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Effectiveness of buccal dental-microwear texture in African Cercopithecoidea dietary discrimination

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Abstract

Objectives: This study compares ISO (ISO/FDIS 25178) roughness parameters, calculated from three-dimensional (3D) molar buccal microtexture surfaces, among African Cercopithecoidea primates with different diets.

Materials and Methods: We examined 98 lower second molars from seven African Cercopithecoidea species with diverse dietary regimes and habitat exploitation. Buccal dental surfaces were analyzed using a Sensofar Plu Neox laser scanning confocal microscope. Thirty-eight, areal surface texture parameters were extracted (Mountain 7® software). Uni- and multivariate statistics were used to obtain diet-related patterns of buccal-microwear textures and feeding ecology to differentiate between species.

Results: Buccal-dental 3D texture parameters discriminate between Cercopithecoidea diets. Analysis of variance (ANOVA) revealed significant variation in microwear texture between forest-adapted *Mandrillus sphinx*, which showed coarse flat features, and grassland forager *Theropithecus gelada*, whose buccal surfaces were characterized by a high density of thin features. Buccal-microwear textures of folivorous species (*Colobus polykomos*) were related to a lower density of thicker surface indentations in comparison to *Papio anubis* and *Cercocebus atys* which are adapted to the consumption of tough and hard foods. The limited interspecific variation in the buccal-microwear textures of savanna dwellers (*Chlorocebus pygerythrus* and *Chlorocebus aethiops*) probably reflects similarities in their foraging diets.

Discussion: Significant variations between-species demonstrate that 3D microwear ISO roughness parameters applied to buccal enamel surfaces can distinguish between the diets of Cercopithecoidea.

KEYWORDS
buccal microtexture, dietary ecology, ISO roughness, microwear, primate

1 | INTRODUCTION

Plant silica-based phytoliths and exogenous quartz dust particles ingested with food have the potential to indent dental-buccal enamel surfaces (Lucas et al., 2013; Romero et al., 2012, 2013). These indentations take the form of scratches with different frequencies, lengths, and orientations that reflect the abrasiveness of the food consumed (Lalueza et al., 1996; Romero et al., 2012). Buccal-microwear analysis based on two-dimensional (2D) scanning electron microscopy (SEM) techniques has been used to determine the potential relationships between specific feeding behaviors and microwear patterns (Galbany et al., 2009; Martínez et al., 2020). These patterns have been used to infer aspects of diet for extinct species (Estebaranz et al., 2009; Estebaranz et al., 2012; Martínez et al., 2016, 2020; Pérez-Pérez et al., 2003, 2017). For instance, primates primarily adapted to folivorous diets exhibit lower densities of shorter buccal scratches than frugivorous and omnivorous species. Others have related high densities of scratches on buccal surfaces to the consumption of hard and gritty food items during mastication (Galbany et al., 2009; Martínez et al., 2020). Terrestrial feeding strategies and ecological constraints among primates also affect interspecific variability in buccal microwear signals (Galbany & Pérez-Pérez, 2004).

Occlusal and buccal dental-microwear can reflect variations in the dietary ecology of extant primates (Calandra & Merceron, 2016; Galbany & Pérez-Pérez, 2004; Scott et al., 2012). There is, however, a disparity between functional morphology and microwear. Species with similar craniodental adaptations can show different microwear pattern, for example, *Paranthropus boisei* from East Africa and *Paranthropus robustus* from South Africa differ in their microwear, however, they both share many craniodental adaptations (Peterson et al., 2018; Ungar et al., 2008). This is in part because the mechanical basis and factors that can contribute to microwear formation are still poorly known (Lucas et al., 2013; Teaford et al., 2020; van Casteren et al., 2020). Studies have also investigated the relative roles of dust and phytoliths, the angle at which an abrasive particle collides with the enamel surface, and particle geometry in microwear formation (Lucas et al., 2013; Teaford et al., 2020; van Casteren et al., 2020). Some authors have tentatively suggested that materials that are softer than enamel may contribute to dental microwear formation, although tooth-to-tooth contact cannot be ruled out (Krueger et al., 2021; Xia et al., 2015).

