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The evolution of facial length and molar proportions in cercopithecoid monkeys

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Introduction: Papionins are a well-studied and morphologically diverse clade of cercopithecoid monkeys. Understanding how craniodental morphology varies in this clade has implications for interpreting taxonomic variation in the fossil record and for our understanding of primate evolution.

Methods: We quantified the phenotypic relationship between facial length and dental proportions in N=314 cercopithecoid individuals across 10 species (six papionins, two cercopithecins, and two colobines) using dental ratios MMC (molar module component, ratio of the lengths of the third and first molars) and PMM (premolar-molar module, ratio of the lengths of the second molar and the fourth premolar) and two metrics of facial length: palatal length and prosthion – glabella.

Results: Facial length and molar dental proportions are significantly correlated interspecifically across cercopithecoids (PGLS, $p < 0.01$), where species with longer faces have relatively longer maxillary and mandibular third molars. These traits are generally not correlated intraspecifically in the cercopithecoids sampled, with some exceptions.

Discussion: Our data demonstrate that prognathic faces evolved convergently at least twice in papionins, with parsimony supporting that *Papio/Theropithecus* shared a prognathic ancestor after the divergence of *Lophocebus*. Additionally, this study lends support to the hypothesis that facial reduction and third molar reduction in human evolution were coordinated and may have been the result of pleiotropy alongside changes in diet.

KEYWORDS

dental proportions, prognathism, Papionini, African fossil record, allometry

Introduction

Papionini is a tribe of monkeys within Cercopithecidae—a speciose extant family of primates distributed across Africa and Asia today—and one of the most well-studied groups of primates due to their widespread use in biomedical studies (VandeBerg et al., 2009). Fossil papionins also commonly co-occur with hominid fossils in African deposits, making them of significant relevance to human evolutionary studies (e.g., Delson, 1984; 1988; Heaton, 2006;

Frost et al., 2022; Jablonski and Frost, 2010; McKee, 1993; McKee et al., 1995; Williams et al., 2007). This diverse tribe is represented by both arboreal and terrestrial taxa with diets that range from grazing herbivorous and folivorous to more omnivorous diets that can include invertebrates and small mammals (Jablonski and Frost, 2010; Nowak, 1999). Most papionins are at least partially frugivorous, and the diets of almost all papionin species consist of more than 50% fruit (DeCasien et al., 2017).

The phylogenetic relationships between papionins have historically been obscured by morphological convergence (Figure 1). *Papio*, *Theropithecus*, and *Mandrillus* are all characterized by elongate faces and palates, and *Macaca*, *Lophocebus*, and *Cercocebus* have shorter faces and palates, more similar to other medium-bodied cercopithecoid primates, with short faces presumed to be the ancestral phenotype (Benefit and McCrossin, 1991, 1993; Collard and O'Higgins, 2001; Fleagle et al., 2010; Pugh and Gilbert, 2018; Pugh et al., 2023; Ravosa and Profant, 2000; Simons et al., 2018; Singleton, 2002, 2005).

The mangabeys, *Lophocebus* and *Cercocebus*, both short-faced papionins, were not recognized as distinct genera belonging to different clades within Papionini until within the last few decades, based primarily on molecular data (Cronin and Sarich, 1975; Fleagle and McGraw, 1999; Groves, 1978; Harris and Disotell, 1998; Page and Goodman, 2001). Current molecular data support three major

groups: 1) *Macaca*, a genus that diverged basally, approximately 8–10 million years ago (Ma), 2) *Papio*, *Lophocebus*, and *Theropithecus*, and 3) *Mandrillus* and *Cercocebus*, with these latter two clades having diverged from each other approximately 6–7 Ma. Even with disagreements about the phylogenetic relationships between *Papio*, *Lophocebus*, and *Theropithecus* (e.g., Chatterjee et al., 2009; Fabre et al., 2009; Guevara and Steiper, 2014; Perelman et al., 2011; Pozzi et al., 2014; Pugh and Gilbert, 2018; Springer et al., 2012), there is consensus that elongate snouts, sometimes referred to as prognathism, evolved at least twice in papionins. Hypotheses for why *Papio* and *Mandrillus* converged on prognathic faces range from allometric explanations, with selection on growth rates or growth spurts likely shaping variation in craniofacial shape in papionins (Leigh, 2007), to adaptive hypotheses focused on the jaw gape necessary to accommodate the long canines that characterize these large-bodied papionins (e.g., Plavcan and Ruff, 2008).

Evolutionary history of the papionins

Tribe Papionini is well-represented in the Plio-Pleistocene African fossil record with extensive fossil samples from eastern and southern Africa (reviewed in Jablonski and Frost, 2010).

