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Aspects of molar form and dietary proclivities of African colobines

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This study investigates aspects of molar form in three African colobine species: *Colobus polykomos*, *Colobus angolensis,* and *Piliocolobus badius*. Our samples of *C. polykomos* and *P. badius* are from the Taï Forest, Ivory Coast; our sample of *C. angolensis* is from Diani, Kenya. To the extent that protective layers surrounding seeds are hard, we predicted that molar features related to hard-object feeding would be more pronounced in *Colobus* than they are *Piliocolobus,* as seed-eating generally occurs at higher frequencies in species of the former. We further predicted that among the colobines we studied, these features would be most pronounced in Taï Forest *C. polykomos*, which feeds on *Pentaclethra macrophylla* seeds encased within hard and tough seed pods. We compared overall enamel thickness, enamel thickness distribution, absolute crown strength, cusp tip geometry, and flare among molar samples. Sample sizes per species and molar type varied per comparison. We predicted differences in all variables except overall enamel thickness, which we expected would be invariant among colobines as a result of selection for thin enamel in these folivorous species. Of the variables we examined, only molar flare differed significantly between *Colobus* and *Piliocolobus*. Our findings suggest that molar flare, an ancient feature of cercopithecoid molars, was retained in *Colobus* but not in *Piliocolobus*, perhaps as a result of differences in the seed-eating proclivities of the two genera. Contrary to predictions, none of the aspects of molar form we investigated tracked current dietary differences in seed-eating between the two *Colobus* species. Finally, we explored the possibility that molar flare and absolute crown strength, when analyzed together, might afford greater differentiation among these colobine species. A multivariate *t* test of molar flare and absolute crown strength differentiated *C. polykomos* and *P. badius*, possibly reflecting known niche divergence between these two sympatric Taï Forest species.

1. Introduction

1.1. Study aims and background

There are well-known differences in molar form between cercopithecines and colobines (Kay, 1978; Lucas and Teaford, 1994; Oates and Davies, 1994; Ulhaas et al., 1999, 2004; Swindler, 2002; Bunn and Ungar, 2009), as well as between African and Asian colobines (Swindler 2002; Pan, 2006). Yet, despite substantial dietary variation among the colobine species of Africa (Oates and Davies, 1994; Fashing, 2011; McGraw et al., 2016), our knowledge of differences in molar form among them is limited (Swindler, 2002; Thiery et al., 2017a, 2017b). Variation in African colobine diets ranges from those consisting of 60% young leaves (*Piliocolobus badius* of the Taï Forest; Korstjens, 2001) to those consisting of 60% seeds (*Colobus satanas* from Cameroon; McKey et al., 1981).

In the present study, we investigate how diet and molar form in African colobines may covary. We use the term ‘molar form’ as we did in our previous work (Guatelli-Steinberg et al., 2022) to refer to multiple molar features. Here, we examine several key aspects of

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molar form (enamel thickness and its distribution, crown strength, molar flare, and cusp geometry) that relate to the mechanics of food breakdown in a large sample of African colobines collected from two field sites: the Taï Forest of the Ivory Coast (*Colobus polykomos, P. badius*) and the suburban town of Diani, Kenya (*Colobus angolensis*). These species present variation in diet, particularly with respect to seed predation, or granivory. Seeds are often encased in hard and/or tough protective layers that pose a mechanical challenge to food breakdown (Lucas et al., 1991; Norconk et al., 2013; McGraw et al., 2016; Ledogar et al., 2018). Thus, in many instances, variable molar form among primates relates to variation in the hardness and/or toughness of seeds in their diets (e.g., Jolly, 1970; Kay, 1981; Lucas and Teaford, 1994; Dumont, 1995; Ulhaas et al., 1999; Strait, 1997; Martin et al., 2003; Lambert et al., 2004; Lucas et al., 2008; Ledogar et al., 2013; McGraw et al., 2014; Thiery et al., 2017a, 2017b; Schwartz et al., 2020).

Here, the first question we ask is whether molar features assumed to be related to seed-eating are shared by the two *Colobus* species but not with *Piliocolobus*, as species of *Colobus* are often more granivorous than those of *Piliocolobus* (McKey et al., 1981; Maisels et al., 1994; Oates, 1994; Davies et al., 1999). The percentage of seeds in *Colobus* diets across six field sites averages 36.0%, reaching a high of 60.1% in *C. satanas* from Gabon (Maisels et al., 1994). By contrast, the percentage of seeds in *Piliocolobus* diets across seven field sites averages 14.0%, with a high of 30.8% in *Piliocolobus tholloni* from Zaire (Maisels et al., 1994). Where species of *Colobus* and *Piliocolobus* are sympatric, their diets are particularly divergent with respect to granivory (Maisels et al., 1994; Korstjens, 2001; McGraw et al., 2016). We suggest that if the proclivity for seed-eating in *Colobus* reflects a dietary divergence with a long evolutionary history, then *Colobus* and *Piliocolobus* should exhibit differences in molar features related to processing these mechanically challenging foods.

We then investigate whether documented differences in granivory between the two species of *Colobus* included in the present study—*Colobus polykomos* and *Colobus angolensis*—are associated with species-level differences in molar form. Unlike either *C. angolensis* from Diani or *P. badius* from the Taï Forest, *C. polykomos* from the Taï Forest consumes significant quantities of *Pentaclethra macrophylla* seeds (McGraw et al., 2016), which make up 12.7% of its diet (Korstjens, 2001). Material analyses reveal that the seed flesh and coating of *Pentaclethra* seeds are soft; however, the outer woody pod is mechanically challenging because it is both hard and tough (McGraw et al., 2016). While *C. polykomos* uses anterior teeth to break into these pods (McGraw et al., 2016), posterior teeth are used to reduce the pods and seeds prior to swallowing. One of the authors (S.M.) as well as field assistants of the Taï Monkey Project have observed these monkeys' oral processing behaviors over many field seasons and are familiar with the routine manner in which portions of pods brought into the oral cavity are masticated with the postcanine battery. This often occurs when seeds are not all fully extracted from pods using incisal preparation. We suggest that if the current diets of these three colobine species relate to differences in molar form among them, then *C. polykomos* should present divergent morphology from *C. angolensis* and *P. badius*. Given that all these species rely on tough foods to varying degrees, our analysis focuses particularly on molar features that are thought to relate to hard-object feeding.

Understanding how the molar features examined in this study vary across colobines with well-documented diets has the potential to inform the dietary reconstruction of ancient colobines (e.g., *Mesopithecus*: Thiery et al., 2017a, 2021; *Cercopithecoides:* Pallas et al., 2019; *Dolichopithecus*: Plastiras et al., 2022). If the colobine species examined here do not vary in molar features that have clear links to the mechanics of food breakdown, then it is reasonable to conclude that these species can process their mechanically variable diets with similar molar forms and that these features are not reliable for dietary inference in fossil colobines. Here, for comparative purposes, we also include the non-colobine *Cercocebus atys*, as its molar anatomy is associated with year-round consumption of hard, mechanically challenging *Sacoglottis gabonensis* seeds (Daegling et al., 2011; McGraw et al., 2014; O'Hara, 2021; Guatelli-Steinberg et al., 2022).

We first examine enamel thickness, which is thought to be highly evolvable over short evolutionary time scales (Hlusko et al., 2004). Quantitative genetic analyses further reveal that enamel thickness has high heritability and can change independently of other phenotypes (Horvath et al., 2014; Ungar and Hlusko, 2016). Diets that include hard (Kay, 1981; Martin, 1983, 1985; Grine and Martin, 1988; Dumont, 1995; Lambert et al., 2004; Vogel et al., 2008; Lucas et al., 2008; Pampush et al., 2013; McGraw et al., 2014; Thiery et al., 2017b) and/or abrasive (Gantt, 1977; Molnar and Gantt, 1977; Lucas et al., 2008; Rabenold and Pearson, 2011; Pampush et al., 2013) foods are thought to select for thick molar enamel, as both kinds of foods can cause loss of tooth function. High bite forces required to break open large hard objects such as seeds or nuts (with radii of 2–20 mm) can cause internal cracks in enamel that propagate to its surface, leading to fracture and potentially tooth crown failure (Lucas et al., 2008). Small hard objects, such as silica phytoliths or grit (with radii of 5–50 μm), are hypothesized to scratch enamel (Olejniczak et al., 2008; Ungar et al., 2008; Cerling et al., 2011), leading to abrasion and enamel loss (Lucas et al., 2008) that reduce the functional life of a tooth (Olejniczak et al., 2008; Ungar et al., 2008; Cerling et al., 2011). If both hard and abrasive foods are included in a species' diet, then it is possible that thick enamel may be an adaptation to both.

The potential for thick enamel to evolve may be more limited in colobines than it is in cercopithecines. Relative to their tooth size and body mass, primate folivores have thinner enamel than frugivores (Gantt, 1977; Ulhaas et al., 1999; Thiery et al., 2017a, 2017b). Thin enamel in folivorous species is thought to be adaptive because wear 'sculpts' (Ungar, 2015) the crown to generate sharp rims of enamel surrounding the softer dentine layer (Ungar and M'Kirera, 2003), exposing a series of compensatory shearing crests (Ungar and M'Kirera, 2003; King et al., 2005). These sharp enamel crests, which in some species increase in length throughout an organism's lifetime, are thought to enhance the shearing function of molars in species that include tough, leafy foods in their diets (Shimizu, 2002; Ungar and M'Kirera, 2003; King et al., 2005; Glowacka et al., 2016). Because all colobines have some dependence on leaves, selection for thin enamel along shearing crests may limit the evolution of thick enamel in these species. Instead, as was suggested for *Mesopithecus* (Thiery et al., 2017a), selection might alter morphological aspects of crown anatomy, and not enamel thickness, as compensatory adaptations to hard food consumption. Thiery et al. (2017a, 2017b) found that relative enamel thickness (RET) does not differ among colobine species despite variation in the degree to which their diets include hard and/or abrasive foods. Sample sizes in these studies, however, were limited to 1–3 individuals per species, limiting the statistical power needed to detect potentially subtle differences in RET that might covary with species' diets.