Three-dimensional (3D) dental-occlusal microtexture analysis based on the use of white-light confocal microscopy, scale-sensitive fractal analysis (SSFA, Ungar et al., 2003), and ISO surface texture parameters (Schulz et al., 2010) are established as a powerful tool from which to infer aspects of diet and the feeding ecology of extant and extinct primates (Calandra et al., 2012; Merceron et al., 2021; Scott et al., 2012). Studies of occlusal microtexture of Cercopithecoidea primates using scale-sensitive fractal analysis found significant differences between species that include resources with different material properties (Scott et al., 2012). Species that consume seeds and hard fruits, such as *C. polykomos* and *C. atys*, tended to have more complex surfaces than species that consumed tough foods, such as *C. guereza*. The diets of folivorous primates, such as *Theropithecus gelada*, which include tough leaves and a lower frequency of hard foods, showed high levels of anisotropy (Scott et al., 2012).

3D ISO texture parameters describe the geometric attributes of a surface, which has been related to the properties of foods (Calandra and Merceron, 2016; Schulz et al., 2013). Surface texture parameters are produced by algorithms, that are reproducible and intra- and inter-observer errors are reduced (Calandra & Merceron, 2016). ISO parameters are grouped into categories of height, spatial, hybrid, functional, and flatness or the deviation of peak and valleys to a reference plane (International Organization for Standardization, 2012; Schulz et al., 2010, 2013).

ISO parameters have been applied in primates to test the deformation and fracture mechanics of occlusal-enamel, and to infer the diet of extinct and extant primates (Calandra et al., 2012; Merceron et al., 2021; Plastiras et al., 2022; Stuhlträger et al., 2019). These studies suggested that hard-fruit eaters *Lophocebus albigena* and *Macaca fascicularis*, whose diets incorporate a large proportion of seeds from fruits, fractured their enamel more heavily and demonstrate great texture relief, with high peaks and deep valleys. Primates that incorporated large amounts of small particles (phytoliths), exhibited flatter surfaces (Calandra et al., 2012). Other studies have suggested that graminivorous primate species such as *T. gelada* show a different occlusal microtexture pattern than other folivorous species (*Colobus guereza*), and savanna dwellers (*Papio hamadryas* or *Chlorocebus aethiops*) due to differences in height distribution and anisotropy-based parameters, reflecting a pattern of finer, longer and denser striations for the colobine and wider striations for the gelada (Merceron et al., 2021).

ISO parameters can be used for dietary assessment because they reflect direct interactions between food particles and enamel surfaces. The comprehensive representation they produce, however, allows for additional functional inferences, as they provide information about the biomechanical properties of the food and the tooth surface that led to their formation or persistence (Calandra et al., 2012).

There are only a few microtexture studies based on buccal-enamel surfaces (Aliaga-Martínez et al., 2017; Hernando et al., 2022). The buccal surface of enamel interacts with food items while processed in the oral cavity. Experimental in vivo studies indicate that buccal microwear patterns exhibit long-term dietary signals and slower turn-over rates in comparison with dental occlusal-microwear (Romero et al., 2012). Sensitive Scale Fractal Analysis (SSFA) on buccal-microtexture studies have indicated that buccal surfaces reflect differences in anisotropy and complexity between species that have diets with different physical properties and hardness (Aliaga-Martínez et al., 2017). Anisotropy has been linked to food toughness, and high anisotropy is found for surfaces that appear to be dominated by parallel scratches (Scott et al., 2006, 2012). Fractal complexity of microwear surfaces has been associated with food hardness, and surfaces that are more complex exhibit pits and scratches of different sizes overlaying each other (Scott et al., 2006).

The positive correlation previously found between microwear density and textural parameters on non-occlusal enamel surfaces, therefore suggest that both methods are informative with regard dietary abrasiveness (Aliaga-Martínez et al., 2017; Purnell et al., 2012). As a recent comparing buccal and occlusal surface, suggested that there are significant differences in complexity and anisotropy, and the combination of both signatures could enable important inferences to be made about dietary reconstruction (Hernando et al., 2022).

This study applies, for the first time, the ISO/FDIS 25178 3D roughness parameters to buccal surfaces, to assess their effectiveness in detecting dietary variability among extant Cercopithecoidea species with diverse feeding ecologies.

