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Further away with dental microwear analysis: food resource partitioning among Plio-Pleistocene monkeys from the Shungura Formation, Ethiopia.

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Abstract

This study aims at improving dietary discrimination among primates through a new analytic approach of dental microwear texture analysis integrating a surface sampling on facets of both phase I and II of mastication. The surface sampling is applied on these two types of molar facets on 104 specimens belonging to four extant cercopithecids, and on 207 Plio-Pleistocene specimens representing four taxa from the Shungura Formation, Ethiopia. The extant species, including *Colobus guereza*, *Theropithecus gelada*, *Papio hamadryas*, *Chlorocebus aethiops*, compose a model covering a wide range of feeding ecology from leaf-eating through grass-eating habits to opportunistic habits.

A principal component analysis built with a selection of the most discriminant variables and extant species as a model displays that the two facets contribute equally to the dispersion of individuals and to the between-species differences. Also, most contributing variables along the components are not central values of texture parameters (mean and median of the parameters measured on subsurfaces or a single value for the whole surface) but rather statistics of their dispersion (percentiles) and distribution (kurtosis, skewness).

Once the fossil specimens are inserted into the extant species model, the two large-bodied colobines, *Paracolobus* and *Rhinocolobus*, are found to differ from the extant *Colobus guereza*, one of the most leaf-eating colobines. This highlights ecological diversity among early African colobines. Besides, the analysis tracks between-genus as well as temporal differences between the extinct species of papionins, attesting of a low ecological overlapping between *Theropithecus* and non-theropith papionins, notably after 2.4 Ma. No significant difference was found between *T. brumpti*, *T. oswaldi*, *Theropithecus* sp. supporting similar feeding habits with the present-day gelada, at least from 2.9 Ma onwards.

Key words: Cercopithecoid, Teeth, Diet, Fossil, Colobines, Papionins, Africa

1. Introduction

Investigating diet is essential, not only to understand how extinct species have shared environmental resources (e.g., Schreier et al., 2009), but also to understand the underlying mechanisms that drove the natural selection of dental phenotypes (Kelley and Swanson, 2008). Among other dietary proxies, such as tooth and masticatory apparatus morphology or stable isotope geochemistry (see the synthetic review Davis and Pineda Munoz, 2016 and citations therein), dental microwear has proven to be an efficient tool in discriminating differences in dietary habits of toothed vertebrates, most notably mammals (Purnell et al., 2007; Calandra and Merceron, 2016; DeSantis, 2016). Although one could argue that exogenous soil mineral particles contribute because they are harder than enamel tissues (Sanson et al., 2007; Lucas et al., 2013; Madden, 2014; Hoffman et al., 2015; Schulz-Kornas et al., 2019), the controlled feeding experiments performed on different species of mammals (Merceron et al., 2016; Ramdarshan et al., 2016; Winkler et al., 2019a, 2019b; Ackermans et al., 2020; Martin et al., 2020; Schulz-Kornas et al., 2020; see also Rodriguez-Rojas et al., 2020) attest that differences in dental microwear texture are mostly driven by differences in diet.

In addition to its higher inter- and intra-observer repeatability, Dental Microwear Texture Analysis (DMTA hereafter) differs from former methods based on 2D analysis in its way of describing the surface. While earlier works classified microwear scars as pits and scratches based on the ratio “length versus width” (Gordon, 1982; Teaford and Walker, 1984; Ungar, 1996; Solounias and Semprebon, 2002; Merceron et al., 2005; Rivals et al., 2015), the dental microwear texture describes the whole surface using Scale Sensitive Fractal Analysis (SSFA; Ungar et al., 2003; Scott et al., 2006) or a set of international standard surface parameters (Purnell et al., 2012; Calandra