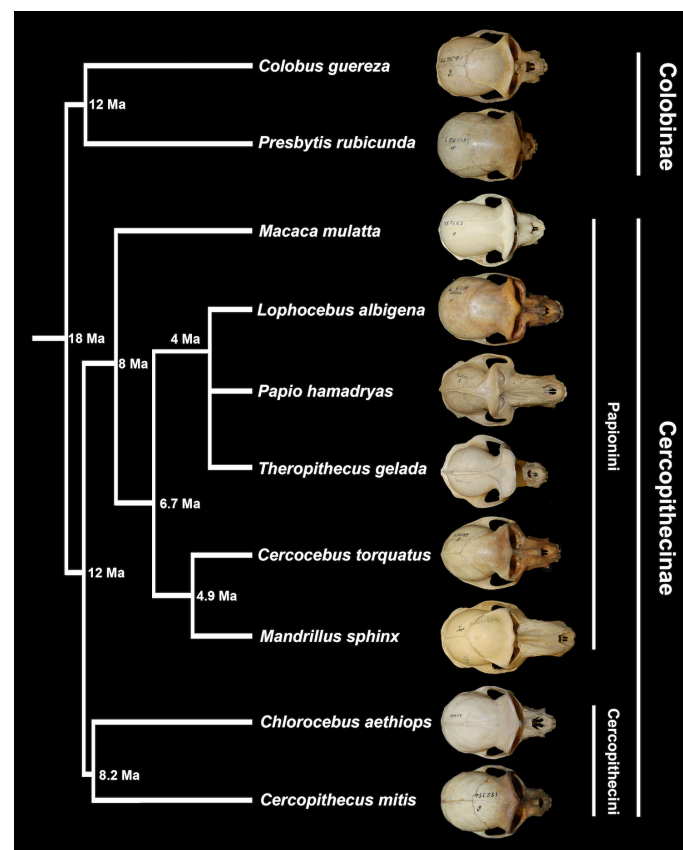


FIGURE 1

Phylogeny of cercopithecids sampled in this study, alongside dorsal views of species-representative crania. Divergence dates are from Perelman et al. (2011). Crania and branch lengths are not to scale. Recently named genus *Rungwecebus*, not included in this study, is inferred to belong to the monophyletic clade including *Papio*, *Lophocebus*, and *Theropithecus* (Davenport et al., 2006).

Papionins begin appearing in the later Miocene of northern Africa with *Macaca*, the sister taxon to all other extant papionins (Figure 1), a genus that is especially well-represented in the later Plio-Pleistocene records of Europe and Asia.

Genus *Parapapio* appears in the later Miocene and early Pliocene record of eastern Africa, followed by larger samples in the Plio-Pleistocene of southern Africa. The exact phylogenetic position of this genus remains unclear, but current data support a basal phylogenetic position for *Parapapio* relative to other extant and fossil genera. *Parapapio* appears to have regionally diversified in the Pleistocene of southern Africa, with some earlier population potentially giving rise to the extant African papionin lineages (Jablonski, 2002; Jablonski and Frost, 2010; Pugh and Gilbert, 2018; Williams et al., 2007).

Following the presumed divergence of *Theropithecus* from *Papio* and *Lophocebus* around 4 million years ago (Figure 1; Cronin and Meikle, 1979; Perelman et al., 2011), *Theropithecus* dominates eastern African assemblages between ~3.5 to 1.5 million years ago, with increases in body size eventually leading to one of the largest monkey species ever known (Jablonski, 2002). During this time, southern African Pleistocene assemblages include representatives of *Parapapio*, *Theropithecus*, and notably, early *Papio* (e.g., Freedman, 1957, 1960, 1961, 1965; Heaton, 2006; Jones, 1937; Pugh and Gilbert, 2018; Szalay and Delson, 1979).

Starting in the Early Pleistocene, *Papio hamadryas* is well documented in southern Africa, and the species has been recognized in the Middle Pleistocene of the eastern African fossil record (Jablonski and Frost, 2010; Frost and Alemseged, 2007; Brasil et al., 2023). While the fossil records for *Theropithecus* and *Papio* are relatively rich among the extant papionin genera, the record of *Lophocebus* is limited to fragmentary remains from a few eastern African sites; *Cercocebus* is even more poorly represented, found only in the Early Pleistocene of southern Africa, and *Mandrillus* is entirely absent from the fossil record (Jablonski, 2002; Jablonski and Frost, 2010). Despite the uneven representation of papionin taxa in the fossil record, the relatively rich records of *Papio*, *Theropithecus*, and their candidate ancestor *Parapapio*, with many relatively complete cranial specimens, provide valuable data for assessing the evolution of craniodental anatomy in several papionin lineages.

Aims and implications of the present study

Significant and pervasive craniofacial covariation characterizes many, but not all, cercopithecoid species, generating species-specific patterns of covariation in this family (Monson, 2020). It has been hypothesized that the evolution of craniofacial morphology in more prognathic species like *Papio* is under greater constraint because of shared underlying genetic and developmental factors (Monson, 2020; Porto et al., 2009). The extent to which dental anatomy covaries with craniofacial anatomy in primates has been less well-studied (but see Polychronis and Halazonetis, 2014) despite the well-documented covariation between many areas of the cranium,

including the face, braincase, and basicranium (e.g., Ackermann, 2002, 2005, 2009; Cheverud, 1982; Dayan et al., 2002; Esteve-Altava et al., 2015; Hallgrímsson et al., 2004, 2007; Lieberman, 2011; Neaux, 2017; Pérez-Claros et al., 2015; Polanski and Franciscus, 2006; von-Cramon-Taubadel and Smith, 2012).

Papio and *Theropithecus* have longer postcanine tooth rows relative to body mass than other cercopithecoids, hypothesized to be related to their prognathic faces (Martin, 1993). Facial length is correlated with *RUNX2* gene expression in anthropoid primates and linked to craniodental disorders in humans, commonly with the presence of extra teeth (Ritzman et al., 2017). Multivariate studies of tooth length also reveal a significant correlation with mandibular length, supporting that larger teeth are associated with larger jaws (Hikita et al., 2018).

Previous work has posed the hypothesis that the long third molars of papionins (relative to the other molars) are phenotypically associated with longer faces among the papionin clade (Monson et al., 2022b). This hypothesis builds from earlier studies that identified a strong correlation between average postcanine tooth area and facial size in a sample of cercopithecoids (Scott, 2011). The aim of the present study is to investigate whether proportions of postcanine tooth length (relative to other postcanine teeth) are correlated with measures of facial length in a comparative phylogenetic framework. We used paired data from individuals to analyze both inter- and intraspecific variation in facial length and postcanine tooth proportions. Quantifying how these phenotypes covary has significant implications for our understanding of craniodental evolution and development; limited covariation suggests that traits may have been evolving independently, while significant covariation suggests shared genetic, developmental, and/or functional networks between traits, often resulting in linked evolutionary histories.

Additionally, this investigation stands to bear on our interpretations of taxonomic diversity in the fossil record. As the majority of primate fossil remains are craniodental, morphological traits of the cranium are commonly used to differentiate fossil species (e.g., Hartwig, 2002; Jablonski and Frost, 2010). In addition to cranial morphology, relative proportions of the third molar, as well as the first molar and fourth premolar, have been cited extensively in taxonomic classification schemes for extant and fossil papionins (e.g., Fleagle and McGraw, 1999; Gilbert, 2013), making an understanding of the allometric relationship between these traits fundamental to refining taxonomic and phylogenetic hypotheses.