2 | MATERIAL AND METHODS

The total sample included 98 mandibular molars (M$_2$s) with unworn or slightly worn occlusal surfaces (Scores 1–3; Meikle, 1977) from wild-caught specimens of seven Cercopithecoidea species with well-defined habitat and dietary preferences (Table 1). The M$_2$ was selected of each specimen because in primates the adult diet is attained when the second molar is erupted and in full occlusion (Romero et al., 2022). The M$_2$ is the most commonly used tooth for both occlusal (Merceron et al., 2021; Scott et al., 2012) and buccal (Galbany et al., 2009; Martínez et al., 2020; Ungar & Teaford, 1996) dental microwear studies among nonhuman primates. Furthermore, a single molar type is chosen for standardization and to prevent the effect of inter-tooth wear-related signatures (Gordon, 1982). We used one tooth per individual, with well-preserved buccal enamel surfaces suitable for microwear analysis. Specimens of the same taxa were chosen, whenever possible, from the same habitat to try and minimize variation in diet due to different locations.

Cercocebus atys is mostly a hard fruit eater (McGraw et al., 2007, 2011), and consumes significantly more quantities of fruit than other sympatric cercopithecoids (McGraw et al., 2011). Several studies suggest that the thick molar and enlarged incisors of mangabeys reflect their common reliance on hard fruits (Hylander, 1975; Kay, 1981). *Mandrillus sphinx* incorporates fruits, leaves, and seeds in their diet, increasing their diversity of food types by eating fallback foods during the fruit-scarce season (Hoshino, 1985; Tutin et al., 1997). *Papio anubis* is characterized by a large variation in foraging and dietary flexibility with a diet dominated by fruits, leaves, and subterranean items, depending on seasonal availability (Hill & Dunbar, 2002; Musyoki & Strum, 2016). Their generalist feeding behavior also includes invertebrates and small mammals. *Theropithecus gelada* has been traditionally described as a graminivorous specialist (Dunbar & Bose, 1991). *Colobus polykomos* is an arboreal primate, traditionally classified as genuine leaf-eater but its diet can also include seeds, fruits, twigs, and flowers (Dasilva, 1994). *Colobus* primates occupy a wide range of habitats, including primary and secondary forests, riverine forests, and wooded grasslands. Their ruminant-like digestive systems have enabled these leaf-eaters to occupy niches that are inaccessible to other primates (McGraw et al., 2016). Finally, two species from *Chlorocebus* genus were included. *Ch. pygerithrus* and *Ch. aethiops* are opportunistic omnivorous species that inhabit savanna woodlands. Both species have a similar feeding ecology that consists mostly of fruits, seeds, and flowers, also including leaves and small mammals, and insects (Dunbar & Dunbar, 1974; Lee, 1984; Struhsaker, 1967).

The M$_2$s were cleaned with acetone and alcohol-soaked cotton swabs, and dental crown impressions were made using President's Jet Regular Body (Coltène-Whaledent™) polyvinylsiloxane. Positive replicas were obtained using polyurethane (Ferropur, Feroca®). Buccal enamel surfaces were scanned with a Sensofar Plu Neox laser scanning confocal microscope from IMF-CSIC (Barcelona), using ×20 (0.45NA) objective, with a spatial sampling of 0.83 mm, an optical resolution of 0.31 mm, a vertical resolution of 20 nm and a z-step interval of 1 μm. All the crowns were placed in the same position, with the buccal surface orientated perpendicular to the objective in a horizontal position. Buccal surface areas of 650 × 500 μm (Figure 1), were obtained and then four fields of 138 × 102 μm were collected on the middle third of the molar buccal surfaces, avoiding the occlusal rim and the cervical area (Aliaga-Martínez et al., 2017). ISO parameters were measured on each buccal surface area, using the Mountain 7® software from Digital Surf (www.digitalsurf.com). The preprocessing template included first, leveling the surface and removing the form alterations to eliminate curvature, using a second degree polynomial, as standard procedure (Calandra et al., 2012), and then, trimming 5% of the extreme values of each parameter following the threshold operator of the software. Finally, the surface roughness was quantified according to 38 ISO (ISO 12781 and ISO 25178; International Organization for Standardization, 2011–2012) parameters (see Table S1; for a detailed definition and categorization of ISO parameters).