et al., 2016; Kaiser et al., 2016). Also, while earlier works (e.g., Solounias and Semprebon, 2002; Merceron et al., 2005) measured the frequencies of specific microwear scars such as large pits, wide scratches as indicators of the consumption of food items hard or tough enough to deeply abrade enamel in different ways, DMTA does not specifically target these isolated scars. One could then claim that DMTA somehow minimizes the potential contribution of these features to dietary discriminations (but see DeSantis et al., 2013). So, using SSFA, a surface finely scratched might have a value similar to that of a polished surface with few scratches (Figures S1a and S1b). Besides, different dental facets with or without few large pits may have similar values in complexity (see Figures S1c and S1d). The only parameter issued from SSFA which explores variations over the surface is the heterogeneity of complexity on a mesh of $n \times n$ cells (Scott et al., 2006). Finally, with some exceptions (Gordon, 1982; Teaford and Walker, 1984; Grine, 1986; King et al., 1999; Merceron et al., 2005; Krueger et al., 2008; Schulz-Kornas et al., 2019; Stuhlträger et al., 2019), most dental microwear analyses on primates were done on phase II molar facets; those facets contributing to the crushing and grinding of the foods during mastication. The dental microwear textures on phase II facets are assumed to better discriminate dietary categories than tooth wear on molar shearing facets, which act during the phase I (King et al., 1999; Krueger et al., 2008). However, phase I molar facets contribute to the comminution by shearing food with slicing movements of homologous facets from upper and lower cheek teeth. Although their dental microwear texture differs from that of phase II molar facets, one may still expect variations in dental microwear textures on phase I molar facets depending on food properties.

We hypothesize that a surface sampling strategy aiming to combine data for multiple texture parameters across

phase I and phase II facets will strengthen the power of DMTA. This sampling strategy may allow the discrimination of species not by the central values of a given parameter, but by the shape of distribution across multiple facets. Using such approaches, we expect a better dietary discrimination. For instance, SSFA and notably the combination of the texture

complexity and anisotropy (Asfc and epLsar) fail to significantly discriminate the arboreal leaf-eating mantled guereza (*Colobus guereza*) from the grass-eating ground-dwelling Ethiopian gelada (*Theropithecus gelada*; Figure S1; Scott et al., 2012), whereas a more thorough surface sampling strategy might be able to do so.