Moreover, the last two million years of *Homo* evolution are characterized by a general reduction in jaw length, dental arcade length, tooth size, and facial length, with variation in these traits used to distinguish among hypothesized Plio-Pleistocene fossil species (e.g., Spoor et al., 2005). Investigating whether these changes are phenotypically linked is important for our understanding of craniodental variation and the selective pressures that shaped human evolution. Extreme facial length has evolved convergently in several cercopithecoid genera, making them an ideal clade in which to investigate phenotypic covariation among craniodental anatomy (Collard and O'Higgins, 2001; Leigh, 2007; Monson, 2020; Singleton, 2005).

Our key goal for this work was to test whether facial length, as captured by palatal length and prosthion - glabella length, is phenotypically correlated with postcanine tooth proportions. A thorough assessment of craniofacial and dental anatomy in extant primates, where traits are paired and measured from the same individual, is essential for interpreting patterns of covariation in these traits. To meet this goal, we measured facial length and postcanine tooth lengths for N=314 extant cercopithecoid individuals spanning 10 species across 10 genera, and addressed the following questions:

1. Are postcanine dental proportions (including relative proportions of the premolars compared to the molars) correlated with measures of facial length in papionin primates?
2. Specifically, do cercopithecoid primates with longer faces also have relatively longer third molars (compared to other postcanine teeth)?

Materials and methods

Data collection

Our sample includes cranial and dental measurements for N=314 extant cercopithecoid individuals, held in osteological collections at the American Museum of Natural History (AMNH) in New York, NY, USA, the Human Evolution Research Center (HERC) and the Museum of Vertebrate Zoology (MVZ) in

Berkeley, CA, USA, the National Museum of Natural History (NMNH) in Washington, DC, USA, the Center for Evolutionary Origins of Human Behavior at Kyoto University (PRISK) in Inuyama, Japan, and the Zurich Natural History Museum (UZH) in Zurich, Switzerland.

All measurements were taken using analog DialMax calipers. Cranial and dental data were matched, measured from the same individual. Matching data requires that specimens are complete and in good condition, and grants the statistical power needed to assess both inter- and intraspecific correlations between traits. All individuals included in this study had a complete cranium and face, with complete maxillary and mandibular postcanine dentitions.

We only measured adult individuals as assessed by the eruption of the third molars. We attempted to measure sex-balanced samples whenever possible, but many papionins (e.g., *Theropithecus*, *Mandrillus*) are extremely rare in museum collections. Our sample includes n=190 papionins, n=57 cercopithecins, and n=67 colobines. See Table 1 for sample size details.

The extant and fossil data used in this study represent years of data collection in many different museum collections around the world. Given the complexity of gathering a dataset of this size, and in favor of maximizing taxonomic breadth and sample sizes, we focused on linear metrics for this study, collecting two cranial and eight dental measurements from all individuals sampled. The two cranial measurements provide different measures of facial length: (1) facial length (measured from prosthion to glabella) and (2) palatal length (measured from orale to staphylion). We did not focus on cranial length as a metric in this study because: 1) cranial length is a proxy for body size, and larger individuals often possess robust muscle attachments on the occipital bone, introducing

TABLE 1 Sample sizes and average trait values for the extant species sampled in this study*.

Taxon	N**	logPL (avg)	logFL (avg)	FL/ML (avg)	XMMC (avg)	XPMM (avg)	DMMC (avg)	DPMM (avg)
<i>Cercocebus torquatus</i>	23 - 24	1.69	1.82	0.51	1.06	1.41	1.30	1.28
<i>Cercopithecus mitis</i>	32 - 35	1.53	1.70	0.49	0.97	1.50	1.09	1.23
<i>Chlorocebus aethiops</i>	10 - 22	1.51	1.61	0.42	0.96	1.49	1.11	1.23
<i>Colobus guereza</i>	32 - 33	1.63	1.67	0.42	1.07	1.46	1.37	1.04
<i>Lophocebus albigena</i>	31 - 33	1.64	1.75	0.47	0.99	1.51	1.23	1.36
<i>Macaca mulatta</i>	30 - 33	1.61	1.73	0.47	1.12	1.63	1.47	1.44
<i>Mandrillus sphinx</i>	29 - 34	1.96	2.06	0.57	1.16	1.46	1.47	1.19
<i>Papio hamadryas</i>	37 - 52	1.90	2.07	0.62	1.21	1.64	1.50	1.46
<i>Presbytis rubicunda</i>	31 - 34	1.39	1.56	0.40	0.97	1.39	1.12	1.05
<i>Theropithecus gelada</i>	9 - 14	1.83	1.93	0.54	1.27	1.91	1.60	1.61
	264 - 314							

*Abbreviations as follows: PL is palatal length, avg is average, FL is facial length, FL/ML is relative facial length, X is maxillary, MMC is molar module component, PMM is premolar-molar module, D is mandibular.

**Range of sample sizes for all traits across species. Range of total sample size for all traits is shown in bold.

measurement error (e.g., resulting from variation in external occipital crest morphology), and 2) very few fossil specimens preserve enough anatomy to confidently measure total cranial length; palatal and facial length, however, are preserved more frequently. Given these caveats, we focused on facial and palatal length, and the phenotypic association between these cranial traits and postcanine dental proportions, for this study. However, we did calculate relative facial length for a subsample (as noted by minimum sample sizes in Table 1) of extant primates (prosthion - glabella length divided by maximum cranial length) to investigate the effects of body size variation on the relationship between facial length and dental proportions.