The variation in enamel thickness distribution in colobines has similarly been understudied. Ulhaas et al. (1999) found colobine molars to have enamel of greater absolute thickness than those of cercopithecines in the region of the occlusal basin. These authors attribute this difference to the 'mortar' function of the occlusal basin, which they suggest may be reinforced in colobines, perhaps owing to the inclusion of (presumably hard) seeds in their diets. This finding raises the possibility that, in colobines, evolutionary changes in the thickness of molar occlusal basins, where food is not sheared but is crushed and ground, may be less constrained than overall enamel thickness. Indeed, occlusal basin enamel appears to be thicker in more durophagous primates, such as orangutans (Schwartz, 2000; Kono, 2004). In addition, O'Hara (2021) found that several measures of occlusal basin thickness, when scaled to average enamel thickness (AET; Martin, 1985), were associated with durophagy in extant catarrhines, including *Ce. atys*, a habitual hard-object feeder. In fact, *Ce. atys* has proportionally thicker occlusal basin enamel in both upper and lower molars than does *Lophocebus albigena,* a fallback consumer of hard foods (Guatelli-Steinberg et al., 2022).

Another feature of molars critical for investigating links between form and function is absolute crown strength (ACS; Schwartz et al., 2020). Absolute crown strength, calculated as the product of AET and a tooth crown's radius, was shown to more closely approximate a crown's resistance to fracture than does RET (Schwartz et al., 2020). Greater correspondence between fracture resistance and ACS than between RET and fracture resistance is consistent with previous studies demonstrating the critical roles of crown size (Constantino et al., 2011) and AET (Lucas et al., 2008; Lawn and Lee, 2009; Lawn et al., 2009) in resistance to fracture. Plastiras et al. (2022) compared ACS in folivorous, fruit/seed-eating, and mixed (or opportunistic) feeding cercopithecids, finding that ACS was lowest and least variable in colobines. Here we build on those observations and ask whether ACS covaries meaningfully in relation to the hardness of foods that *C. polykomos*, *C. angolensis*, and *P. badius* consume.

We also quantify cusp tip sharpness and functional cusp flare to evaluate whether morphological variation in African colobines is related to hard-food consumption to a greater degree than RET or AET, given the functional importance of thin enamel in promoting sharp shearing crest formation in folivores. Sharp cusp tips and long shearing crests in folivores play a key role in puncturing and slicing through tough plant material (Lucas and Teaford, 1994; Ulhaas et al., 2004). Hard foods, by contrast, have the potential to break sharp-tipped cusps and are therefore thought to select for bunodonty (Kay, 1978). Furthermore, dull (vs. sharp) cusps have been suggested to be more efficient in the breakdown of hard foods (Lucas and Luke, 1984; Singleton, 2003; Berthaume et al., 2020). Toughness and hardness, then, are expected to drive selection for

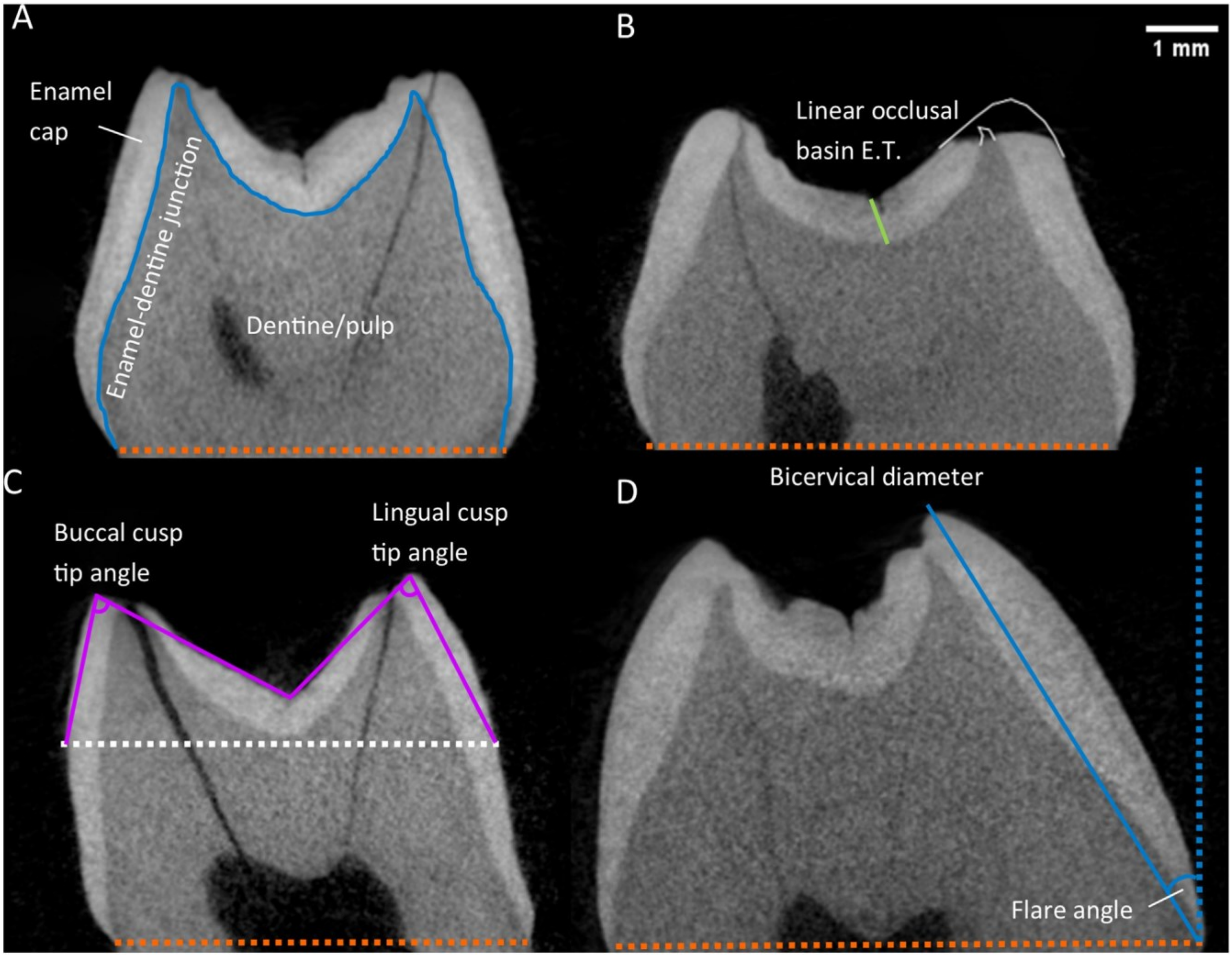

Figure 1. Virtual slices from 22 mm scans through the mesial cusps of four upper right third molars of *Colobus polykomos* (A; specimen 9067), *Colobus angolensis* (B; specimen 9037), *Piliocolobus badius* (specimen TF 22-22), and *Cercocebus atys* (D; specimen TF 16-11). A, B) Reference lines for the enamel-dentine junction (EDJ; blue line), the bicervical diameter (BCD; orange dotted line), and occlusal basin enamel thickness (green solid line). The dentine-pulp crown area is bounded by the EDJ and BCD, the area of the enamel cap is visible in white, bounded by the EDJ and the outer enamel surface (OES). C) As a guide for measuring cusp tip geometry, a line was drawn parallel to BCD that was tangent to the EDJ at the lowest point of the occlusal basin (white dotted line). Lingual and buccal cusp tips angles (purple lines) were measured between the point where the white dotted line intersected the OES to the cusp tip (vertex of the angle) to the lowest point of the occlusal basin. D) molar flare was measured as the angle between the solid blue line (extending from the cemento-enamel junction to the cusp) and a line perpendicular to the BCD (blue dotted line). Abbreviation: E.T. ¼ enamel thickness.

cusp tip geometry in different directions. Here we explore whether variation in the hardness of colobine diets might be a critical factor in predicting variation in their molar cusp tip angles.

Molar cusp flare (Fig. 1) refers to the angulation of the cusp from the cervix to the cusp tip (Shimizu, 2002; Singleton, 2003; Macho and Shimizu, 2009). Greater degrees of flare have been suggested to buttress crowns against laterally directed forces during chewing (Macho and Shimizu, 2009). In support of this suggestion, an association between molar flare and hard-object feeding has been found in extant hominoids (Singleton, 2003) and Asian colobines (Wright and Willis, 2022). In addition, *Ce. atys* has greater molar flare than *L. albigena*, consistent with differences between these two species in the frequency with which they process hard foods (Guatelli-Steinberg et al., 2022). Here we examined flare on ‘functional’ cusps—that is, cusps involved in Phase II of the chewing cycle (see Schwartz, 2000; Kono, 2004; and references therein), which are the lingual cusps of upper molars and the buccal cusps of lower molars (Hillson, 1996). We use this terminology—functional vs. nonfunctional cusps—simply as a convenient shorthand aligning our work with the recent literature, knowing full well that all cusps are ‘functional’ in the sense that they are involved in some facet of food breakdown. Shimizu (2002) compared molar flare in *P. badius* and *Macaca fuscata*, suggesting that minimal molar flare combined with thinner enamel in *P. badius* serves to reduce the width of enamel rims that are formed as wear exposes underlying dentine, thus enhancing the shearing function of *P. badius* molars. Similarly, Singleton (2003) showed that reduced flare is associated with greater shearing-crest length in hominoid molars. Thus, molars regularly recruited for shearing are expected to have reduced molar flare.

1.2. Dietary variation in the sample

Efforts to link molar form to function require as firm a grasp as possible on the material properties of consumed foods, with a particular focus on hardness, toughness, and abrasiveness. To estimate abrasiveness, differences in the ingestion rates of exogenous abrasive particles and the phytolith content of foods are evaluated. Dust-laden Harmattan winds deposit abrasives in the Taï Forest canopy each year (Geissler et al., 2018; Schulz-Kornas et al., 2019); however, at Taï, the amount of grit adhering to plant foods is greater near the soil than it is higher in the canopy (Geissler et al., 2018). Phytolith consumption is calculated below and incorporated into the discussion of our findings.