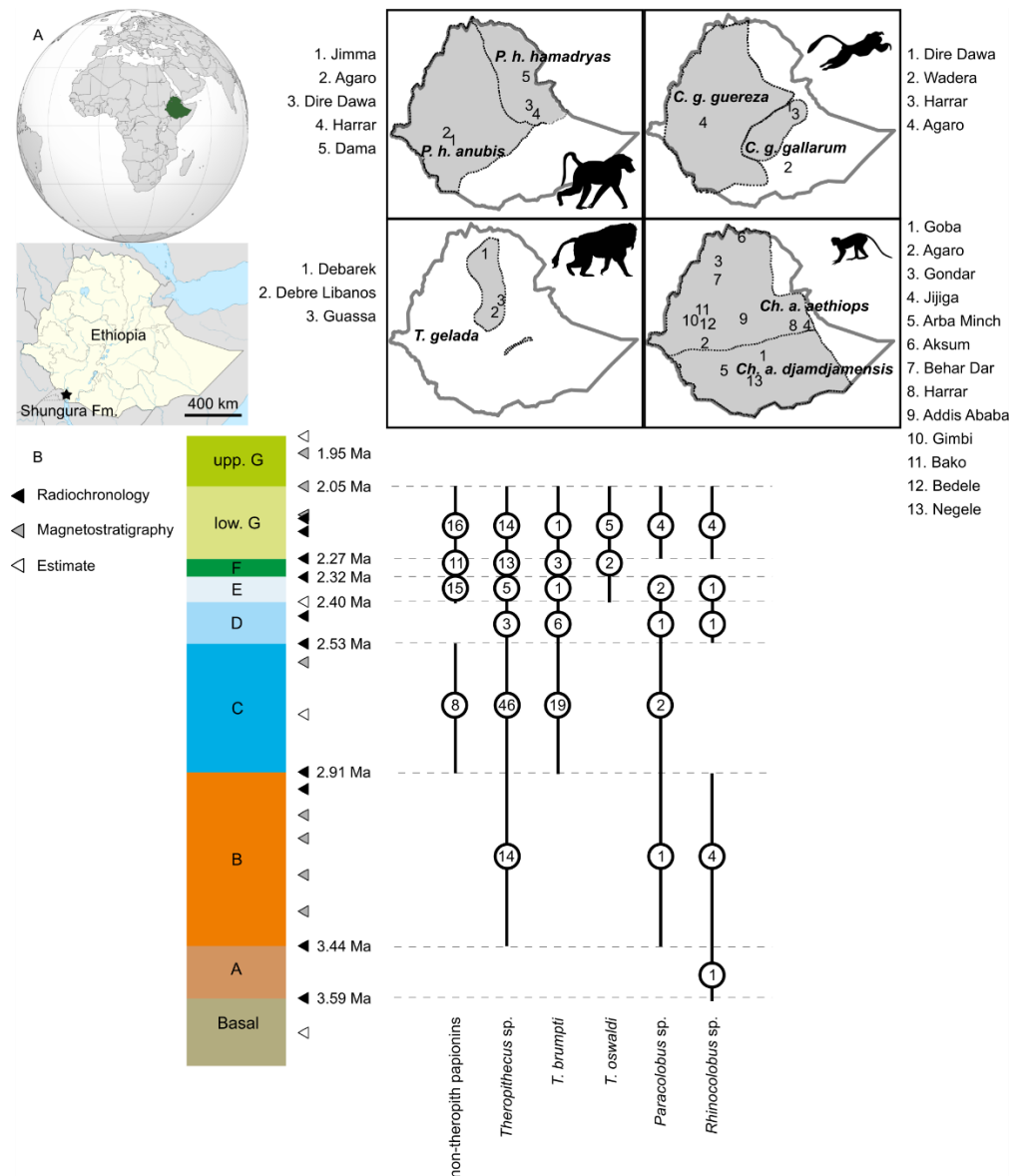


Figure 1. Geographic origin of wild caught specimens and geographic distribution of extant species used as model and location of the Shungura Formation (A) and chronostratigraphic distribution of analysed samples of fossil specimens (number given in the circles) and extinct species (B) within the geological Plio-Pleistocene members (with dating point symbolized as triangles, Member A to Member lower-G) of the Shungura Formation along the Omo Valley River, southern Ethiopia. Geographic distribution of extant species are issued from IUCN map (<https://www.iucnredlist.org/>), Butynski *et al.* (2013), Haus *et al.* (2013), Lauck *et al.* (2013), Fashing *et al.* (2014), Abu *et al.* (2017), and Fischer *et al.* (2017). It is worth noting that some specimens, notably *C. guereza* have been sampled near Wadera (in the late 60' and early 70's) out of the geographic distribution shown in the map. One specimen belonging to the extinct genus *Paracolobus* and three to *Rhinocolobus* considered in the present study, having no precise stratigraphic assignation, are not listed here (but in SI Appendices).

To test the hypothesis mentioned above, we apply our procedure to a dataset of four extant species of Cercopithecidae, all coming from Ethiopia: *Colobus guereza*, *Theropithecus gelada*, *Papio hamadryas*, and *Chlorocebus aethiops* (Figure 1). These species have different feeding preferences. *Theropithecus gelada* is a terrestrial papionin that lives only in the Ethiopian Highlands and feeds mostly on the herbaceous layer, including both monocots and dicots (Iwamoto, 1993; Fashing et al., 2014; Abu et al., 2017; Jarvey et al., 2018; Souron, 2018). *Papio hamadryas* ssp. is a semi-terrestrial omnivorous papionin (Nagel, 1973; Dunbar and Dunbar, 1974; Norton et al., 1987; Kamilar, 2006; Okecha and Newton-Fisher, 2006; Swedell et al., 2008). Although their extinct relatives have evolved in sympatry, and thus in competition for food resources with early hominins, extant baboons and geladas have been intriguingly assumed to be also appropriate for modelling early hominin ecology (Swedell et al., 2008; Fashing et al., 2014; Macho, 2014; Wood and Schroer, 2012). *Chlorocebus aethiops* is a semi-terrestrial cercopithecine and has opportunistic feeding habits (Hall, 1965; Struhsaker, 1967). Lastly, *Colobus guereza* is an arboreal colobine feeding mostly on fresh and mature leaves along with few fruits as a third dietary source during wet seasons. The genus *Colobus* actually contains the most leaf-eating species of colobine monkeys (Rose, 1978; Ibrahim et al., 2017; Shumet and Yihune, 2017). Keeping in mind that seasonal variations in dietary composition (Dasilva, 1994; Fashing et al., 2014; Jarvey et al., 2018; Oelze et al., 2014; Swedell et al., 2008; Wrangham et al., 1998) and in subsequent dental microwear textures may blur the signal, we assume that the ecological disparity of this assemblage of four extant species would reflect a maximum range of dental microwear textures on phase II and phase I molar facets. Indeed, two of these species (*T. gelada* and *C. guereza*) are