We also measured the lengths of the fourth premolar and all three molars (P4-M3) for both the maxilla and the mandible to calculate two dental ratios: MMC (molar module component, measured as M3 length divided by M1 length), and PMM (premolar-molar module, measured as M2 length divided by P4 length; Hlusko et al., 2016). Quantitative genetic analyses demonstrate that these dental ratios are heritable (e.g., h^2 mandibular MMC=0.69, h^2 mandibular PMM=0.45) and do not covary with sex or body size in baboons (genus *Papio*; Hlusko et al., 2016; Monson et al., 2022a). Because molar lengths are guided by iterative developmental processes (e.g., Kavanagh et al., 2007), ratios of relative third molar length are more informative than absolute tooth lengths or widths, which are frequently linked to body size (e.g., Hlusko et al., 2016). The MMC and PMM dental ratios also have strong phylogenetic signal in mammals (e.g., Monson et al., 2019a; Zuercher et al., 2021). Additionally, because these dental ratios carry taxonomic signal, and teeth are relatively abundant in the hominid fossil record, MMC and PMM have already been employed in paleoanthropological investigations (e.g., Brasil et al., 2020; Monson et al., 2018, 2022a).

As part of our analysis, we also collected data on molar, fourth premolar, and facial/palatal lengths for $n=50$ fossil papionins from genera *Parapapio*, *Procercopithecus*, *Papio*, and *Theropithecus*. Data for *Victoriapithecus*, a putative early ancestor of the cercopithecoid primate family, were taken from the literature (Benefit, 1993; Benefit and McCrossin, 1997) and represent compiled data for multiple specimens. All other cranial and dental fossil data were measured by the authors and are matched, measured from individual fossils that retain all relevant morphology. The fossils are held in repositories at the Ditsong Museum of Natural History and the Evolutionary Studies Institute at the University of the Witwatersrand (South Africa), the National Museum of Ethiopia, and the University of California Museum of Paleontology (USA). See SI for raw data used in this study.

Analytical methods

We log-corrected all cranial measurements and tested that all traits were distributed normally prior to analysis. We used the describeBy function in the *psych* package (Revelle and Revelle, 2015) to generate descriptive statistics and characterize the data. Average values for all traits are reported in Table 1 (extant

cercopithecids). Average values for each trait were used to run a series of phylogenetic generalized least squares (PGLS) analyses, which test for covariation between traits while accounting for phylogenetic relationships. These analyses examine whether traits are correlated more than would be expected from neutral evolution and phylogenetic relatedness. All phylogenetic analyses were conducted using a published molecular supertree trimmed to species of interest (Faurby and Svenning, 2015). We chose this molecular phylogeny because it retains *Papio*, *Lophocebus*, and *Theropithecus* as sister taxa in an unresolved polytomy (in contrast to 10ktrees [Arnold et al., 2010] which places *Lophocebus* as sister to *Theropithecus* in a monophyletic clade with *Papio* placed basally, and more recent mammalian supertrees [e.g., Upham et al., 2019] that continue to place *Lophocebus* and *Cercocebus* in a monophyletic mangabey clade in contrast to current consensus that these species are within different clades of the papionin phylogeny [P/L/T vs. C/M]).

We ran PGLS analyses comparing trait variation between palatal length, facial length, relative facial length, and the two dental ratios (PMM and MMC, for both the maxillary and mandibular dentitions), using the *pgls* function in *caper* (Orme et al., 2013). All PGLS analyses are interspecific comparisons of quantitative trait values. We also compared trait values across clades with phylogenetic ANOVA using *aov.phylo* in *geiger* (Harmon et al., 2008). We performed a preliminary assessment of the impact of sexual dimorphism on trait covariation in our extant sample using ANOVA.

To assess intraspecific variation in craniodental traits, we calculated correlations between trait values within a single species using the *rcorr* function in the *Hmisc* package (Harrell and Harrell, 2019). We aimed for sample sizes of $n=30$ for each species included in the analyses. Seven species had adequate sample sizes for correlation analyses: *Cercopithecus mitis*, *Cercocebus torquatus*, *Lophocebus albigena*, *Macaca mulatta*, *Papio hamadryas*, *Colobus guereza*, and *Presbytis rubicunda*. We also included *Mandrillus sphinx*, with a minimum sample size of $n=28$, in the correlation analyses.

Craniodental trait variation was visualized at species and subfamily/tribe levels for both extant and fossil taxa using bivariate regressions, plotted with *ggplot2* (Wickham, 2016). We plotted dental ratios, as well as one dental length (which increased fossil sample size), against palatal and facial length. All analyses were conducted in the statistical programming software R version 4.3.2 (R Core Team, 2021).

Results

Facial length and palatal length, as well as relative facial length, are all highly correlated with relative third molar length in the maxilla and mandible (as reflected by MMC) in extant cercopithecoid primates (Figure 2; Supplementary Figure S1; Table 2). Specifically, species with longer faces and palates tend to have relatively longer third molars (as compared to M1, measured via MMC). Three extant taxa—*Mandrillus sphinx*, *Papio*