2.1 | Statistical analyses

Analyses followed previous procedures outlined for tooth surface textural parameters (Francisco et al., 2018; Purnell et al., 2012). All analyses were conducted using both IBM® SPSS® Statistics v. 22.0 (IBM) and Addinsoft XLSTAT 2020.5. The significance level was set to $p = 0.05$. The median of the ISO parameters was calculated for the four extracted surfaces of each specimen (Calandra et al., 2012; Schulz et al., 2010). A Shapiro–Wilk test indicated that most of the buccal enamel textural parameters (78.94%; 30 of 38 parameters) were non-normally distributed. Data were thus log-transformed [Log (1 + parameter)]. The outliers of log-transformed variables were identified according to their studentized residual values (absolute value greater than three) and removed from the final data set (Schulz et al., 2010). Because of the high number of parameters generated, the data were first explored using analysis of variance (ANOVA) combined with a Tukey HSD post-hoc test to identify significant differences between groups. A Welch's ANOVA was used when Levene's test revealed homogeneity of variance was unequal (Wilcox, 2005). Finally, a linear stepwise discriminant function analysis (LDA) was performed on the texture parameters that were found to differ significantly between groups.

2.2 | Results

Twenty-nine buccal enamel microtextural parameters out of the 38 original (76.31%) showed significant differences (ANOVA; $p < 0.05$) among the analyzed Cercopithecoidea species (Table 2; see Table S2 for descriptive statistics of the parameters). The non-

TABLE 1 African Cercopithecoidea sample and dietary information

Species	*N*	Origin	Habitat	Dietary category[a]	Museum[b]
Colobus polykomos	11	Liberia	Forest	Folivore-seed eater	IMAZ
Mandrillus sphinx	7	Cameroon and Gabon	Forest	Folivore-Frugivore-seed eater	IMAZ
Chlorocebus aethiops	15	Kenya	Savanna-woodland	Oportunistic omnivore	NMK
Papio anubis	25	Kenya	Savanna	Oportunistic omnivore	NMK
Cercocebus atys	13	Cameroon, Congo and Liberia	Forest	Hard object feeder	RMCA, IMAZ
Chlorocebus pygerithrus	11	Tanzania	Savanna-woodland	Oportunistic omnivore	NMK
Theropithecus gelada	16	Ethiopia	Grasslands-highland plateaus	Grass eater	FMNH, MNHN

[a] Dietary information based on feeding preferences (see Material and Methods section).

[b] Museum abbreviation corresponds to University of Zurich (IMAZ), Zurich; National Museum of Kenya (NMK), N; Royal Museum for Central Africa (RMCA), Brussels; Field Museum of Natural History (FMNH), Chicago; Muséum National d'Histoire Naturelle (MNHN), Paris.