highly specialized towards two contrasting types of folivory and the two other species (*P. hamadryas* and *Ch. aethiops*) share opportunistic feeding habits and may be confronted, depending on season and location, to a wider range of mechanical challenges, from the large and fibrous fruits of doum palm to the small and hard seeds of acacia trees (Wrangham and Waterman, 1981; Whitten, 1983; Swedell et al., 2008; Schreier et al., 2009). *Papio hamadryas* can also fall back on hard and tough underground storage organs (Dominy et al., 2008). In contrast, *Ch. aethiops* avoids hard foods with the exception of *Acacia* seeds (Wrangham and Waterman, 1981). This extant monkey model is likely to assess niche partitioning among Plio-Pleistocene cercopithecoid monkeys (*Rhinocolobus*, *Paracolobus*, *Theropithecus*, and non-theropith papionins) from the Shungura Formation, Ethiopia (Figure 1). A previous dental microwear texture analysis has found variations in food resources for the extinct *Theropithecus* from the Shungura Formation (Martin et al., 2018), but failed to see significant chronological variations among the sample of extinct non-theropith papionins. We propose here to re-investigate the cercopithecids from the Shungura Formation by inserting their dental microwear textures into the model based on extant Ethiopian monkeys as a mean to assess niche overlapping between extinct taxa.

2. Material and methods

2.1. Material

The model is built from 104 wild-shot individuals belonging to four extant species. All specimens of *Colobus guereza* and *Chlorocebus aethiops* and most of *Papio hamadryas* and *Theropithecus gelada* are stored at the Muséum National d'Histoire Naturelle, Paris, France. When known, dates of sampling are reported in the supplementary information (SI). It is worth noting that most of the specimens from the Muséum National d'Histoire Naturelle, Paris, France were collected in

late nineteen-sixties and early nineteen-seventies during several field and sampling missions headed by the museum. The other specimens of *P. hamadryas* and *T. gelada* (except two) are stored at the Authority for Research and Conservation of Cultural Heritage in Addis Ababa, Ethiopia. The last two specimens of extant gelada are stored at the Musée des Confluences, Lyon, France.

The sample of *Colobus guereza* is composed of 19 individuals. Most specimens belong to three main populations. A few isolated specimens complete the sample of *Colobus guereza*. The sample of *Papio hamadryas* is composed of 27 individuals. Most of them are from two main lots, along with untracked individuals from different localities and times. Regarding this sample, there is also heterogeneity in terms of taxonomic assignment: six specimens are assigned to the subspecies *P. hamadryas hamadryas*, four to the subspecies *P. hamadryas anubis*. The other specimens were not identified at the subspecific level. However, their skull morphology suggests that these specimens should be assigned to the latter subspecies. The sample of extant gelada, *Theropithecus gelada*, is formed of two sampled localities from Debarq and Debre Libanos, and some isolated specimens leading to 21 individuals. The sample of *Chlorocebus aethiops* is composed of three lots leading to a total of 37 individuals. The taxonomic status is heterogeneous as *Chlorocebus aethiops* is composed of several subspecies. Details are given in the supplementary information. In the present study, we consider these species at the specific level assuming that the subspecies share similar feeding ecology.

All the fossil specimens considered in this study were collected by the International Omo Research Expedition (IORE, 1967–1976) and the Omo Group Research Expedition (OGRE, since 2006) in the Shungura Formation, Lower Omo

Valley, Ethiopia (Boisserie et al., 2008 and citations therein). They were all gathered between Member B and the lower part of Member G (stratigraphic units 1–13), covering a time span ranging from 3.44 Ma to 2.05 Ma (Fig. 1B). More than 2,500 dental remains of Shungura cercopithecids attributed with certainty to the genus *Theropithecus* and 173 attributed to the genus *Papio* are stored at the Authority for Research and Conservation of Cultural Heritage in Addis Ababa. Among these specimens, only 132 molars of *Theropithecus* and 50 of *Papio* were selected for this study due to an important number of specimens with post-mortem damages (see Teaford et al., 2008). Most of these teeth with badly preserved enamel surfaces were discarded either by naked eyes or using a $\times 10$ magnifying glass. Then, a second selection was made after surface scanning. Indeed, many specimens among the 500 dental replicas attributed to the papionins show dental microwear textures with apparent post-mortem alteration. Absence of scratches combined with a homogeneous texture all over the scan with little variation in scar dimensions, and especially the absence of differences between phase I and phase II molar facets help to identify altered specimens (see figure 2 in Martin et al., 2018). Following the same procedure, only 11 and 14 molars of the two large-bodied colobines, *Paracolobus* and *Rhinocolobus* respectively, were considered to still represent diet-related surface wear among 98 molars assigned to one of the two large colobines. Because of the scarce number of colobines distributed across different geologic members (see Figure 1), and taking into account that dental microwear texture bears a short-term ecological information (Teaford and Oyen, 1989; Teaford et al., 2017; Winkler et al., 2020), we decided not to explore variations through time for these two colobines.