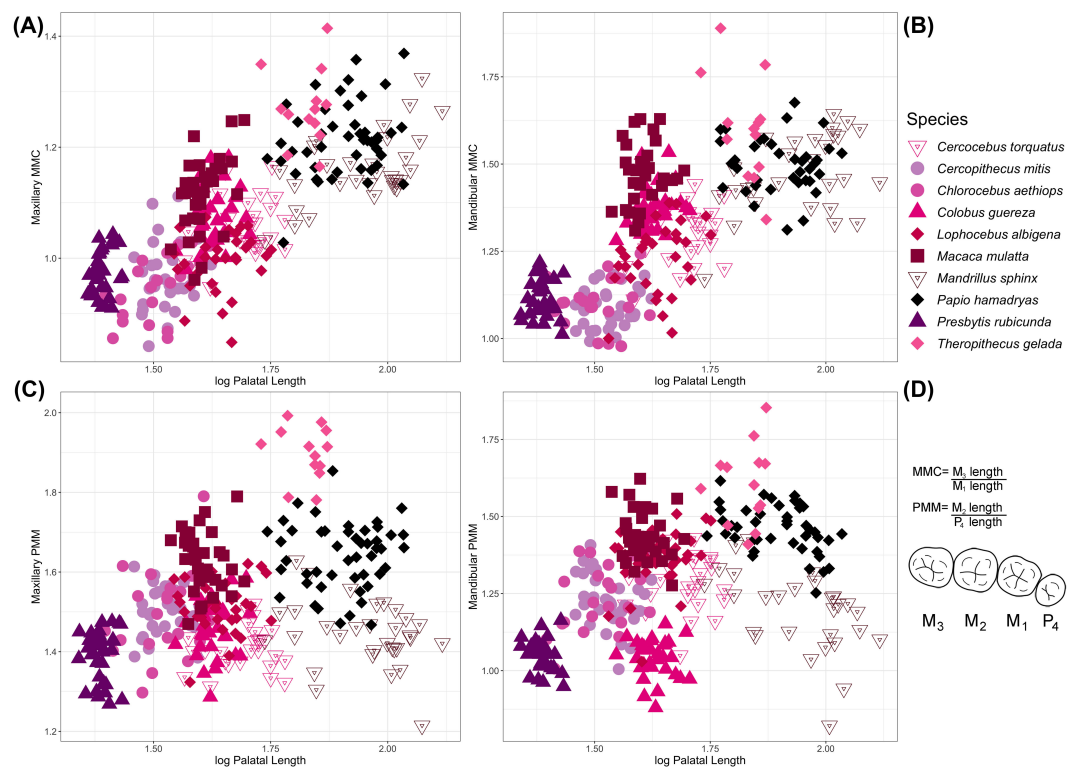


FIGURE 2

Species-level variation in palatal length compared to (A) maxillary and (B) mandibular MMC, and (C) maxillary and (D) mandibular PMM. The mathematical formulas for calculating MMC and PMM are presented to the right of panel (D) alongside a diagram of primate (human) postcanine dentition (mandibular). See [Supplementary Figure S1](#) for bivariate comparisons of tooth proportions with facial length. Palatal and facial lengths are significantly correlated with maxillary and mandibular MMC but not PMM.

hamadryas, and *Theropithecus gelada*—sit at the upper end of the regression between molar proportions and facial/palatal length and are differentiated from other cercopithecids by having longer faces and palates, as well as relatively longer third molars (Figure 2, [Supplementary Figure S1](#)).

In contrast to relative third molar length, other postcanine tooth proportions are not correlated with facial and palatal length, or relative facial length, in extant cercopithecids. For example, raw metrics for maxillary second molar and fourth premolar lengths are correlated with palatal length (PGLS $p < 0.001$), but the ratio of second molar to fourth premolar length is not ($p > 0.05$), likely at least partially driven by the range of palatal lengths observed in extant *Mandrillus*. Likewise, we note a wide range of PMM values exhibited by cercopithecids, where taxa with similar facial and palatal lengths can have either high PMM values (relatively larger second molars, e.g., *Theropithecus*) or low ones (second molars and fourth premolars are more similar in size, e.g., *Mandrillus*).

Our data demonstrate that individuals cluster by species in postcanine proportions vs. prognathism morphospace (Figure 2). We note high taxonomic discrimination across cercopithecids when comparing facial and palatal length with PMM, which captures relative second molar to fourth premolar lengths. Mandibular PMM is the only trait that is significantly different between clades when assessed using phylogenetic ANOVA. The mandibular PMM dental ratio is significantly larger in *Papio/Lophocebus/Theropithecus* relative to

Cercopithecus/Mandrillus, Colobinae, Cercopithecini, and *Macaca*, likely driven by the higher PMM values (i.e., relatively longer second molars) of *Theropithecus*. Although statistical power is limited by small sample sizes, covariation between most traits varies significantly between males and females, likely related to the extreme sexual dimorphism that characterizes some cercopithecoid species.

We also assessed PMM in fossil cercopithecids, including *Parapapio* (a putative ancestor of *Papio* and possibly other modern African papionins, *Lophocebus* and *Theropithecus*), and *Procercopithecus* (hypothesized to be more closely related to *Cercopithecus* and *Mandrillus*). The larger-bodied papionins have longer palates and second molar lengths and are distinguished in trait morphospace. While extant *Papio* and *Mandrillus* are distinguished by second molar and palatal lengths, fossil *Papio* overlaps with both extant taxa. Fossil *Theropithecus* clusters well outside the range of variation for extant *Theropithecus* and is quite distinct from other taxa in this study. *Parapapio* and *Procercopithecus* have palatal lengths that are intermediate to the short- and long-faced extant papionins. Both *Parapapio* and *Procercopithecus* overlap in morphospace with fossil and extant *Papio* but are distinct from *Cercopithecus* and almost all specimens of *Mandrillus* (Figure 3).

Victoriapithecus, a short-faced basal cercopithecoid, looks very similar to *Lophocebus*, *Macaca*, and *Colobus* in relative and absolute second molar length, and palatal length. Maxillary second molar length compared to palatal length discriminates among several

TABLE 2 Results of the PGLS analyses comparing trait values across extant species*.

Trait Comparison**	Adjusted R-squared	p-value
Palatal length ~ XMMC	0.67	0.002
Palatal length ~ DMMC	0.62	0.004
Facial length ~ XMMC	0.62	0.004
Facial length ~ DMMC	0.51	0.012
Relative facial length ~ XMMC	0.54	0.009
Relative facial length ~ DMMC	0.39	0.031
Palatal length ~ XPMM	0.01	0.325
Palatal length ~ DPMM	0.17	0.131
Facial length ~ XPMM	0.00	0.343
Facial length ~ DPMM	0.20	0.108
Relative facial length ~ XPMM	0.04	0.276
Relative facial length ~ DPMM	0.26	0.075

*Significant correlations are bolded.
**Abbreviations as follows: X is maxillary, MMC is molar module component, PMM is premolar-molar module, D is mandibular.

papionin taxa, short and long-faced taxa in particular. All prognathic taxa, including all fossil papionins included in this sample, sit at the upper end of the regression, with longer second molars and palates.