Table 1 presents comparisons of dietary hardness, likelihood of grit in the diet, and dietary toughness for the four study species. Brief descriptions of the species' diets follow.

Colobus polykomos Taï's king (or western black-and-white) colobus primarily eats tough, mature leaves and fruit (McGraw et al., 2016). As noted, *C. polykomos'* fruit consumption is dominated by *Pe. macrophylla* seeds protected by woody pods, which are both hard and tough. Processing these hard, tough pods, in addition to mature tough leaves, results in more chewing bouts per ingestive event in *C. polykomos* than in sympatric *P. badius* (McGraw et al., 2016).

Table 1
Key features of species' diets.[a]

Species	Hardness of diet	Abrasiveness: grit in diet	Toughness of diet
Ce. atys	Hard	High	Low
C. angolensis	Soft	Low	Medium
C. polykomos	Medium	Low	High
P. badius	Soft	Low	Medium

Abbreviations: *P. badius* ¼ *Piliocolobus badius*; *C. angolensis* ¼ *Colobus angolensis*; *C. polykomos* ¼ *Colobus polykomos*; *Ce. atys* ¼ *Cercocebus atys*.

[a] Hardness, abrasiveness due to grit, and toughness are our relative assessments based on the studies cited in the dietary descriptions in the main text.

Colobus angolensis Dunham (2017) documented the diets of *C. angolensis* from the Diani Forest, Kenya, the source population for the dental sample of this species that is included here. Most of the diet consisted of young leaves (58%), with smaller percentages of mature leaves (13%), flowers (14%), and fruits/seeds (14%). Given that only 2.8% of the diet consisted of leguminous seeds with tough outer pods, leaves reflect the ‘majority of the dietary challenges faced by *Colobus angolensis palliatus* with regard to toughness’ (Dunham and Lambert, 2016: 345). A diet of primarily young leaves is considerably less tough than that of *C. polykomos*. At the town of Diani, *C. angolensis* spends considerable time in all three forest strata—sapling, lower, and upper canopy—with less than two percent in the emergent layer (Dunham and McGraw, 2014). Less than one percent of their time is spent on the ground (Dunham and McGraw 2014) eating provisioned foods, playing, and moving between locations that provide limited options for remaining aerial such as trees, house roofs, fences, and walls. Based on the amount of time *C. polykomos* spends in the trees vs. on the ground at Diani, grit consumption is expected to be relatively low.

Piliocolobus badius Taï red colobus consumes mostly young leaves, fruit, and flowers (Wachter et al., 1997; Korstjens, 2001). These foods are generally less tough than the mature leaves consumed by *C. polykomos.* Red colobus does not eat *Pe. macrophylla* seeds, and this fact, together with their consumption of young leaves, is reflected in a chewing rate lower than that of *C. polykomos* (McGraw et al., 2016).

Cercocebus atys. The sooty mangabey is predominantly a terrestrial, hard-food specialist, collecting food items amid leaf litter (McGraw et al., 2007, 2014). *Cercocebus atys* frequently consumes the seeds of *S. gabonensis*, a food with an outer casing almost twice as hard as a cherry pit (Daegling et al., 2011). *Cercocebus atys* processes *S. gabonensis* seeds year-round by placing them posterior to their canines and crushing them on their premolars and molars with a powerful isometric bite (Daegling et al., 2011; McGraw et al., 2014). The foraging behavior of Taï sooty mangabeys (searching for *S. gabonensis* seeds on the forest floor) leads to a substantial amount of grit ingestion (Geissler et al., 2018). Of the Taï monkey species for which the number of masticatory cycles per ingestive event have been recorded (*Ce. atys*, *C. polykomos*, and *P. badius*), values for *Ce. atys* are the lowest (Kane et al., 2020, 2022).

1.3. Hypotheses and predictions

The following hypotheses and predictions are tested in this study.

1. Hypothesis 1) Enamel thickness variation in folivorous colobines is constrained by selection for thin enamel and shearing crests that are efficient at breaking down tough, leafy foods. Prediction: RET and AET values will not differ among the colobine species sampled here.
2. Hypothesis 2) With the exception of RET and AET, molar features related to hard-object feeding will be more pronounced in *Colobus* than they are in *Piliocolobus* owing to the more frequent inclusion of seeds in *Colobus* diets (Maisels et al., 1994; Daegling and McGraw, 2001; Daegling et al., 2011; McGraw et al., 2016). Of the two colobus species, *C. polykomos* is expected to exhibit more pronounced features related to hard-object feeding, owing to this species' mastication of hard (and tough) *Pe. Macrophylla* seed pods.

   Prediction 2.1) Absolute crown strength should track dietary variation in hardness among the three colobine species.

Although AET is not expected to vary greatly in these species, differences in molar size will result in statistically significant ACS differences among them.

Prediction 2.2) If the evolution of thicker enamel in the occlusal basins of colobine molars is less constrained than RET or AET, then occlusal basin thickness will track variation in dietary hardness, with *Colobus* having thicker occlusal basin enamel than *Piliocolobus* and with *C. polykomos* having the greatest thickness of enamel in this molar region.

Prediction 2.3) Colobines will differ in molar cusp tip geometry in relation to the hardness of their foods, as hard foods have the potential to cause fracture/failure of sharp cusp tips. *Colobus* will have molar cusp tips that are more rounded than those of *Piliocolobus*, with *C. polykomos* having the roundest cusp tips.

Prediction 2.4) The degree of functional cusp flare in colobine molars will vary in proportion to the hardness of their foods. *Colobus* will have greater flare than *Piliocolobus. Colobus angolensis* will have less flare than *C. polykomos*, as the latter consumes harder (and tougher) foods that require more bouts of chewing, necessitating greater buttressing against the increased masticatory loads required for penetrating and triturating mechanically challenging *Pe. Macrophylla* seed pods.

2. Materials and methods

2.1. Sample history and preparation

The samples of *C. polykomos* and *P. badius* included in this study are from the Taï Forest of the Ivory Coast. These samples are housed in the Primate Laboratory in the Department of Anthropology at The Ohio State University. Also housed in this laboratory, on loan from the National Museums of Kenya (Permit # NMK/GVT/8/6; CITES # KE001 17US063307), is the sample of *C. angolensis palliatus* (noted as *C. angolensis* in this manuscript) included in this study. This collection originated in the town of Diani, southeastern Kenya. It was collected by N.D., P.M.K.C., and A.D. between 30 October 2012 and 8 December 2015. The full dental sample, subsets of which were used for specific analyses, is listed in Table 2. Both upper and lower molars were included. However, uppers were always analyzed separately from lowers. Treatment of tooth type varies by analysis, as detailed in section 2.4 on statistical methods.

The least worn molar of each antimeric pair was chosen for scanning. Sex was known for only some specimens and so remains an unknown source of potential variation in our analyses. Molars were manually extracted from jaws and sterilized with ultraviolet light.

2.2. Phytoload

Following Rabenold and Pearson (2011), phytolith ingestion was calculated as time spent feeding on plant species belonging to families that Piperno (1988: 22) classifies as ‘often common to abundant’ phytolith producers. These are plant families in which over 50% of species studied produce phytolith quantities equal to or greater than those commonly reported for grasses (2e5% of plant dry weight). Recent data on phytolith production in Piperno (2006) and Mercader et al. (2009) allowed an update for taxa missing from Piperno (1988) to be classified. Rabenold and Pearson (2011) calculated what they termed ‘Phytoload A’ as follows: the percentage of feeding time on high phytolith-producing plant foods as a percentage of plant foods identified at the family level. Their

Table 2
Full dental sample of teeth used in this study.

Species	Individual	Tooth types
Cercocebus atys	TF 16-5	M^1, M^2, M_1, M_2
	TF 16-9	M^3
	TF 16-11	M^3
	TF 22-26	M^2, M^3, M_2, M_3
	TF 22-29	M^2, M^3, M_3
	TF 22-46	M^1, M^2
	TF 23-10	M^2, M^3
	TF 24-3	M^2, M_1
	TF 94-7	M^2
	TF 94-9	M^2, M^3, M_3
	TF 94-25	M^1, M^2
	TF 2001	M^1, M^2
	TF 2008	M^3
	TF 2010-1	M^1
	TF 2010-2	M^2, M^3
	TF 2016	M^1, M^2, M^3
	TF 2019	M^1, M^2
	TF 2020	M^1, M_1
	TF 2040	M_1
	TF 2041	M^1
	TF 2106	M^3, M_3
	TF 2108	M^2, M^3, M_3
	TF 2138	M^3
	TF 22-46	M^1, M^2
	TP-91	M^2
Colobus polykomos	TF 1040	M^3, M_1, M_2, M_3
	TF 16-8	M^3
	TF 21-00	M^2, M^3, M_3
	TF 21-19	M^1, M^2
	TF 21-23	M^2
	TF 22-11	M^3
	TF 22-38	M^3
	TF 22-45	M^3
	TF 23-8	M^1, M^2, M_2
	TF 90-67	M^3
	TF 94-11	M^3
	TF 94-18	M^2
	TF 94-26	M^3
Colobus angolensis	2052	M_1, LM2, M_3
	9037	M^1, M^3, M_3
	9038	M^1, M^2, M_1, M_2, M_3
	9041	M^1, M^2, M^3, M_1
	9042	M^1, M^2, M_1, M_2
	9045	M^3, M_3
	9046	M^1, M^2, M^3, M_2, M_3
	9052	M^3
	9053	M^3, M_1
	9056	M^2, M^3, M_1, M_2, M_3
	9059	M^1, M^2
	9061	M^2, M^3, M_2, M_3
	9064	M^1
	9065	M^2, M_1, M_2
	9067	M^3, M_1, M_2
	9068	M^1, M^2, M^3, M_1, M_2, M_3
	9069	M^1, M_1, M_2
	9071	M^1
	9078	M^1
	9079	M_1
Piliocolobus badius	TF 10-10	M_3
	TF 10-28	M^3
	TF 10-34	M_3
	TF 2005	M^2, M^3
	TF 2109	M_2, M_3
	TF 2115	M^1, M^3, M_2, M_3
	TF 21-18	M^3
	TF 22-19	M_3
	TF 22-20	M^3, M_3
	TF 22-22	M^3, M_3
	TF 22-7	M^3, M_3
	TF 23-2	M^1, M^2, M_3
	TF 94-15	M^3
	TF 94-6	M^2, M_2