Among the papionins recovered in the Shungura Formation, the species *Papio quadratiostris* has been identified from

Member D to the lower part of Member G (Frost, 2001). However, Frost (2001) suggested that the genus *Papio* is present from Member A to Member L as Eck (1976) had already suggested (see also Gilbert et al., 2018). Besides, several specimens composed of dental remains were assigned to the genus *Soromandrillus* by Gilbert (2013), which are not included in the present analysis. However, other African papionins such as *Parapapio* are present in the Turkana basin, and more generally in East Africa. So, we here made the choice to use the term “non-theropithecine papionins” (Elton and Dunn, 2020) instead of the genus name *Papio* as there is no guarantee that all of the specimens belong to the very same genus. Two species of *Theropithecus* are represented: *T. brumpti* (n = 30) and *T. oswaldi* (n = 7). Due to small sample sizes for some species when focusing at the Member scale, the supra-specific level was preferred to assess chronological variations among papionins.

2.2. Methods

Upper and lower second molars M2 composed most of the sample of extant species. The fossil sample is composed of upper and lower molars (M1 to M3) with priority given to M2. M1 and M3 completed the sample if the M2 was either dirty, too worn or not worn enough. Ramdarshan et al. (2017) found no significant variation from M1 to M3 when focusing on the same molar facet once molars are functional (i.e. showing wear facets).

After standard molding procedures (see details in Merceron et al., 2016; Martin et al., 2018), two scans per tooth were done: one on each of the molar facet types (phase I shearing and phase II crushing facets, scans are shown in SI). Scans were produced using “TRIDENT”, the Leica DCM8 white light confocal profilometer housed at the PALEVOPRIM lab (CNRS and University of Poitiers; Numerical aperture: 0.90; working

distance: 0.9 mm; Leica Microsystems), and pre-treated under LeicaMap v. 8.0 (Leica Microsystems; Mountain technology; see Figures 2 and 3; Merceron et al., 2016 for details). Following Maier (1977), molar facets #9, #10, #11, #12 and #13 contribute to the crushing and grinding of food items during the phase II and molar facets #1, #2, #3, #4, #5, #6, #7, and #8 to the shearing of food items during the phase I of the mastication (see also Percher et al., 2018; Schultz et al., 2018). Scans were done directly on silicone molds without making replicas. To avoid difficulties in scanning facets with sharp slopes, dental facets were individually cut and manually positioned horizontally under the objective lens. Scans for both extant and extinct specimens are shown as photosimulations and false color elevation maps in SI.

The surfaces ($200 \times 200 \mu\text{m} - 1551 \times 1551$ pixels) thus obtained were subjected to a numeric treatment to automatically extract surface parameters for all surfaces and subsurfaces at once, using a Python routine (Jupyter 5.7.8) developed by Francisco et al. (2018b; see Figure 4). In complement of gathering a single value per parameter and per surface, this procedure generates x subsurfaces per scan and thus x values for each parameter. From these x values, different statistics are produced: median, mean, skewness, kurtosis, standard deviation, values at the first and last quartiles, mean of the values above and below the first and last quartiles (Table S2; Francisco et al., 2018a, 2018b). In order to enhance the finest scale roughness (Francisco et al., 2018b), the 8th-order least square polynomial (PS8) surface is extracted from the raw surface. It is considered that the geometry of a dental facet surface is nearly a second order polynomial. Thus the relief due to wear is better visualized on a surface from which its polynomial surface PS2 has been subtracted. However, the surface may have spalls with superimposed scratches. This is why a higher order polynomial PS8 should also be subtracted. Francisco et al. (2018a,

2018b) have found that an 8th order is the most efficient to discriminate diets. Simulations have yielded efficient results with 256 [256 × 256 pixel] sampling, meaning that for each scanned surface the analysis generates 257 values per parameter: one is issued from the analysis of the whole surface and the 256 others from the 256 subsurfaces.

Sixteen surface parameters quantifying height, spatial and topologic (combining both spatial and height) information are here considered (Table S1). They are either ISO 25178 (*Sa*, *Sp*, *Sq*, *Sv*, *Ssk* and *Sku*) or ISO 25178-based (*Sdar* = *Sdr* - 1, *Stri* = 1/*Str* and *Sal* together with *Stri* are averaged on three heights $r_s = 0.3, 0.4, 0.5$) or self-defined parameters (*Sm*, *Smd*, *Sh*, *b.sl*, *s.sl*, *r.sl*, and *Rmax*, the latter being averaged on three heights $r_s = 0.3, 0.4, 0.5$; see Table S1; Francisco et al., 2018b). For each of these parameters, a set of ten statistics is extracted from the 256 subsurfaces batch (see above; Table S2). All these steps generate a total of 160 variables for each scan made on each of the two molar facets.