While facial and palatal length are significantly correlated with molar proportions across cercopithecids interspecifically, we do not find strong support for intraspecific correlations for most traits. There are some exceptions: *Mandrillus* is distinct in having dental proportions that are significantly correlated with facial and palatal lengths, excepting relative maxillary fourth premolar length (Table 3); *Macaca* is also characterized by significant correlations between maxillary molar proportions and facial and palatal lengths; Mandibular MMC is correlated with palatal length in *Colobus*, and mandibular PMM is correlated with both palatal and facial length in

Papio and *Cercopithecus*; Relative facial length is also correlated with maxillary molar proportions in *Presbytis* and *Cercopithecus*, mandibular molar proportions in *Presbytis*, maxillary molar/premolar proportions in *Colobus*, and mandibular molar/premolar proportions in *Mandrillus*.

Discussion

Cercopithecoid monkeys with longer faces and palates are characterized by relatively longer third molar lengths (as compared to first molars). This evolutionary allometry has significant implications for our understanding of craniodental variation and evolution in primates and may also bear on hypotheses about human morphological evolution.

The tight interspecific correlation between cranial and dental traits speaks to potential genetic constraints underlying the evolution of facial/palatal length and molar proportions. As papionin faces evolved to be longer over the last 5 million years, third molars in these species also increased in relative length, potentially due to pleiotropy and/or overlapping developmental effects. Although the developmental and genetic mechanisms regulating facial length are still relatively unknown (Boughner and Hallgrímsson, 2008; Boughner et al., 2008; Usui and Tokita, 2018), there is a growing body of evidence that the *RUNX2* gene is implicated in primate facial length (Ritzman et al., 2017). *RUNX2* has also been implicated in early and late tooth development, as well as enamel and root formation (e.g., Chu et al., 2018; Komori, 2010; Wen et al., 2020), providing a potential genetic mechanism for covariation between facial length and molar proportions in primates.

There have been many attempts to characterize patterns of phenotypic covariation in this anatomical region, and there is strong evidence for conserved craniofacial covariation structure across mammals (e.g., Cardini, 2019; Cardini and Polly, 2013; Monson, 2020; Monson et al., 2017), although patterns of covariation can differ significantly across even closely related taxa

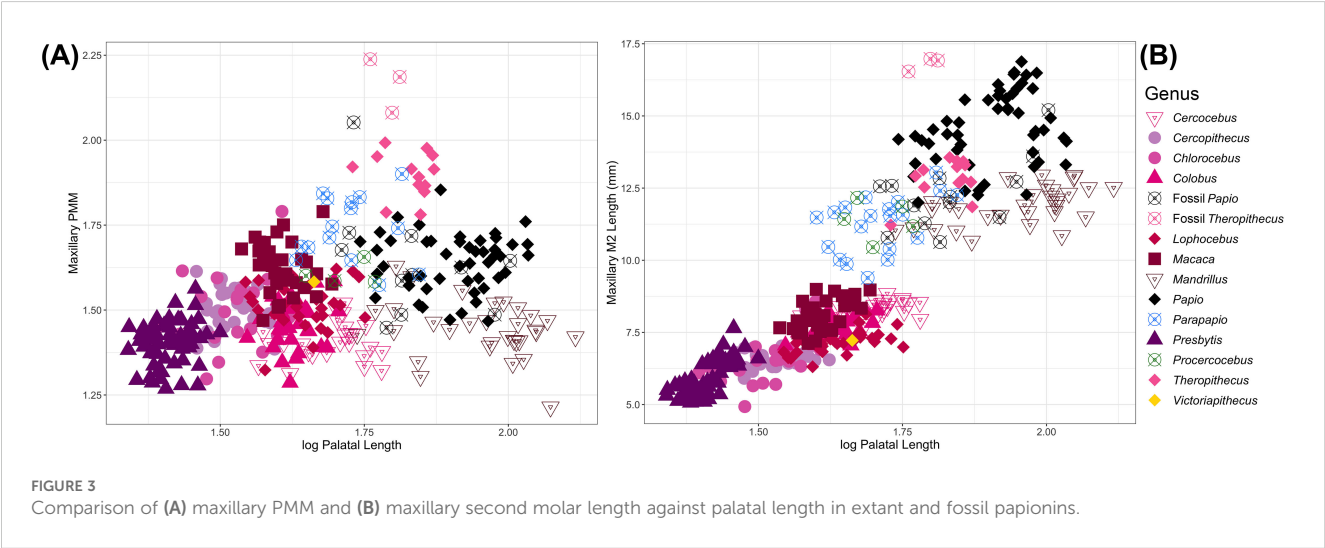


TABLE 3 Intraspecific correlations in facial length and postcanine dental proportions*.