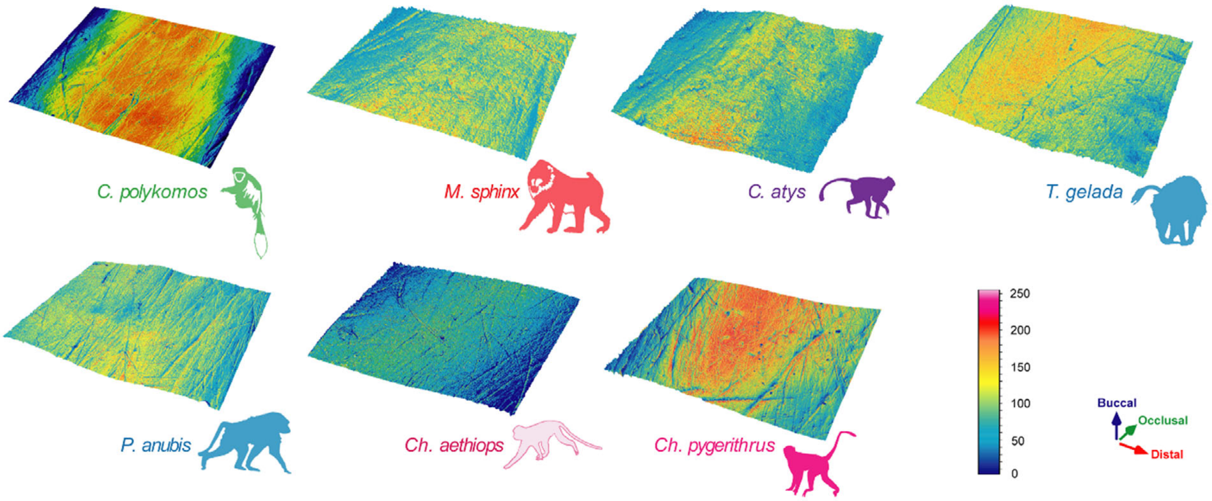

FIGURE 1 Digital elevation models (650 x 500 μm) of M_2s buccal enamel surfaces showing microwear textures in Cercopithecoidae species (color gradient depicts topographic scale in micrometers)

significant parameters (23.68%; 9 out of 38) were therefore discarded. Tukey's HSD procedure indicated that 24 surface texture parameters (82.75% of the remaining 29 parameters) differed significantly among species (Table 3). The greatest pairwise differences were found for *Papio anubis* and *Theropithecus gelada*, which differed significantly from *Mandrillus sphinx* for 19 and 14 surface texture parameters, respectively (most corresponded to height and volume parameters). Fewer pairwise significant differences (Tukey HSD; $p < 0.05$) were found for other species comparisons (1 to 4 parameters in range) and only related to area (*Sha*), density (*Sal* and *Spd*), and material ratio (*Smr1* and *Smr2*) surface texture categories (Table 3).

The stepwise LDA, including the 24 textural parameters that showed post hoc significant differences, yielded five significant parameters to better discriminate among groups (*Spd*, *Smr2*, *Sdv*, *FLTq*, *Sal*). The LDA revealed highly significant between-species differences according to dietary-related textural parameters (Wilks' $\lambda = 0.240$; $F = 4.991$; $p < 0.001$). The two first discriminant functions (DF1-2) accounted for 82.27% of total variance. Overall, 54.08% of teeth were correctly assigned (post-hoc correct classification). DF1 (58.2% of variance; eigenvalue 1.097) significantly differentiated between species (ANOVA: $F = 15.83$; $p < 0.001$). The area material ratio, indicative of surface roughness (*Smr2*: $r = 0.725$; $p < 0.001$) and peak density (*Spd*: $r = 0.308$, $p = 0.002$) and the autocorrelation length (*Sal*: $r = 0.221$; $p = 0.028$), were among the textural categories loading most heavily on the DF1 axis (Figure 2). Pairwise comparisons (Tukey's HSD for DF1) revealed that the enamel textural patterns of savanna-dwellers *P. anubis* and *Chlorocebus* species resembled each other, however, they displayed more significant differences than *T. gelada*, *C. atys*, *M. sphinx* and *C. polykomos* (Tukey's HSD for DF1; $p < 0.001$).

DF2 accounted for 24.1% of total variance (eigenvalue of 0.454), also capturing species-specific microtextural trends (ANOVA: $F = 8.86$; $p < 0.001$). DF2 was positively correlated with *Spd* ($r = 0.804$; $p < 0.001$), and *Sal* ($r = -0.900$; $p < 0.001$), *FLTq* ($r = -0.423$; $p < 0.001$), and *Sdv* ($r = -0.216$; $p = 0.032$) showed significant negative loadings. Pairwise differences (Tukey's HSD for DF2;