Then, for each of two types (phase I and phase II) of facets of the extant species model, a statistical routine introduced by Francisco et al. (2018b; Figure 4) is run to target which variables show discriminant variations among species. This routine starts with a Box-Cox transformation and ends with the extraction of the TOP-3 most discriminating variables. In the present study, we have implemented the last section as follows: after Fisher's LSD tests (Figure 4), each set of the discriminant variables (84 and 86 variables on phase I and phase II facets, respectively; Table S3) is ordered by decreasing number of significant differences (up to six per variable because of four groups of extant species of primates) among extant species (see Figure 4, box 1), and the mean of significant *p*-values of each variable (Figure 4, boxes 2 and 3). The first

variables (meaning with the lowest average *p*-values) of each of the two sets of phase I and the phase II molar facets are picked out for each parameter to compose a smaller data set (see Figure 4, box 4). Finally, 13 and 12 variables gathered, respectively, on the phase I and phase II molar facets are assumed to be the most discriminant ones for the extant monkey model (individual values for extant specimens are shown in SI appendices). Using this selection (Table S4), a principal component analysis (PCA; Figures 5 and S2) combining both phase I and phase II facets of extant individuals is produced (Figure 4, box 5). SSFA variables, complexity (*Asfc*) and anisotropy (*epLsar*) on the two facets, were used as supplementary variables because it helps readers to connect the sets of surface parameters issued from the routine with the two most popular and intuitive variables (Figure 5 and S2). Individual values of fossil monkeys (SI) are inserted into the PCA as supplementary individuals meaning that they do not contribute to the model (see Figure 4, box 6).

Two sets of analyses of variance are performed on PC coordinates to test significant differences (Table S5). First, differences between (extinct and extant) taxa are treated through a one-way anova. Then, a nested anova is specifically produced to test significant variations between the extinct papionins and among members for each of the two taxa. The nested scheme is here preferred as the sample of non-theropithecine papionins is not symmetrical to the one of *Theropithecus* (Ungar et al., 2007). PC coordinates are first Box-Cox transformed for each of the two analysis of variances to meet the assumptions of normal distribution of residuals and homoscedasticity. The combination of Tukey's test of Honestly Significant Differences (HSD) and Fisher's test of Least Significant Difference (LSD) is used to pinpoint significant differences (Table S6).