Taxon**	Statistic	logPL v XMMC	logFL v XMMC	FL/ML v XMMC	logPL v DMMC	logFL v DMMC	FL/ML v DMMC	logPL v XPMM	logFL v XPMM	FL/ML v XPMM	logPL v DPMM	logFL v DPMM	FL/ML v DPMM
<i>Colobus guereza</i>	n	30	32	30	33	33	30	32	32	30	32	32	30
	R ²	0.28	0.25	0.19	0.39	0.06	-0.2	0.11	-0.17	-0.46	-0.04	-0.2	-0.27
	p-value	0.1341	0.1735	0.3187	0.0234	0.7381	0.2817	0.5551	0.3573	0.0111	0.8265	0.283	0.1542
<i>Presbytis rubicunda</i>	n	31	31	28	32	32	28	34	34	28	33	33	28
	R ²	0.26	-0.21	-0.38	0.03	-0.32	-0.41	0.06	-0.15	-0.33	-0.33	-0.13	0.03
	p-value	0.1563	0.2585	0.0479	0.8687	0.0711	0.03	0.7515	0.3936	0.083	0.0589	0.4639	0.8857
<i>Macaca mulatta</i>	n	33	33	33	30	30	30	33	33	33	33	33	33
	R ²	0.46	0.48	0.26	0.16	0.1	0.16	-0.28	-0.03	0.21	-0.15	0.04	0.13
	p-value	0.0073	0.0045	0.1439	0.4105	0.5816	0.4065	0.1087	0.8899	0.2327	0.3972	0.8289	0.4651
<i>Mandrillus sphinx</i>	n	31	31	28	28	28	28	31	31	28	28	28	28
	R ²	0.48	0.42	0.22	0.43	0.41	0.25	-0.28	-0.2	-0.03	-0.55	-0.54	-0.38
	p-value	0.0062	0.019	0.2692	0.0231	0.0305	0.1982	0.1326	0.2738	0.8704	0.0022	0.0032	0.0445
<i>Lophocebus albigena</i>	n	31	31	30	31	31	30	31	31	30	32	32	30
	R ²	0.28	0.26	0.31	0.33	0.23	0.07	0	0.06	0.14	0.29	0.26	0.2
	p-value	0.1314	0.163	0.0946	0.0664	0.2189	0.7111	1	0.7424	0.4551	0.1015	0.155	0.2817
<i>Papio hamadryas</i>	n	33	33	33	33	33	33	33	33	33	33	33	33
	R ²	0.23	0.21	0.23	-0.1	-0.05	0.17	-0.06	-0.07	0.03	-0.42	-0.44	-0.14
	p-value	0.202	0.2327	0.2007	0.5967	0.7732	0.3546	0.7339	0.6938	0.8811	0.014	0.0109	0.4337
<i>Cercopithecus mitis</i>	n	32	32	30	32	32	30	34	34	30	34	34	30
	R ²	0.19	-0.01	-0.37	0.26	0.17	-0.06	0.09	-0.01	-0.19	-0.39	-0.38	-0.25
	p-value	0.2857	0.9555	0.0453	0.1538	0.3452	0.7676	0.6286	0.9706	0.321	0.0222	0.0256	0.1904

*Significant correlations are bolded.
**Abbreviations as follows: PL is palatal length, v is versus, FL is facial length, FL/ML is relative facial length, X is maxillary, MMC is molar module component, PMM is premolar-molar module, D is mandibular.

(e.g., baboons and macaques; Monson, 2020). The lack of intraspecific correlation, or static allometry, between cranial and dental morphology in the majority of cercopithecoid species sampled is consistent with other allometric trends, where environmental variation within species drowns out the anatomical covariation that shapes clade-level morphological diversification (e.g., Hlusko et al., 2006; Laughlin et al., 2017).

Cardini et al. (2015) proposed an evolutionary pattern called craniofacial allometry (CREA), arguing that small species tend to have short faces, and large species tend to have long faces (Cardini et al., 2015) and relatively smaller braincases (Cardini, 2019). Postnatal changes in body size can also result in changes in facial length, and allometry may enable craniofacial diversification in some clades (Cardini and Polly, 2013; Monson, 2020). We extend this previous work by demonstrating that long faces are significantly correlated with relatively longer third molars. As the third molars are the last teeth to develop (Kavanagh et al., 2007), the ontogeny of facial morphology may also play a role in craniodental covariation (Collard and O'Higgins, 2001; Singleton, 2002; Simons and Frost, 2021).

Papionins occupy distinct craniodental morphological niches

The strong taxonomic discrimination provided by measures of facial length and relative premolar size supports that these traits are heritable (as has already been demonstrated for relative premolar size; Hlusko et al., 2016; Monson et al., 2022a) and may be important for facilitating occupation of distinctive morphospaces associated with ecological and dietary niches.

Extant cercopithecoids occupy distinctive morphospaces of postcanine dental proportions and facial/palatal lengths. While PMM does not appear to be associated with diet broadly across mammals (Monson et al., 2019a), this study clearly demonstrates the diversity of second molar and fourth premolar lengths relative to facial/palatal length in cercopithecoid primates (Figure 3). These craniodental traits also partition the *Cercocebus/Mandrillus* and *Papio/Lophocebus/Theropithecus* clades (Figure 2D), aligning with previous work by Fleagle and McGraw (1999, 2002) demonstrating the relatively larger fourth premolar in *Cercocebus* and *Mandrillus* compared to *Papio*, *Lophocebus*, and *Theropithecus*, which they attribute to feeding behaviors and hard-object processing. Fleagle and McGraw (2002) also demonstrate that *Macaca*, which they use as an analogue for the papionin ancestor, has relatively larger fourth premolars, and they hypothesize that the enlarged first molars of *Papio/Lophocebus/Theropithecus* evolved independently in that clade.

A growing body of work has identified a strong allometric component to primate craniofacial variation with important implications for fossil taxonomy and paleontological studies (e.g., Collard and O'Higgins, 2001; Gilbert, 2013; Monson et al., 2017; Plavcan, 2002, 2003; Shirai and Marroig, 2010). Our work supports these previous studies and emphasizes that dental variation, and particularly molar proportions, should also be considered in

assessments of primate craniofacial allometry and evolutionary relationships.

Evolution of prognathism in papionins

Most researchers now agree that prognathism is derived and evolved convergently in papionins (Benefit and McCrossin, 1991, 1993; Collard and O'Higgins, 2001; Cronin and Sarich, 1975; Delson, 1975; Disotell, 1994, 1996; Harris, 2000, 2002; Jolly, 1970; Strasser and Delson, 1987). The position of *Victoriapithecus*, a basal cercopithecoid, in trait morphospace suggests that the ancestral papionin morphology of dental proportions and facial lengths is likely similar to that seen in extant *Macaca*, *Cercocebus*, and *Lophocebus*. Fossil *Papio*, *Parapapio* and *Procercocebus* all look similar to extant baboons, although they tend to have relatively shorter third molars and shorter faces than extant taxa. These findings support that *Parapapio* and *Procercocebus* may represent an intermediate fossil morphology between the ancestral phenotypes typified by *Victoriapithecus* and other short-faced papionins, and the derived longer face in extant *Papio* and *Mandrillus* (see Brasil et al. [2025, this same issue] for a detailed history of the taxonomy and phylogenetic hypotheses for *Parapapio*). Further assessment of the relationships between postcanine tooth length proportions and facial/palatal length may help provide some indication of ancestor-descendent relationships, although additional fossils will be required to more thoroughly test these hypotheses.