Table 3

Summary statistics by tooth type for relative enamel thickness (RET; dimensionless), average enamel thickness (AET; mm.), bicervical diameter (BCD; mm.), absolute crown strength (ACS; dimensionless), linear enamel thickness of the occlusal basin (LOB; mm), proportional linear occlusal basin thickness (pLOB; dimensionless), flare (degrees), functional cusp tip angle (degrees), and nonfunctional cusp tip angle (degrees).[a]

Taxon	Tooth	RET (*n*)	AET (*n*)	BCD (*n*)	ACS (*n*)	LOB (*n*)	pLOB (*n*)	Flare (*n*)	Functional cusp tip angle (*n*)	Nonfunctional cusp tip angle (*n*)
Ce. atys	M^1	12.4 ± 1.4 (7)	0.576 ± 0.07 (7)	7.6 ± 0.9 (7)	1.48 ± 0.15 (7)	e	e	28.5 ± 5.1 (6)	100.0 (1)	99.4 (1)
	M^2	13.3 ± 1.6 (15)	0.715 ± 0.08 (15)	8.5 ± 0.7 (15)	1.74 ± 0.14 (15)	1.14 ± 0.24 (8)	1.54 ± 0.17 (8)	27.8 ± 3.2 (13)	88.1 ± 12.0 (8)	91.9 ± 9.5 (8)
	M^3	14.8 ± 1.6 (12)	0.747 ± 0.05 (12)	8.1 ± 0.7 (12)	1.74 ± 0.09 (12)	1.06 ± 0.13 (8)	1.43 ± 0.12 (8)	30.0 ± 4.0 (12)	89.5 ± 8.1 (8)	97.3 ± 10.3 (7)
	All uppers	13.6 ± 1.8 (34)	0.697 ± 0.09 (34)	8.2 ± 0.8 (34)	1.68 ± 0.16 (34)	1.10 ± 0.19 (16)	1.48 ± 0.15 (16)	28.8 ± 3.9 (31)	89.5 ± 10.0 (17)	94.7 ± 9.7 (16)
	M_1	12.2 ± 0.8 (4)	0.526 ± 0.04 (4)	5.9 ± 0.8 (4)	1.24 ± 0.13 (4)	0.84 ± 0.07 (2)	1.69 ± 0.04 (2)	31.9 ± 6.5 (4)	92.0 ± 6.4 (2)	93.9 ± 0.07 (2)
	M_2	12.0 ± 0.8 (2)	0.680 ± 0.01 (2)	7.8 ± 0.0 (2)	1.63 ± 0.01 (2)	0.81 (1)	1.20 (1)	39.9 ± 1.6 (2)	68.5 (1)	79.7 (1)
	M_3	14.5 ± 1.6 (5)	0.732 ± 0.04 (5)	7.3 ± 0.7 (5)	1.74 ± 0.09 (5)	1.21 ± 0.09 (4)	1.56 ± 0.13 (4)	36.1 ± 4.3 (5)	92.8 ± 7.7 (3)	92.7 ± 4.2 (4)
	All lowers	13.2 ± 1.7 (11)	0.648 ± 0.10 (11)	6.9 ± 1.0 (11)	1.49 ± 0.21 (11)	1.10 ± 0.17 (7)	1.54 ± 0.19 (7)	35.3 ± 5.4 (11)	88.5 ± 11.3 (6)	91.2 ± 5.9 (7)
C. polykomos	M^1	9.3 ± 1.7 (2)	0.371 ± 0.06 (2)	5.8 ± 0.6 (2)	1.03 ± 0.03 (2)	e	e	20.5 ± 4.1 (2)	e	e
	M^2	10.4 ± 1.3 (5)	0.464 ± 0.06 (5)	6.8 ± 0.3 (5)	1.26 ± 0.08 (5)	e	e	20.3 ± 3.0 (5)	e	e
	M^3	11.2 ± 0.7 (9)	0.490 ± 0.03 (9)	6.0 ± 0.4 (9)	1.22 ± 0.06 (9)	0.77 ± 0.16 (5)	1.56 ± 0.30 (5)	17.6 ± 3.1 (9)	86.0 ± 2.9 (5)	84.8 ± 7.1 (5)
	All uppers	10.7 ± 1.2 (16)	0.469 ± 0.06 (16)	6.3 ± 0.6 (16)	1.21 ± 0.09 (9)	0.77 ± 0.16 (5)	1.56 ± 0.30 (5)	18.8 ± 3.3 (16)	86.0 ± 2.9 (5)	84.8 ± 7.1 (5)
	M_1	9.4 (1)	0.355 (1)	4.9 (1)	0.94 (1)	e	e	22.8 (1)	e	e
	M_2	10.7 ± 1.0 (2)	0.450 ± 0.05 (2)	5.4 ± 0.03 (2)	1.10 ± 0.06 (2)	e	e	22.2 ± 1.4 (2)	e	e
	M_3	11.0 ± 0.6 (2)	0.460 ± 0.04 (2)	5.6 ± 0.11 (2)	1.13 ± 0.03 (2)	0.77 (1)	1.59 (1)	26.6 ± 2.2 (2)	e	68.7 (1)
	All lowers	10.5 ± 0.9 (5)	0.435 ± 0.06 (5)	5.4 ± 0.28 (5)	1.08 ± 0.09 (5)	0.77 (1)	1.59 (1)	24.1 ± 2.7 (5)	e	68.7 (1)
C. angolensis	M^1	10.1 ± 0.7 (10)	0.425 ± 0.03 (10)	5.7 ± 0.4 (10)	1.10 ± 0.56 (10)	0.49 ± 0.10 (8)	1.20 ± 0.15 (7)	18.8 ± 3.9 (10)	92.7 ± 4.6 (3)	92.4 ± 5.1 (7)
	M^2	11.2 ± 0.8 (10)	0.513 ± 0.03 (10)	6.2 ± 0.4 (10)	1.26 ± 0.06 (10)	0.68 ± 0.10 (9)	1.34 ± 0.18 (9)	17.3 ± 2.7 (10)	89.3 ± 3.2 (7)	92.9 ± 5.5 (8)
	M^3	11.8 ± 0.9 (10)	0.516 ± 0.05 (10)	5.5 ± 0.7 (10)	1.19 ± 0.07 (10)	0.72 ± 0.15 (10)	1.37 ± 0.28 (9)	14.8 ± 5.0 (10)	89.5 ± 5.8 (7)	85.2 ± 3.8 (8)
	All uppers	11.0 ± 1.1 (30)	0.485 ± 0.06 (30)	5.8 ± 0.6 (30)	1.18 ± 0.09 (30)	0.63 ± 0.15 (26)	1.31 ± 0.22 (25)	17.0 ± 4.1 (29)	90.0 ± 4.6 (17)	90.1 ± 5.9 (23)
	M_1	10.1 ± 0.7 (11)	0.402 ± 0.03 (11)	4.6 ± 0.2 (11)	0.96 ± 0.04 (11)	0.65 ± 0.09 (2)	1.48 ± 0.25 (2)	21.9 ± 3.1 (11)	84.2 (1)	78.3 ± 1.0 (2)
	M_2	11.8 ± 0.6 (10)	0.509 ± 0.03 (10)	5.6 ± 0.9 (10)	1.2 ± 0.11 (10)	0.77 ± 0.19 (7)	1.51 ± 0.31 (7)	20.2 ± 2.2 (10)	79.8 ± 4.5 (2)	80.3 ± 8.8 (6)
	M_3	11.9 ± 1.3 (8)	0.487 ± 0.06 (8)	4.9 ± 0.5 (8)	1.09 ± 0.09 (8)	0.77 ± 0.23 (8)	1.35 ± 0.34 (8)	19.4 ± 1.9 (8)	78.4 ± 9.7 (3)	76.2 ± 5.5 (8)
	All lowers	11.2 ± 1.2 (29)	0.463 ± 0.06 (29)	5.0 ± 0.7 (29)	1.07 ± 0.13 (29)	0.71 ± 0.20 (17)	1.43 ± 0.31 (17)	20.6 ± 2.7 (29)	80.0 ± 6.8 (2)	78.1 ± 6.6 (16)
P. badius	M^1	10.9 (1)	0.487 (1)	5.7 (1)	1.18 (1)	e	e	5.9 ± 0.0 (2)	e	e
	M^2	12.1 ± 1.4 (4)	0.482 ± 0.04 (4)	5.4 ± 0.7 (4)	1.14 ± 0.09 (4)	0.68 (1)	1.43 (1)	15.6 (4)	e	83.3 (1)
	M^3	10.4 ± 0.9 (7)	0.445 ± 0.05 (7)	5.9 ± 0.2 (7)	1.15 ± 0.08 (7)	0.68 ± 0.16 (2)	1.58 ± 0.25 (2)	16.3 ± 5.7 (7)	71.6 (1)	76.9 ± 5.3 (2)
	All uppers	11.0 ± 1.3 (12)	0.461 ± 0.04 (12)	5.7 ± 0.5 (12)	1.15 ± 0.08 (12)	0.68 ± 0.11 (3)	1.56 ± 0.30 (5)	14.5 ± 6.3 (13)	71.6 (1)	79.0 ± 5.3 (3)
	M_1	e	e	e	e	e	e	e	e	e
	M_2	12.0 ± 1.1 (3)	0.495 ± 0.02 (3)	4.9 ± 0.5 (3)	1.10 ± 0.08 (3)	0.77 ± 0.06 (2)	1.55 ± 0.03 (2)	16.2 ± 2.5 (3)	e	87.2 ± 0.34 (2)
	M_3	12.8 ± 1.3 (9)	0.492 ± 0.04 (9)	4.4 ± 0.5 (9)	1.03 ± 0.05 (9)	0.86 ± 0.12 (4)	1.75 ± 0.11 (4)	16.1 ± 2.6 (8)	73.4 ± 8.4 (4)	73.1 (1)
	All lowers	12.6 ± 1.3 (12)	0.493 ± 0.03 (12)	4.5 ± 0.5 (12)	1.05 ± 0.06 (12)	0.83 ± 0.11 (6)	1.68 ± 0.14 (6)	16.1 ± 2.5 (11)	73.4 ± 8.4 (4)	82.5 ± 8.2 (3)

[a] For each variable, values are reported as follows: mean ± 1 SD.