TABLE 2 Results of ANOVA comparing texture parameters between species

				ANOVA[a]	
Category	Parameter	Levene	p	F	p
Area	*Sda*	1.138	0.347	2.564	**0.024**
Area	*Sha*	0.949	0.464	4.379	**0.001**
Density	*Sal*	3.752	**0.002**	10.198	**0.000**
Density	*Spd*	2.573	**0.024**	3.828	**0.005**
Direction	*Str*	1.549	0.171	2.499	**0.028**
Direction	*Std*	2.142	0.056	0.678	0.668
Height	*S10z*	1.126	0.354	2.151	0.073
Height	*S5p*	1.203	0.312	3.651	**0.007**
Height	*S5v*	0.783	0.585	1.640	0.167
Height	*Sa*	1.239	0.294	2.588	**0.036**
Height	*Sku*	1.089	0.375	0.722	0.633
Height	*Sp*	0.779	0.589	3.235	**0.013**
Height	*Sq*	1.057	0.394	2.776	**0.027**
Height	*Ssk*	0.555	0.765	3.086	**0.017**
Height	*Sv*	1.005	0.427	2.537	**0.039**
Height	*Sxp*	0.809	0.566	3.173	**0.014**
Height	*Sz*	0.801	0.572	2.801	**0.026**
Height	*FLTt*	1.456	0.202	4.134	**0.003**
Height	*FLTp*	1.403	0.222	4.490	**0.002**
Height	*FLTv*	1.595	0.157	4.599	**0.002**
Height	*FLTq*	2.363	**0.036**	3.921	**0.005**
Hybrid	*Sdq*	1.686	0.133	1.970	0.099
Hybrid	*Sdr*	1.771	0.114	2.001	0.094
Peak sharpness	*Spc*	1.795	0.109	2.146	0.074
Plateau size	*Smc*	1.184	0.322	2.865	**0.023**
Material ratio	*Sk*	2.074	0.064	3.170	**0.014**
Material ratio	*Spk*	1.631	0.147	2.641	**0.034**
Material ratio	*Svk*	0.561	0.760	1.578	0.185
Material ratio	*Smr1*	1.833	0.101	3.099	**0.008**
Material ratio	*Smr2*	0.109	0.995	6.840	**0.000**
Volume	*Sdv*	0.574	0.750	2.570	**0.024**
Volume	*Shv*	0.397	0.879	1.947	0.082
Volume	*Vm*	0.883	0.511	2.820	**0.025**
Volume	*Vmc*	1.350	0.243	2.599	**0.036**
Volume	*Vmp*	0.883	0.511	2.820	**0.025**
Volume	*Vv*	1.155	0.338	2.893	**0.022**
Volume	*Vvc*	1.351	0.243	2.840	**0.024**
Volume	*Vvv*	0.981	0.443	2.674	**0.031**

Note: Significant differences at $p < 0.05$ in bold type.

[a] Welch ANOVA for parameters with unequal variances (Levene test).

$p < 0.05$) demonstrated that the negative values along DF2 for *C. polykomos* (lowest *Spd* and greatest *Sal* values) significantly differed from *Ch. aethiops*, *C. atys*, *P. anubis*, and *T. gelada*, showing a clear microtextural-dietary spectrum which extended from those species with less coarse features on buccal surfaces to high density of peaks. *T. gelada* had the lowest wavelength (*Sal*) and surface flatness (*FLTq*) values, and also presented a significantly different textural pattern compared with *M. sphinx* and *P. anubis* (Tukey's HSD for DF2; $p < 0.05$).

TABLE 3 Significant pairwise differences (Tukey HSD) on the textural parameters between species.

Paired comparisons (species)		Percentage[a]	Significant parameters[b]
Ch. aethiops	*Ch. pygerithrus*	3.4	*Sal*
	C. polykomos	3.4	*Sal*
	C. atys	3.4	*Smr2*
	T. gelada	3.4	*Smr2*
Ch. pygerithrus	*M. sphinx*	3.4	*Smr2*
	C. polykomos	10.3	*Sal, Smr1, Smr2*
	C. atys	6.8	*Spd, Smr2*
	T. gelada	6.8	*Spd, Smr2*
P. anubis	*T. gelada*	6.8	*Spd, Sha*
	C. atys	10.3	*Spd, Sha, Smr2*
C. polykomos	*P. anubis*	6.8	*Sal, Smr1*
	T. gelada	10.3	*Sal, Spd, Sha*
	C. atys	13.8	*Sal, Spd, Sha, Smr1*
M. sphinx	*C. atys*	3.4	*Spd*
	P. anubis	65.5	*Sq, Sp, Sv, Sz, Sa, Smc, Sxp, Vm, Vv, Vmp, Vmc, Vvc, Vvv, S5p, Sdv, FLTt, FLTp, FLTv, FLTq*
	T. gelada	48.2	*Sq, Sp, Sa, Smc, Sxp, Sal, Vv, Vmc, Vvc, Spd, FLTt, FLTp, FLTv, FLTq*

[a] Percentage of textural parameters denote differences between species after pairwise testing (Tukey HSD) at $p < 0.05$.
[b] Pairwise tallies include 29 parameters that exhibited significant ANOVAs differences (see Table 2).

