulus expression is a byproduct of size—larger molars have more frequent and greater degree of interconulus expression. However, genetic analyses have shown interconulus expression to be independent of molar tooth size within *Papio* (Hlusko and Mahaney, 2003), suggesting that although the papionins sampled here represent the largest extant cercopithecids in this study, significant interconulus expression in only the papionins is not likely merely a byproduct of sampling. Further evidence for independence between size and interconulus expression is the lack of correlation between metameric patterns of molar length and interconulus expression as observed in this study (see Fig. 3). However, it is interesting that at least one large-bodied colobine (*Kuseracolobus hafu*) does have an interconulus (Hlusko, 2006). A detailed paleontological study is needed to elucidate the specific pattern of interconulus expression in extinct cercopithecoids to further test our hypothesis proposed here.

Selection operates most readily on phenotypic variation that is influenced by strong additive genetic effects, i.e., traits that are heritable. Quantitative genetic analyses have reported high levels of additive genetic variance for interconulus variation within *Papio hamadryas* (Hlusko and Mahaney, 2003). Hlusko and Mahaney (2003) also reported that interconulus expression did not yield significant genetic covariance with other dental phenotypes such as molar crown size (as noted above), or other systemic factors such as sex. This relative genetic independence, or rather lack of evidence of significant pleiotropy with other dental phenotypes, suggests that the interconulus could readily respond to selective pressure as has been proposed for other similarly characterized dental phenotypes such as enamel thickness (Hlusko et al., 2004), although it remains to be determined whether or not this response could be fast enough to evolve and be lost in multiple lineages within the Quaternary.

As widely recognized, molar cusp morphology correlates with diet (e.g., Jernvall, 2000). Bilophodonty as a defining feature of cercopithecids has long been hypothesized to be a dietary adaptation for frugivory and seed-eating, with occlusal contact between the lophs allowing for effective crushing and chewing motions (Delson, 1975; Maier, 1977; Kay, 1984; Happel, 1988; Lucas and Teaford, 1994; Ungar, 2010). Colobines are further defined by molars with high, columnar cusps, postulated to be an adaptation for shearing mechanics in a highly frugivorous diet (Sirianni, 1974; Delson, 1975; Benefit, 2000). In contrast, papionin molars frequently demonstrate lingual traits and enamel foldings, with the most extreme expression seen in *Theropithecus* (Jablonski, 2002). In cercopithecids, lingual features such as the interconulus are proposed to have adaptive function, providing structural support and protection for the gums (e.g., Delson, 1975; Happel, 1988; Slaughter, 1970). The frequent and extreme expression of the interconulus is specifically associated with papionins, a tribe characterized by primarily terrestrial locomotion and a diverse diet ranging from fruits, seeds, leaves and grasses to invertebrates, intertidal organisms and small vertebrates. Based on the results we have presented here, the morphologies recorded in the cercopithecid fossil record, and the molecular divergence dates of cercopithecids, we propose that the high frequency of larger interconulus morphologies evolved in the Miocene, and significant expression may possibly have been selected for during a time when OWM were facing rapid environmental changes in Africa between 16-8 Ma.

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