‘Phytoload B,’ on the other hand, is calculated by multiplying Phytoload A by the percentage of the total diet comprising plants; this is the value calculated and reported here.

2.3. X-ray microtomography

Molars were scanned at a resolution of 22 mm with a Bruker SkyScan 1172 High Resolution Ex Vivo 3D X-Ray Tomography Scanner located in the Do-Gyoon Kim Laboratory at The Ohio State University College of Dentistry. RAW output files were processed with N.Recon v. 1.7.4.2 (Bruker MicroCT, Kontich) and then saved as TIFFs. Two-dimensional buccolingual planes of section (across the mesial molar cusps, passing through buccal and lingual dentine horns, and situated perpendicular to the cervical margin) were generated from three-dimensional (3D) digital renderings of the teeth (following Skinner et al., 2015) using Dragonfly v. 2021.1.0.977 (Object Research Services, Montre□al). Each virtual section was then saved as a TIFF and imported into Adobe Photoshop v. 22.2 (Microsoft, San Jose) where crown outlines were reconstructed (when necessary; see below) prior to performing measurements.

2.4. Measurements

Figure 1 depicts measurement reference points and lines. AET was calculated as the enamel cap area divided by the enamel-dentine junction (EDJ) length (Martin, 1985, Fig. 1A). RET was

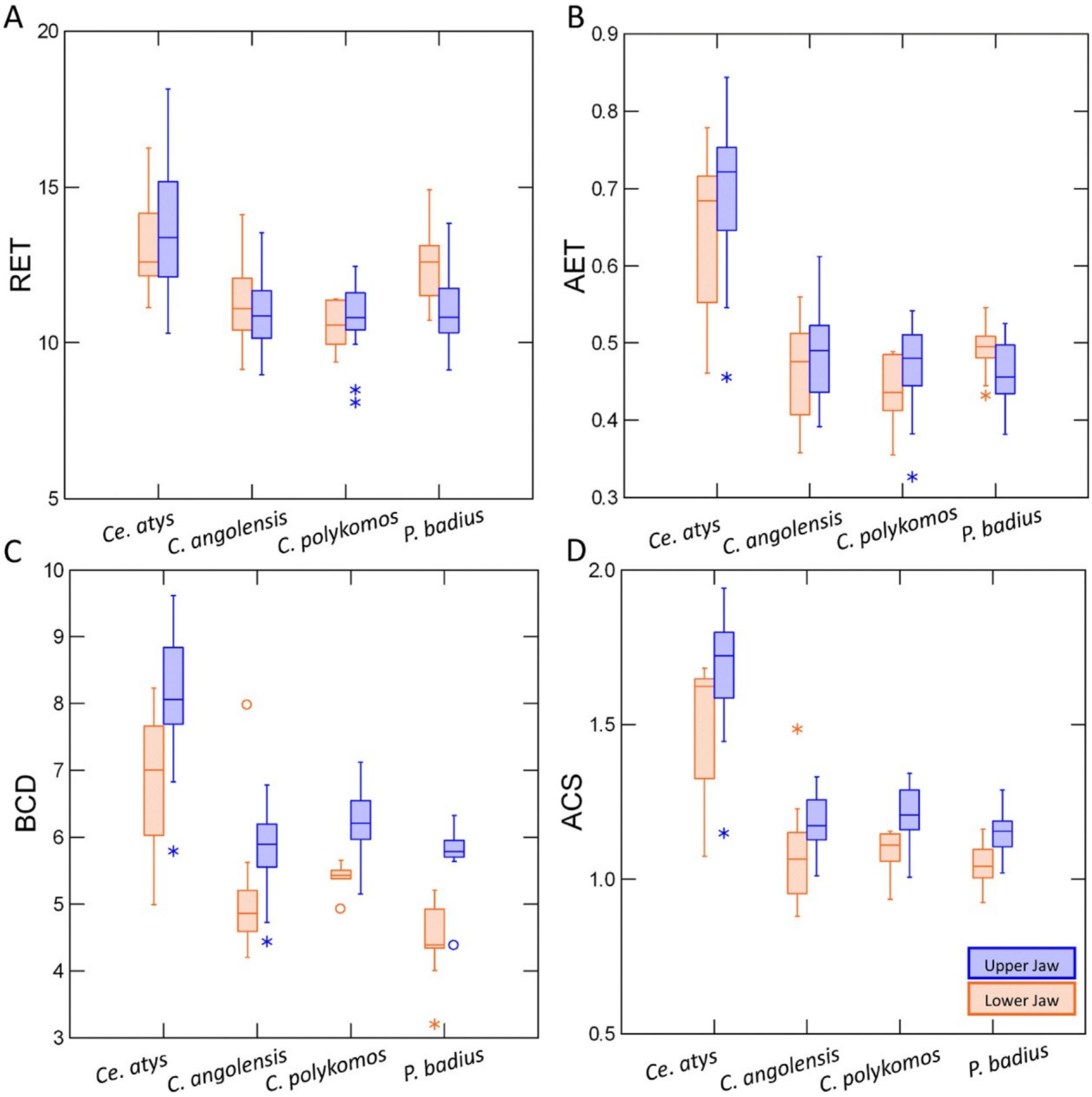

Figure 2. Box plots for relative enamel thickness (RET; A), average enamel thickness (AET; B), bicervical diameter (BCD; C), and absolute crown strength (ACS; D) for four species. In these plots, all upper molar types are combined, as are all lower molar types. The distribution of the data is shown in each set of box and whiskers, with outliers represented by asterisks, the box representing 50% of the data, and the line within the box representing the median. Abbreviations: *Ce. atys* ¼ *Cercocebus atys*; *C. angolensis* ¼ *Colobus angolensis*; *C. polykomos* ¼ *Colobus polykomos*; *P. badius* ¼ *Piliocolobus badius*.

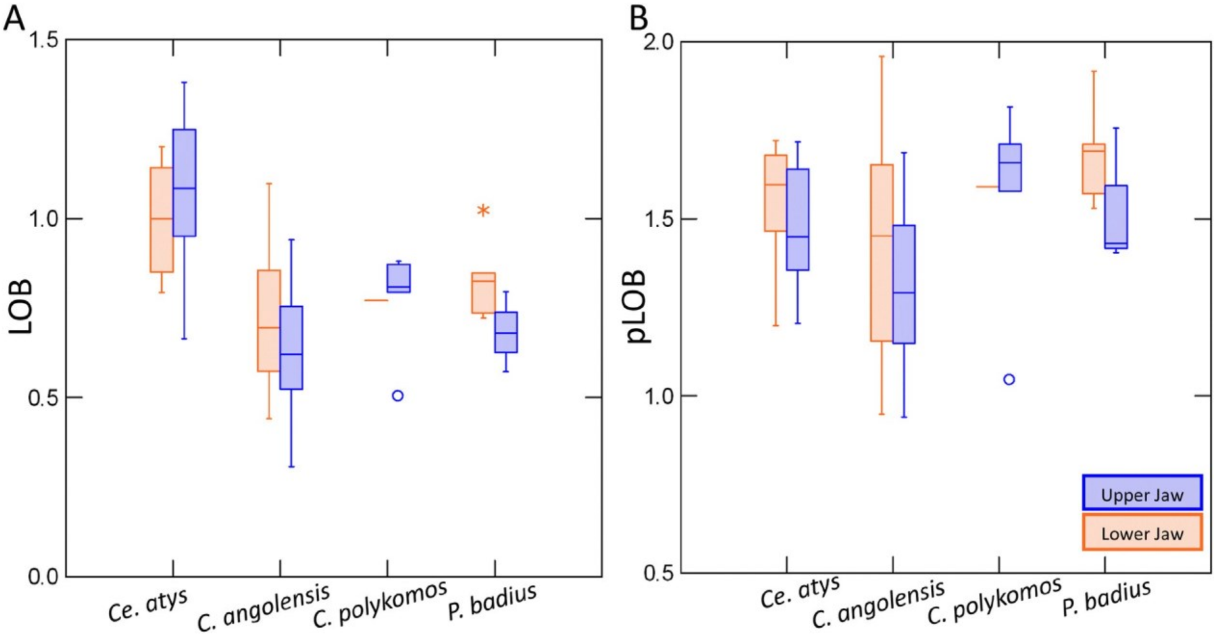

Figure 3. Box plots for linear enamel thickness of the occlusal basin (LOB; A) and proportional linear occlusal basin thickness (pLOB; B) for four species. In these plots, all upper molar types are combined, as are all lower molar types. The distribution of the data is shown in each set of box and whiskers, with outliers represented by asterisks, the box representing 50% of the data, and the line within the box representing the median. Abbreviations: *Ce. atys* ¼ *Cercocebus atys*; *C. angolensis* ¼ *Colobus angolensis*; *C. polykomos* ¼ *Colobus polykomos*; *P. badius* ¼ *Piliocolobus badius*.

calculated as AET divided by the square root of the dentine-pulp area enclosed by the EDJ and bicervical diameter (BCD) and multiplied by 100 (Martin, 1985). ACS was calculated as the square root of the product of the coronal dentine radius (half of the BCD) and AET (Schwartz et al., 2020). Linear enamel thickness of the occlusal basin (LOB) was measured as the distance between the lowest point of the occlusal basin at the EDJ and the lowest point of the occlusal basin at the outer enamel surface (OES; Macho and Thackeray, 1992, 1993; Macho and Berner, 1994; Kono-Takeuchi et al., 1998; Schwartz, 1997, 2000; Olejniczak and Grine, 2006; Fig. 1B). Linear occlusal basin thickness was divided by AET to obtain the variable proportional linear occlusal basin thickness (pLOB); values greater than 1 represent relatively thicker enamel in the occlusal region relative to the AET of a molar (O'Hara, 2021; Guatelli-Steinberg et al., 2022).