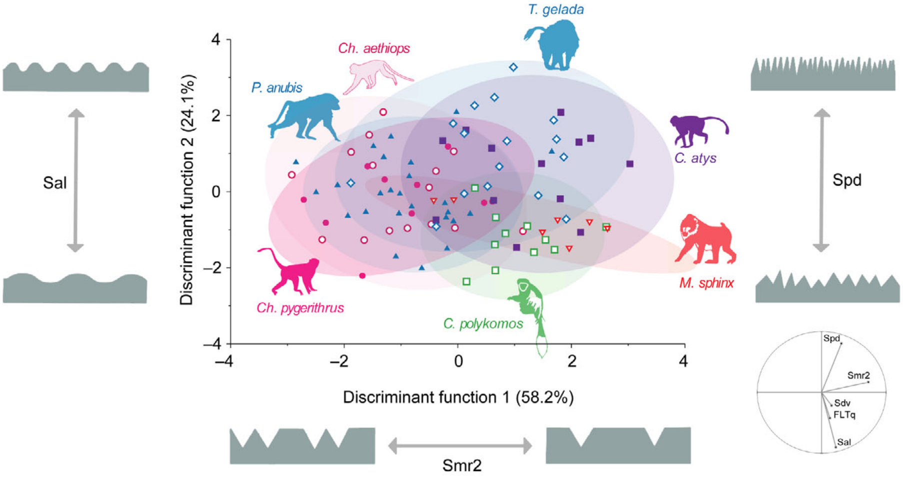

FIGURE 2 Plot of the two first discriminant functions (DF1-2) of buccal-dental textural parameters. Ellipses show 95% confidence limits for each species. The labeled rays show the loadings of the ISO texture parameters onto DFs. Schematic models for texture parameters (*Smr2*, *Spd*, *Sal*) displaying significant higher correlations (Pearson's *r*) between species

3 | DISCUSSION

Analyses of ISO standardized enamel surface roughness and flatness parameters revealed microwear varied between African Cercopithecoidea primates with different diets. Overall, the results showed that higher values of area material ratio (*Smr2*) were observed in species with higher dietary abrasive potential (*C. atys* and *M. sphinx*) derived from ingesting hard items and that savanna-dwellers, adapted to a more opportunistic diet (*Chlorocebus* and *Papio*) demonstrated the lowest values. Density textural parameters (*Spd* and *Sal*) were inversely related. Grass and hard-object specialist (*C. atys* and *T. gelada*) had a higher density of thin peaks (greater *Spd* values), and less coarse and deeper enamel surface textures (lower *Sal* and *Sdv* values) than *M. sphinx* and *C. polykomos*, a leaf-eater with a small contribution from fruits and seeds.

The discriminant function analysis revealed significant differences in ISO roughness parameters. *C. atys* and *T. gelada*, with diets based on processing hard exocarp and high proportions of phytoliths respectively, showed the highest density of sharp peaks (*Spd*) and valley material portion (*Smr2*) compared with the rest of the species. Their surfaces are therefore characterized by a great relief with high and deep features. Previous analysis of occlusal microtexture with ISO parameters (Calandra et al., 2012) reported similar results grouping *T. gelada* with hard-object feeders, according to their high frequency of peaks. *C. atys* is a hard fruit eater that consumes fruits with hard exocarp all year-round, and the high density of peaks could be correlated with the high scratch density pattern previously described (Estebaranz et al., 2012). The autocorrelation length (*Sal*) parameter provides a numerical index of the density of similar structures in units of length. Accordingly, *T. gelada* showed the lowest *Sal* values, characterized by sharper and thinner features compared with *C. polykomos* and *M. sphinx*. Although the *T. gelada* diet is described as mainly graminivorous, recent studies in relatively undisturbed habitats revealed a more diverse diet than expected, incorporating large quantities of forbs (Fashing et al., 2014; Souron, 2018), with considerable seasonal variations, although gelada's diet might not include seeds such as *Mandrillus* and *Colobus*. *C. polykomos*, with a diet based on leaves, seeds, and soft fruits, exhibited a buccal roughness characterized by slightly flatter features, lower peaks and less thinness (moderate *FLTq* and high *Sal* values).