If some early population of *Parapapio* is ancestral to other papionins, this would support that long faces evolved convergently in *Papio/Theropithecus*, and *Mandrillus*, with *Parapapio* as a likely medium-faced ancestor (this scenario supports that *Lophocebus* is an outgroup to *Papio/Theropithecus*). Alternatively, long faces may have evolved separately in all three lineages (*Papio*, *Theropithecus*, and *Mandrillus*) with short faces retained, or secondarily evolved, in *Lophocebus* and *Cercocebus*. A third scenario, less parsimonious based on available evidence, is that papionins shared a prognathic ancestor, currently undiscovered in the fossil record, and that *Lophocebus* and *Cercocebus* secondarily evolved shorter faces convergently.

In all scenarios, prognathic faces evolved convergently at least twice in papionins, and potentially three times, supporting that this trait is highly labile in this clade. The most parsimonious explanation is that *Papio* and *Theropithecus* shared a prognathic ancestor after the divergence of *Lophocebus*, and that long faces evolved twice in papionins (the first scenario described in the paragraph above). There continues to be debate about the phylogenetic relationships among papionins (e.g., Guevara and Steiper, 2014), with many researchers settling on a polytomy for *Lophocebus/Papio/Theropithecus*. Our work weighs in on this debate by providing morphological evidence that *Lophocebus* more likely diverged earliest in this clade, and prognathic faces evolved in a more recent common ancestor shared by *Papio/Theropithecus*.

It is possible that long-faced primates converged on relatively longer third molars through selection for longer teeth and/or selection for longer faces, as both traits have been hypothesized to

assist in chewing and digesting a diet dominated by tough C4 plants and other abrasive materials (e.g., Cerling et al., 2011; Jablonski, 1993; Singleton, 2005). Future comparative studies looking at facial elongation in other mammals (e.g., Carnivora; Machado et al., 2018; Sears et al., 2007; Tamagnini et al., 2017), particularly herbivorous species (e.g., horses; Janis et al., 2024), as well as the biomechanics of chewing and muscular anatomy, may provide additional insights into the likely convergent evolution of prognathism in papionins.

Applications to human evolutionary studies

Facial retraction in humans remains one of the most enigmatic changes in hominid cranial evolution. Decades of hypotheses attempting to explain the reduction of supraorbital robusticity and facial length in humans have focused on diet and the biomechanics of chewing, cognition and brain size, and other functional adaptations (e.g., Demes, 1987; Gómez-Robles et al., 2017; Preuschoft and Witzel, 2004). More recently, research has demonstrated the strong roles of craniodental integration and evolutionary allometry in shaping primate facial morphology. Although there is a large and growing body of research on cranial variation and modularity in anthropoids (e.g., Cummings et al., 2012; Grunstra et al., 2021; Kay and Kirk, 2000; Ravosa and Profant, 2000), key unanswered questions about the evolution of cranial anatomy remain, particularly for traits related to facial retraction.

Relative third molar lengths also reduced dramatically in *Homo* throughout the Plio-Pleistocene, leading to small maxillary and mandibular third molars in modern humans (e.g., Gómez-Robles et al., 2017; Ungar, 2012). High rates of agenesis of these teeth are also reported in humans, with occurrence of agenesis significantly associated with shorter facial and jaw lengths (e.g., Fekonja and Čretnik, 2022; Gkantidis et al., 2021). The identification of a common set of genes influencing both craniofacial development and tooth size has led researchers to hypothesize that reductions in prognathism and changes in tooth size proportions in human evolution are pleiotropically linked (e.g., Polychronis and Halazonetis, 2014). The impetus for reduced third molar length remains unexplained in human evolution, although a growing body of evidence suggests that these evolutionary changes may also be linked to changes in fetal growth and gestation (Monson et al., 2019b; 2022b).

Previous investigation of evolutionary changes in craniofacial and dental anatomy in fossil hominids has suggested that these traits may not be tightly linked (Gómez-Robles et al., 2017). However, this previous work focused on fossil samples and brain size rather than facial projection, and data for craniofacial and dental anatomy are often collected from unassociated specimens. Given the anatomical relationship between cranial and dental morphology seen in cercopithecids in this study, it is reasonable to hypothesize that the relatively reduced third molar length in humans may be associated with our shorter faces rather than resulting exclusively from any adaptive or functional role. Further analysis of morphological covariation between facial/palatal length and postcanine dental proportions across a broader sample of primates, particularly apes, will help test this hypothesis.

Conclusion

Facial and palatal lengths are significantly correlated with relative third molar length in cercopithecoid primates. Species with longer faces have relatively longer third molars (as compared to first molars). The allometric relationship between cranial and dental variation in primates illuminates the tangled genetic and developmental networks that guide morphological diversification in this clade. Long prognathic faces evolved at least twice, and potentially three times in papionins (in *Papio*, *Theropithecus*, and *Mandrillus*), but the evolutionary history of this convergence remains obscured. Given the current morphological data, parsimony supports an evolutionary scenario where *Papio* and *Theropithecus* share a prognathic ancestor, and *Lophocebus* is a more basal sister species. Bringing a more comprehensive understanding of craniofacial covariation to paleontological studies promises to inform our approach to taxonomy and phylogenetic inference in the fossil record. We also highlight the possibility that selection for shorter faces, and/or relatively shorter third molars, may help explain coordinated patterns of facial reduction and reduced third molar length throughout the last several million years of human evolution.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

TM: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Project administration, Visualization, Writing – original draft, Writing – review & editing. MB: Conceptualization, Data curation, Funding acquisition, Investigation, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2025.1492411/full#supplementary-material>

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