To measure cusp tip geometry (i.e., cusp sharpness), a reference line parallel to the BCD and tangent to the lowest point on the EDJ at the occlusal basin was drawn (Fig. 1C). Cusp tip geometry for the buccal and lingual cusps was measured as the included angle between where the reference line intersects the OES on either crown wall and the deepest point of the occlusal basin at the OES. To measure cusp flare, a reference line was drawn perpendicular to the BCD (Fig. 1D). The included angle between that reference line and a line connecting the CEJ to the apex of the cusp (or reconstructed cusp) on the OES defines that degree of molar flare (Shimizu, 2002); a greater angle is associated with a cusp tip that is positioned more toward the center (i.e., occlusal basin) of a crown than toward the crown wall.

Worn crowns were reconstructed following the recommendations of O'Hara and Guatelli-Steinberg (2021), using either the ‘Profile’ or ‘Pen Tool’ methods. The first of these methods involves filling in wear on enamel cusps and dentine horn tips based on OES curvature profiles of unworn teeth of the same tooth type (Smith et al., 2011). The second of these methods involves the ‘Pen Tool’ in Adobe Photoshop, which is used to find the intersection of the two sides of the worn cusp, creating a rounded shape representing the unworn cusp tip (Saunders et al., 2007; Guatelli-Steinberg et al., 2009; O'Hara et al., 2019).

O'Hara and Guatelli-Steinberg (2021) found that for AET and crown height measurements, for crowns with limited wear (for which wear did not reach the dentine horns and/or the deepest point of the occlusal basin), accurate values were achievable with both the Profile and Pen Tools. O'Hara and Guatelli-Steinberg (2021) also found that, for crowns on which wear exposed the tips of dentine horns (what they termed ‘extensive wear’), it was possible to obtain accurate AET values using the Profile method. The O'Hara and Guatelli-Steinberg (2021) recommendations were followed here for AET, RET, and measurements of molar flare using the Profile method on teeth with extensive wear and incorporating the Pen Tool method if a reference tooth was not available but wear was limited.

Measurements of cusp tip geometry and occlusal basin thickness were not taken on crowns with any occlusal basin wear and/or on any reconstructed crowns. All measurementsÐother than flareÐwere made by J.R., whose measurements were compared to those of K.G. in Guatelli-Steinberg et al. (2022). The interobserver error between K.G. and 5 ranged from 0.5% (for BCD) to 7.4% (for LOB measurements). Flare measurements for *Ce. atys* were made by K.G. (whose intraobserver error was assessed previously as 0.8% [Guatelli-Steinberg et al., 2022]). As noted in that work, the higher error of the occlusal basin thickness measurements, we believe, reflects small variations in how the measurement line is angled from the lowest point of the occlusal basin to the EDJ. Flare measurements for all colobines were taken by D.G.S., whose calculated intraobserver measurement error for the present study is 2.3% (across 15 measurements).

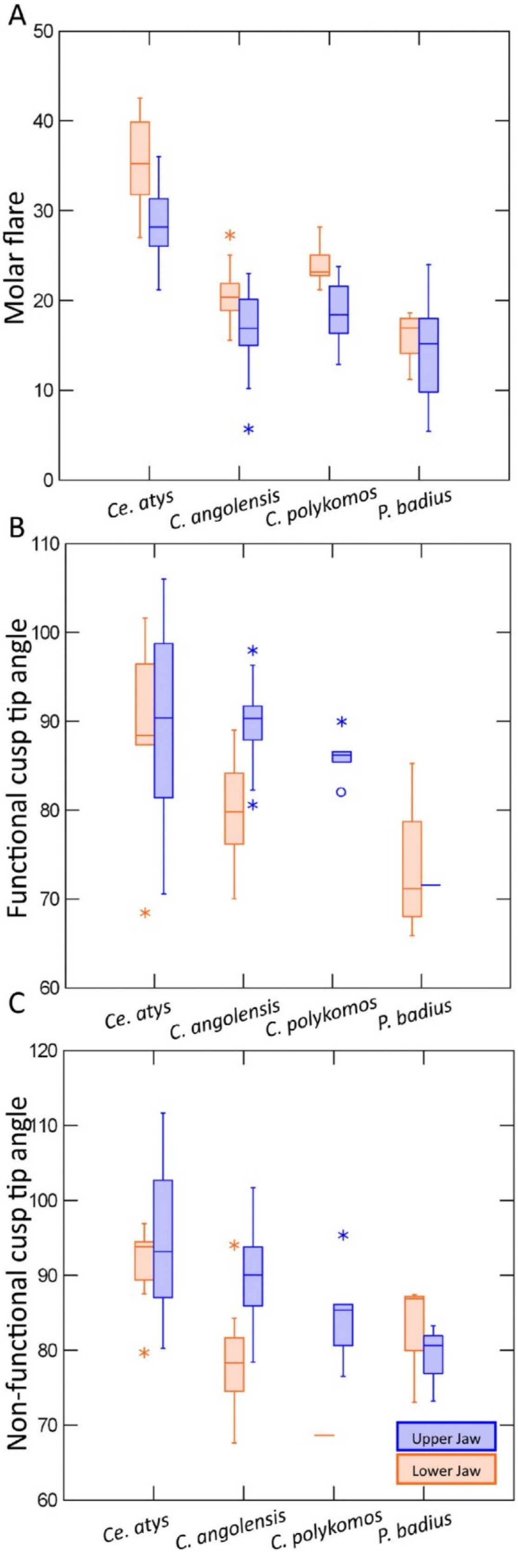

Figure 4. Box plots for molar flare (A) and cusp tip angles (B, C) for four species. In these plots, all upper molar types are combined, as are all lower molar types. The distribution of the data is shown in each set of box and whiskers, with outliers represented by asterisks, the box representing 50% of the data, and the line within the box representing the median. Abbreviations: *Ce. atys* ¼ *Cercocebus atys*; *C. angolensis* ¼ *Colobus angolensis*; *C. polykomos* ¼ *Colobus polykomos*; *P. badius* ¼ *Piliocolobus badius*.

2.5. Statistical methods

Descriptive statistics (means and standard deviations) were calculated per tooth type, and box plots were generated for both upper and lower molars in SYSTAT v. 13 (SPSS, Chicago, Illinois). Analytical statistics were performed only for upper molars, as lower molar sample sizes were limited. For the variables RET, AET, BCD, ACS, and flare, repeated measures linear mixed models were run with a procedure called 'PROC MIXED' in SAS v. 9.4 (SAS Institute, Cary) to analyze how each of these dental parameters varied across species, tooth types, and the interaction between species and tooth type. For each of these five variables, values for the different tooth types of an individual were treated as repeated measures. The fixed effects of species, tooth type, and their interaction were evaluated for statistical significance. Each model was run with different covariance structures, and the model with the smallest Akaike Information Criterion (AIC), representing the best fit, is reported here. Regressions were checked for the normality of their residuals. Post hoc pairwise comparisons for each species pair (based on the familywise error rate) were evaluated as the difference of least squares means between them. The least squares means for species reflect adjustment for the within-individual factor of tooth type and the interaction of species and tooth type.

For LOB, pLOB, and cusp tip angles measured on functional and nonfunctional cusps, sample sizes were too limited for analysis using linear mixed models. To evaluate species and generic differences for these variables, bootstrapped *t* tests were performed on combined samples of M^2s and M^3s, the two tooth types with the largest sample sizes. We chose to use *t* tests rather than a nonparametric equivalent because *t* tests are generally more powerful and can be used when data are normal. All four of the variables, LOB, pLOB, functional and nonfunctional cusp tip angles had Shapiro-Wilk values greater than 0.05, indicating no significant departure from normality. Finally, we extended our analysis to explore whether colobine species could be differentiated from one another using two key variables: ACS and molar flare, which we chose a priori because of their hypothesized connections to crown strength and buttressing against high occlusal loading. For this analysis, all upper molars were combined, and the multivariate Hotelling T^2 test was performed to evaluate the statistical significance of differences in bivariate means among colobines. The two variablesdACS and molar flaredare not highly correlated for the colobine sample (Pearson r ¼ 0.33), the sample on which the Hotelling T^2 test was performed. To visualize all species differences in bivariate means, we generated a scatterplot of ACS vs. flare showing the 95% confidence ellipses around centroids.

3. Results

All phytoload calculations are included in Supplementary Online Material (SOM) Tables S1eS4. Notable results include the high phytoload for *C. polykomos* (85.3%) followed by the much lower phytoloads of *C. angolensis* (23.9%), *P. badius* (19.8%), and *Ce. atys* (17.8%). Our value for *Ce. atys* is slightly lower than the 20.6% reported in the study by Pampush et al. (2013).

Table 3 provides sample sizes, means, and standard deviations for all dental variables by tooth type and dental arcade. Figures 2e4 are box plots comparing species for all upper and lower molars. Figure 2 suggests that *Ce. atys* has greater RET, AET, BCD, and ACS than any of the colobines. However, there is a clear overlap among

Table 4
Results of comparisons for relative enamel thickness (RET), average enamel thickness (AET), bicervical diameter (BCD), absolute crown strength (ACS), and flare computed with Proc Mixed.[a]

Variable	Null model likelihood ratio test (*p* > ChiSq)	Fixed effect	Numerator df	Denominator df	F value	*p* greater than F
RET	<0.0001	Species	3	61	26.49	<0.0001
		Tooth type	2	19	8.53	0.0023
		Species by tooth type interaction	6	19	4.72	0.0042
AET	0.0029	Species	3	61	78.43	<0.0001
		Tooth type	2	19	14.15	0.0002
		Species by tooth type interaction	6	19	4.67	0.0044
BCD	<0.0005	Species	3	61	62.18	<0.0001
		Tooth type	2	19	5.29	0.0149
		Species by tooth type interaction	6	19	3.33	0.0206
ACS	<0.0001	Species	3	61	114.87	<0.0001
		Tooth type	2	19	9.82	0.0012
		Species by tooth type interaction	6	19	4.42	0.0059
Flare	0.0100	Species	3	59	48.78	<0.0001
		Tooth type	2	18	1.23	0.3166
		Species by tooth type interaction	6	18	3.49	0.0182

Abbreviation: df ¼ degrees of freedom.