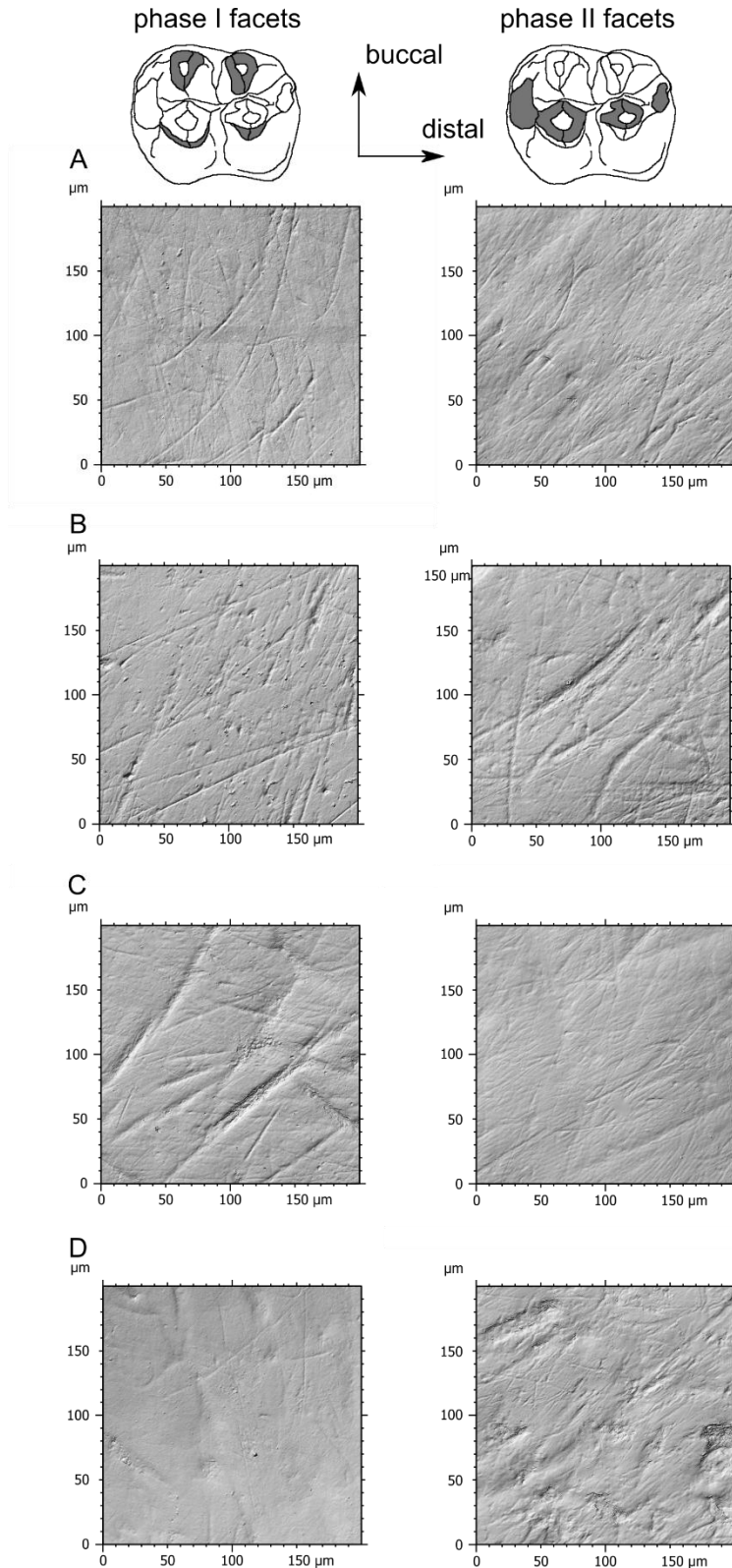


Figure 2. Photosimulations ($200 \times 200 \mu\text{m}$) generated with LeicaMap v. 8.0 of shearing (phase I) and crushing/grinding (phase II) molar facets of four specimens of extant species from Ethiopia. *Colobus guereza* MNHN 1962-1398 (A), *Papio hamadryas* MNHN 1969-444 (B), *Theropithecus gelada* MNHN 1969-449 (C), *Chlorocebus aethiops* MNHN 1972-305 (D).