Mandrillus sphinx showed the largest number of significant differences in the ISO parameters compared with the rest of analyzed species, especially with *T. gelada* and *P. anubis*. The buccal microtexture signatures of *M. sphinx* were quite characteristic and different from the rest of the African Cercopithecoidea species. *M. sphinx* was characterized by a surface with more coarse flat features (high *Sal* values and *FLT*) along with *C. polykomos*, however, *M. sphinx* features were higher (had increased height parameters) and deeper, with dale regions (high *Sdv*), than *C. polykomos*. *Mandrillus* mostly feeds on mechanically protected plant foods, such as hard-shell fruits, similar to *C. atys*. *Mandrillus* also relies on seeds, and this feeding behavior could explain the differences in *Spd* between both species and the similarity with *C. polykomos* which also consumes seeds. The occlusal microtexture pattern of *M. sphinx* has been characterized by a low complexity, however, which might be affected by abrasive particles that could smooth occlusal relief through hard rubbing (Percher et al., 2018). This "rubbing effect" contrasts with the microtexture pattern with high relief found in the present study, and resembles the high number of buccal-enamel scratches previously observed (Martínez et al., 2016, 2020) suggesting specific mechanisms of microwear formation on occlusal and buccal surfaces.

Papio showed differences in *Sha* (closed hill area) compared with *Theropithecus* and *Cercocebus* and a valley material proportion (*Smr2*) lower than *Cercocebus* and *Mandrillus*. *Papio* inhabit dry open environments, where they feed on the ground. Grit and dust may therefore play a role in smoothing the surface while the food is processed in the oral cavity, reducing the dales. It is worth noting that the species which inhabit savanna ecosystems, *Papio* and *Chlorocebus*, had similar buccal surfaces with flatter texture reliefs (low values in *Smr2* and *Sdv*). Previous results based on buccal microwear patterns shown that *Papio* has less density of scratches than *Mandrillus* and *Cercocebus* (Estebaranz et al., 2012), suggesting a close relationship with the lower volume values and flatter texture reliefs observed. Similar results were described for the microtexture of the buccal surfaces of *P. anubis*, characterized by low total fill volume (*Tfv*) and relatively shallow scratches (Aliaga-Martínez et al., 2017), and those described on occlusal surfaces for *Papio* and hard fruit eater species (Calandra et al., 2012). Finally, the three species that inhabited savanna ecosystems (*Papio* and *Chlorocebus*) shared a similar microtexture buccal pattern, with fewer differences between them than with the rest of analyzed species.

In summary, 3D ISO roughness parameters discriminate between African Cercopithecoidea primates of different diets. Hard food eaters have molar buccal surfaces with more microscopic relief. Graminivorous *T. gelada* have microwear features with less volume but with a high density of sharp peaks and thin features. The discrimination of buccal microtexture patterns and their relationship with dietary regimes in extant species indicates that the buccal microtexture pattern with ISO parameters can distinguish among diets and can be applied to the interpretation of extinct species.

AUTHOR CONTRIBUTIONS

Laura M. Martínez: Conceptualization (equal); investigation (lead); methodology (equal); resources (equal); supervision (lead); writing – original draft (lead); writing – review and editing (equal). **Ferran Estebaranz-Sánchez:** Conceptualization (equal); data curation (equal); formal analysis (equal); investigation (lead); methodology (equal); resources (equal); writing – original draft (equal); writing – review and editing (equal). **Alejandro Romero:** Conceptualization (equal); investigation (equal); methodology (equal); writing – original draft (equal); writing – review and editing (equal). **Juan José Ibáñez:** Funding acquisition (equal); software (lead). **Yasmina Avià:** Formal analysis (equal); writing – review and editing (equal). **Luis Hidalgo-Trujillo:** Formal analysis (equal); writing – review and editing (equal). **Alejandro Pérez-Pérez:** Conceptualization (equal); funding acquisition (equal); project administration (equal); resources (equal); writing – review and editing (equal).

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CONFLICT OF INTEREST

The authors declare that there are no conflicts of interest.

DATA AVAILABILITY STATEMENT

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

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