[a] Significant *p*-values are highlighted in bold.

the colobines for all these variables. BCD appears to show slightly more differentiation among the colobines, with crown sizes largest in *C. polykomos*. Figure 3 suggests that LOB is greater in *Ce. atys* than it is in the colobines, but all four of the species appear to be similar for pLOB. Figure 4 suggests greater flare and less acute cusp tip angles in *Ce. atys* than in any of the colobines. Among the colobines, molar flare appears to be highest in *C. polykomos*. With respect to cusp tip angles, it appears that those of *P. badius* are most acute. These plots also suggest that upper molars possess generally higher values of BCD and ACS than lower molars, but that lower molars tend to exhibit a greater degree of functional cusp flare.

Table 5
Post hoc pairwise comparisons among species for relative enamel thickness (RET), average enamel thickness (AET), bicervical diameter (BCD), absolute crown strength (ACS), and flare (from Proc Mixed models).[a]

Variable	Difference of least squares means between species pairs (*n*)[a]	df	t-value	*p*-value greater than absolute value of t
RET	*C. ang.* vs. *C. poly.*	61	1.25	0.2159
	C. ang. vs. *Ce. atys*	61	−7.22	<0.0001
	C. ang. vs. *P. bad.*	61	−0.16	0.8716
	C. poly. vs. *Ce. atys*	61	−7.11	<0.0001
	C. poly. vs. *P. bad.*	61	−1.13	0.2641
	Ce. atys vs. *P. bad.*	61	4.92	<0.0001
AET	*C. ang.* vs. *C. poly.*	61	1.67	0.1006
	C. ang. vs. *Ce. atys*	61	−12.61	<0.0001
	C. ang. vs. *P. bad.*	61	0.66	0.5118
	C. poly. vs. *Ce. atys*	61	−11.41	<0.0001
	C. poly. vs. *P. bad.*	61	−0.71	0.4777
	Ce. atys vs. *P. bad.*	61	9.21	<0.0001
BCD	*C. ang.* vs. *C. poly.*	61	−1.54	0.1286
	C. ang. vs. *Ce. atys*	61	−12.18	<0.0001
	C. ang. vs. *P. bad.*	61	0.56	0.5744
	C. poly. vs. *Ce. atys*	61	−7.98	<0.0001
	C. poly. vs. *P. bad.*	61	1.68	0.0976
	Ce. atys vs. *P. bad.*	61	8.79	<0.0001
ACS	*C. ang* vs. *C. poly.*	61	0.22	0.8625
	C. ang. vs. *Ce. atys*	61	−15.99	<0.0001
	C. ang. vs. *P. bad.*	61	0.82	0.4141
	C. poly. vs. *Ce. atys*	61	−12.42	<0.0001
	C. poly. vs. *P. bad.*	61	0.55	0.05839
	Ce. atys vs. *P. bad.*	61	9.54	<0.0001
Flare	*C. ang.* vs. *C. poly.*	59	−1.39	0.1705
	C. ang. vs. *Ce. atys*	59	−9.43	<0.0001
	C. ang. vs. *P. bad.*	59	2.98	0.0042
	C. poly. vs. *Ce. atys*	59	−6.05	<0.0001
	C. poly. vs. *P. bad.*	59	3.74	0.0004
	Ce. atys vs. *P. bad.*	59	10.37	<0.0001

Abbreviation: df ¼ degrees of freedom; *P. bad.* ¼ *Piliocolobus badius*; *C. ang.* ¼ *Colobus angolensis*; *C. poly.* ¼ *Colobus polykomos*; *Ce. atys* ¼ *Cercocebus atys*.

[a] Significant *p*-values are highlighted in bold.

Results of the linear mixed models are given in Tables 4 and 5. There are significant effects for species and the species vs. tooth type interaction for RET, AET, BCD, ACS, and flare. Tooth type itself is statistically significant for the analysis of all variables except for molar flare. Post hoc comparisons among species testing for significant differences in their least squares means reveal the following: (1) *Ce. atys* is significantly different from every colobine species for each variable, with *Ce. atys* having greater means for RET, AET, BCD, ACS, and flare. With the exception of flare, no differences in these variables were found among the colobine species. It is worth noting, however, that the ACS difference between *C. polykomos* and *P. badius* was close to significance (*p* ¼ 0.0584). For flare, all species differences were significant except for the difference between *C. polykomos* and *C. angolensis*. Relative to the molars of *P. badius*, those of both *C. angolensis* and *C. polykomos* were more flared.

Results of bootstrapped *t* tests are provided in Table 6. For LOB and pLOB, these tests revealed statistically significant differences only for LOB, and these were for *Cercocebus* vs. the combined *Colobus* sample and for *Cercocebus* vs. *Piliocolobus*. Similarly, significant differences in cusp tip sharpness were found only for comparisons between *Cercocebus* vs. the combined *Colobus* sample and for *Cercocebus* vs. *Piliocolobus*. These bootstrapped *t* tests, however, are conservative in that they assume unequal variances. Under the equal variance assumption, there was an additional significant difference for the comparison between *Piliocolobus* and *Colobus* in nonfunctional cusp tip angle (df ¼ 22, t ¼ 2.233, $p < 0.0297$).

A scatterplot of ACS vs. flare is shown in Figure 5. It appears to show some distinction among colobines, but the 95% confidence ellipses surrounding colobine centroids overlap. The Hotelling T^2 value (run on the full colobine upper molar sample) is statistically significant for the comparison between *P. badius* and *C. polykomos* ($p < 0.045$) but not for the comparison between *P. badius* and *C. angolensis* (Table 7).

We note that we had a small sample of worn *Procolobus verus* (olive colobus) molars available to us that we did not ultimately include in the full data set, owing to their degree of wear. In two M_3 specimens of *Pr. verus*, there was, however, enough of a cusp preserved to estimate where unworn cusp tips would have been located. The average of the two flare estimates for these teeth is

Table 6
Bootstrapped *t* tests for upper second and third molars combined.[a,b]

Comparison (*n*)	Variable	Variances	df	t-value	*p*-value
C. poly. (5) vs. *C. ang.* (18)	LOB	Unequal	5.5624	−0.97	0.3704
C. poly. (5) vs. *C. ang.* (18)	pLOB	Unequal	5.3749	−1.42	0.2112
C. poly. (14) vs. *C. ang.* (5)	F. ANGLE	Unequal	11.464	1.89	0.0847
C. poly. (16) vs. *C. ang.* (5)	N. ANGLE	Unequal	5.9475	1.22	0.2700
Pilio. (3) vs. *Colobus* (23)	LOB	Unequal	2.7915	0.45	0.6839
Pilio. (3) vs. *Colobus* (23)	pLOB	Unequal	2.9703	−1.04	0.3742
e	F. ANGLE	e	e	e	e
Pilio. (3) vs. *Colobus* (21)	N. ANGLE	Unequal	2.9296	2.71	0.0748
Colobus (23) vs. *Cercocebus* (16)	LOB	Unequal	24.654	6.88	<0.0001
Colobus (23) vs. *Cercocebus* (16)	pLOB	Unequal	36.315	1.26	0.2166
Colobus (19) vs. *Cercocebus* (16)	F. ANGLE	Unequal	19.791	0.12	0.9087
Colobus (21) vs. *Cercocebus* (15)	N. ANGLE	Unequal	22.166	2.18	0.0399
Pilio. (3) vs. *Cercocebus* (16)	LOB	Unequal	4.6618	5.14	0.0044
Pilio. (3) vs. *Cercocebus* (16)	PLOB	Unequal	2.4734	−0.40	0.7188
e	F. ANGLE	e	e	e	e
Pilio. (3) vs. *Cercocebus* (21)	N. ANGLE	Unequal	5.5019	3.89	0.0096

Abbreviations: df ¼ degrees of freedom; *Pilio.* ¼ *Piliocolobus*; *C. ang.* ¼ *Colobus angolensis*; *C. poly.* ¼ *Colobus polykomos;* LOB ¼ linear occlusal basin (thickness), pLOB ¼ proportional linear occlusal basin (thickness), F. Angle ¼ functional (cusp tip) angle; N. Angle ¼ non (-functional cusp tip) angle.

[a] Significant *p*-values are highlighted in bold.

[b] Lines with no entries represent comparisons for which there were too few specimens to perform a *t* test. These are for *Piliocolobus* vs. *Colobus* in F. Angle and for *Piliocolobus* vs. *Cercocebus* in F. Angle.

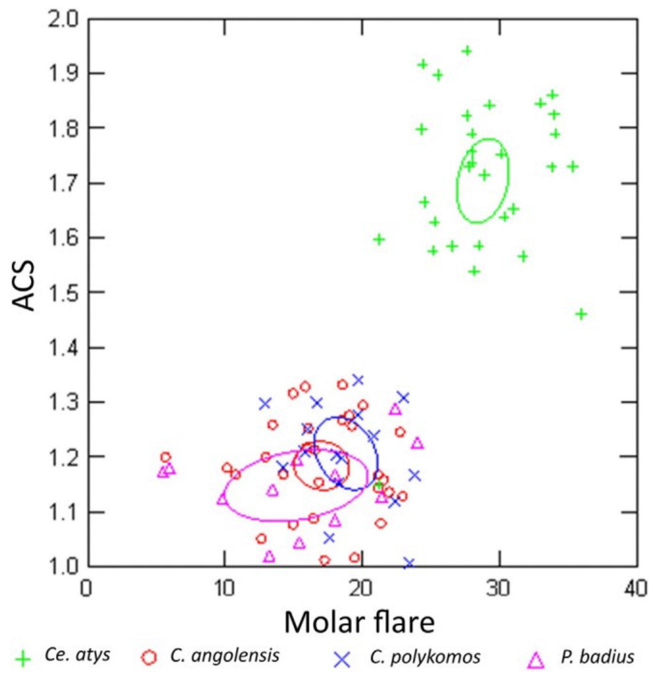

Figure 5. Scatterplot of absolute crown strength (ACS) against molar flare for four species. Ellipses represent 95% confidence intervals for bivariate means. Note: these are not confidence intervals for the sample but are bivariate confidence intervals on the centroid, analogous to the standard error of the mean in univariate comparisons. Abbreviations: *C. angolensis* ¼ *Colobus angolensis*; *C. polykomos* ¼ *Colobus polykomos*; *Ce. atys* ¼ *Cercocebus atys*; *P. badius* ¼ *Piliocolobus badius*.

Table 7
Bivariate comparison for colobines of flare and absolute crown strength for all upper molars combined.[a]

Comparison (*n*)	Hotelling's T-Square	F-ratio	df	*p*-value
C. poly. (16) vs. *P. bad.* (12)	7.349	3.533	2, 25	0.045
C. ang. (29) vs. *P. bad.* (12)	2.670	1.301	2, 38	0.284
C. ang (29) vs. *C. poly.* (16)	3.109	1.518	2, 42	0.231

Abbreviations: df ¼ degrees of freedom; *P. bad.* ¼ *Piliocolobus badius*; *C. ang.* ¼ *Colobus angolensis*; *C. poly.* ¼ *Colobus polykomos*.

[a] Significant *p*-values are highlighted in bold.

15.4^0. Below, we incorporate these estimates into our discussion of the evolution of molar flare in colobines (Table 7).

4. Discussion and conclusions

This study investigated variation among African colobines in several aspects of molar form. We included *Cercocebus atys*, a consummate hard-object feeder (McGraw et al., 2014), as a comparator to the colobines. Two-dimensional sections of each of the species included in this study are shown in Figure 1, which reflects some of the similarities and differences among them. Unsurprisingly, differences between *Ce. atys* and colobines were statistically significant for RET, AET, ACS, LOB, and molar flare. In all cases, *Ce. atys* exhibited higher values. Thus, *Ce. atys* presents many molar features expected to be associated with both the hardness of its foods and the inclusion of abrasive grit in its diet related to terrestrial foraging.

With respect to molar form variation within the colobines, we tested two hypotheses. We suggested in Hypothesis 1 that selection for thin enamel in these folivorous species would limit the evolution of differences in overall enamel thickness (RET or AET) among them. Hypothesis 1 gains strong support from our analysis, as no statistically significant differences among these species in RET or AET were found. This result lends credence to the hypothesis that Thiery et al. (2017a) first proffered: the evolution of thickened enamel in colobines as a response to hard-object feeding may be heavily constrained by the functional role of thin enamel in shearing. In addition, it is possible that phylogenetic inertia might help explain these results, particularly with respect to the lack of enamel thickness differences between *C. polykomos* and *C. angolensis*. It is further possible that the lack of variation in enamel thickness among these colobines is related to constraints arising from the effect that thick enamel would have on reducing OES curvature.

In Hypothesis 2, we suggested that features related to hard-object feeding would be more pronounced in *Colobus* compared to *Piliocolobus*, as well as in *C. polykomos* relative to both *C. angolensis* and *P. badius*. We anticipated that while selection for thin enamel in these folivorous species would limit the evolution of thick enamel overall (RET or AET), differences in hard-object feeding among them might be reflected in aspects of crown form that are related to increased buttressing against higher, more repetitive bite forces: ACS (Prediction 2.1), occlusal basin enamel thickness (Prediction 2.2), cusp tip geometry (Prediction 2.3), and degree of molar flare (Prediction 2.4).

Prediction 2.1, relating to ACS differences among colobines, is not supported, as no statistically significant differences in ACS were detected among them. It was expected that even though there would be minimal variation in enamel thickness among the colobines, differences in tooth size among them might endow them with differences in ACS. That expectation was not realized, as tooth size (BCD) was not significantly different among colobine species. Thus, even though in our sample *C. polykomos* consumes the most mechanically challenging foods, it does not have a significantly greater ACS. More work is required to understand how food material properties, chewing rates, and crown strength covary across primates. In that context, it is interesting that western lowland gorillas possess molars with high ACS and have also been documented to feed on hard objects, but only at one study site (Loango National Park, Gabon; van Casteren et al., 2019); whether this behavior exists in other gorilla populations remains unknown.

Our results also failed to support Prediction 2.2, as no statistically significant differences were present among colobines for LOB and pLOB. These two variables were predicted to be greater in *Colobus* than *Piliocolobus,* and then within the genus *Colobus,* to be greatest in *C. polykomos* on the basis of dietary hardness differences among them. We note that the greater phytoload of *C. polykomos* relative to the other colobines in this study would also lead to the expectation of greater LOB and pLOB in this species. Yet, for *C. polykomos*, neither greater dietary hardness nor abrasiveness in terms of phytoload is associated with thickened occlusal basin enamel.

As an added note, the finding that LOB values were higher in *Cercocebus* than in any of the colobines is at odds with the suggestion that, in comparison to cercopithecine molars, those of colobines might possess absolutely thicker occlusal basin enamel (Ulhaas et al., 1999). Comparing a more diverse set of colobine and cercopithecine species would help clarify whether there are broad differences between the two subfamilies in occlusal basin enamel thickness. It is also noteworthy that despite the finding that pLOB is greater in *Cercocebus* than it is in other cercopithecines (O'Hara, 2021), there is no difference in pLOB between *Cercocebus* and any of the colobines included in the present study. The pLOB results of the present study suggest that while this variable may be useful at identifying hard-object feeders within cercopithecines (O'Hara, 2021), it may not be useful within the higher taxonomic level of the Cercopithecoidea, encompassing both subfamilies.

Prediction 2.3, which stated that cusp tip geometry would differentiate colobine taxa based on their food hardness profiles, was not supported in our analysis. Cusp tip angles were only statistically significantly different between *Cercocebus* and the colobines and were statistically indistinguishable among colobine taxa. Of interest, the *Piliocolobus* vs. *Colobus* contrast in nonfunctional cusp tip angle was close to significance at $p < 0.078$ and, as noted, reached significance under an assumption of equal variances ($p < 0.045$). Thus, there is some indication that *Piliocolobus* has sharper cusp tips than *Colobus*, which lends a modicum of support to Prediction 2.3 at the genus, though not species, level.

Prediction 2.4, stipulating a relationship between the degree of molar cusp flare and food hardness, gains partial support from our analyses. Both species of *Colobus* did possess greater flare than *P. badius*, suggesting a genus-level difference that might relate to divergent evolutionary histories of these genera in terms of seed-eating. Contrary to our expectations, however, *C. polykomos* did not possess greater flare than *C. angolensis.*

Molar flare is an ancient feature of Cercopithecoidea, present in the 22 Ma nonbilophodont stem cercopithecoid *Alophia* and becoming more pronounced in victoriapithecids in conjunction with increased bilophodonty, ca. 15.5 Ma (Rasmussen et al., 2019). Bilophodonty has been suggested to have originated in a seed-eating context, with the lophs acting as wedges in the breakdown of very tough (Lucas and Teaford, 1994) and/or hard food items (Benefit, 1999). Molecular data suggest a final divergence between *Colobus* and *Piliocolobus* between 9.0 and 7.5 Ma (Roos and Zinner, 2022), roughly coinciding with an increase in leaf consumption for colobines in the Late Miocene (Pallas et al., 2019). Perhaps as these two genera diverged, selection acted to reduce flare in *Piliocolobus*, enhancing the shearing function of its molars (as per Shimizu, 2002).

The 15.4^{0} average flare for our two *Pr. verus* third molar specimens is closer to the average lower molar flare value of *P. badius* (16.1^{0}) than it is to the means for either of the *Colobus* lower third molar average values (19.4^{0} for *C. angolensis* and 24.1^{0} for *C. polykomos*). *Procolobus verus* is the sister taxon of *P. badius* (Ting, 2008; Roos and Zinner, 2022). Taï olive colobus' preferred food items are soft, young leaves and soft fruit (Oates, 1988; Korstjens, 2001; McGraw and Zuberbühler, 2007). Although a recent analysis revealed that olive colobus engages in more mastication than might be expected given the prevalence of young leaves in its diet, none of the olive colobus foods appear to require high, sustained bite forces to breach (Traff et al., 2022). *Procolobus verus* would therefore be expected to have minimal functional cusp flare, which is indeed what our estimates suggest. Though these estimates for *Pr. verus* are tentative, they align with expectations of reduced molar flare in a species that relies on young leaves and soft fruit. They also suggest the possibility that reduced molar flare was present in the common ancestor of *Piliocolobus* and *Procolobus*.

On the whole, then, there seems to be more variation in molar flare in these colobines than there is in either average or RET, ACS, or absolute or proportional linear occlusal basin enamel thickness. Cusp tip angles hint at a morphological difference between *Colobus* and *Piliocolobus*. Among colobines, only the *C. polykomos* vs. *P. badius* multivariate *t* test for ACS and molar flare was significantly different. We tentatively suggest that this result reflects the known niche separation between these two Taï Forest species, and possibly character displacement, as no significant difference was present between *C. angolensis* and *P. badius*. An important caveat is that this result, which combines all upper molars, would be strengthened through additional tests on larger samples, for which the possible effect of molar position can be assessed.

Based on evidence from our study, it seems that some aspects of molar crown anatomy, such as RET, AET, ACS, and occlusal basin enamel thickness, would not be useful for dietary inference in fossil colobines, while others (molar flare, cusp geometry) may be better suited. For instance, our analyses suggest that ACS in conjunction with molar flare might provide some insight into fossil colobine diets. Given that some aspects of crown morphology examined in this study bore a relationship to dietary variation, dental topographic parameters (e.g., relief, curvature, and complexity; Thiery et al., 2017a) may be more promising for dietary reconstruction in African colobines. Such topographic features, Thiery et al. (2017a) argue, might compensate for thin enamel when hard foods constitute critical elements of colobine diets.

Conflict of interest statement

The authors have no conflicts of interest.

Data sharing

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supplementary Online Material

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