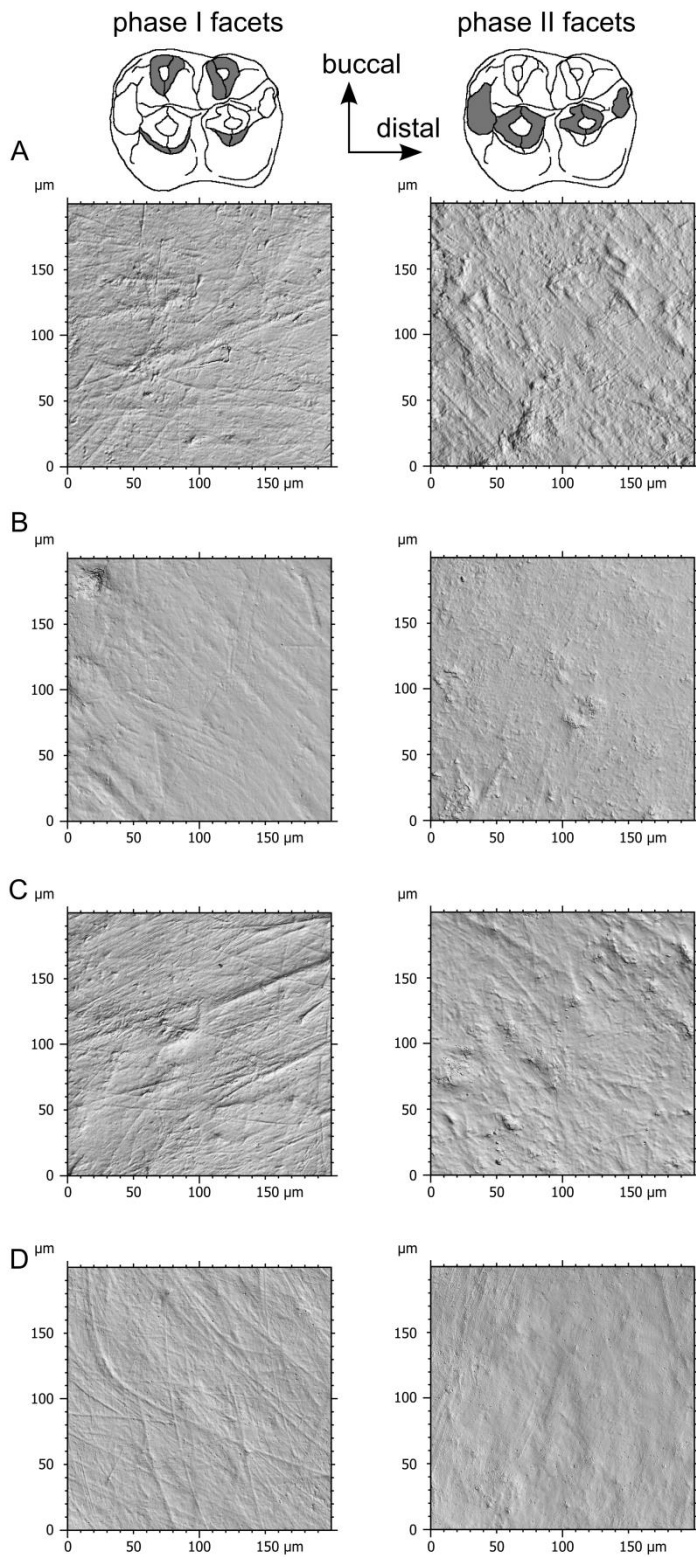


Figure 3. Photosimulations ($200 \times 200 \mu\text{m}$) generated with LeicaMap v. 8.0 of shearing (phase I) and crushing (phase II) molar facets of four specimens of extinct genera from the Shungura Formation, Ethiopia. *Paracolobus* OMO 18-1970-294 (A), *Rhinocolobus* L 668-51 (B), non-theropith papionins OMO 57/5-1972-187 (C), *Theropithecus oswaldi* OMO 75/i-1970-1000 (D).

3. Results

3.1. Subsampling surfaces, extracting parameters, and identifying discriminant variables

On the 160 variables, issued from one global value and nine statistics generated for 16 parameters extracted from 256 samples per surface, 84 and 86 are discriminant on the shearing and crushing molar facets, respectively (Figure 6; Table S4). From this dataset, 13 and 12 variables are then selected on shearing and crushing/grinding molar facets, respectively (Table S4). The central statistics and single values for the whole surface make 12 of the 25 most discriminant variables; the other 13 ones are related to either dispersion or distribution (Table S4).

3.2. PCA on the extant monkey model

The eigenvalues of the PCA show that the PC1 (34.2%) is more than twice as informative as the second PC (12.8%; Figure 5A). The present analysis shows that the most contributing variables to the variance along PC1 are equally derived from shearing and crushing molar facets (Figure 5B and C). Along PC1, *Colobus guereza* shows the lowest values and *Chlorocebus aethiops* the highest. *Theropithecus gelada* and *Papio hamadryas* plot together along PC1 (Figures 6 and S3). The central and dispersal statistics of height parameters on both crushing/grinding and shearing facets pull specimens with complex textures towards high values along PC1 (Figures 5B and C; Figure S4). By contrast, the mean of the absolute smallest height (*Sv*) on the two facets as well as statistics for the high percentage of nearly horizontal facets (*Sh*) help to pull specimens with flatter surfaces such as the ones seen on *C. guereza* towards negative values. It is worth noting that the weight of the supplementary Asfc-SSFA parameters, and notably the one on the molar shearing facets, mirrors this trend towards more complex surfaces

associated with positive values along PC1 (Figure 5B).

Although PC2 contributes more than PC3 and PC4, respectively 12.8, 10.0, and 8.4% of the total variance (Figure 5A), PC2 does not provide significant discrimination between species (Table S5). PC3 (Figures S2 and S3; Table S5) and most notably PC4 (Figures 5 and 6; Table S5) are actually more discriminant than PC2. The significant differences along PC3 and PC4 are driven by differences in spatial and topological parameters mostly on shearing facets for PC3 and on crushing ones for PC4 (Figures 5, S2 and S4; Table S5). *C. guereza* differs from *T. gelada* along PC3 notably due to the higher values in statistics derived from anisotropy-based parameters (*Stri* and *Sal*), reflecting a pattern of finer, longer and denser striations on shearing molars facets for the colobine (Figures S2-S4). Along PC4, *T. gelada* differs from *P. hamadryas* and *Ch. aethiops* notably due to differences in height distribution (*Sku* and *Ssk*) and anisotropy-based parameters (*Stri*, *Sal* and *r.sl*), reflecting a pattern of wider striations on crushing molars facets for the gelada (Figures 5, 6 and S4).

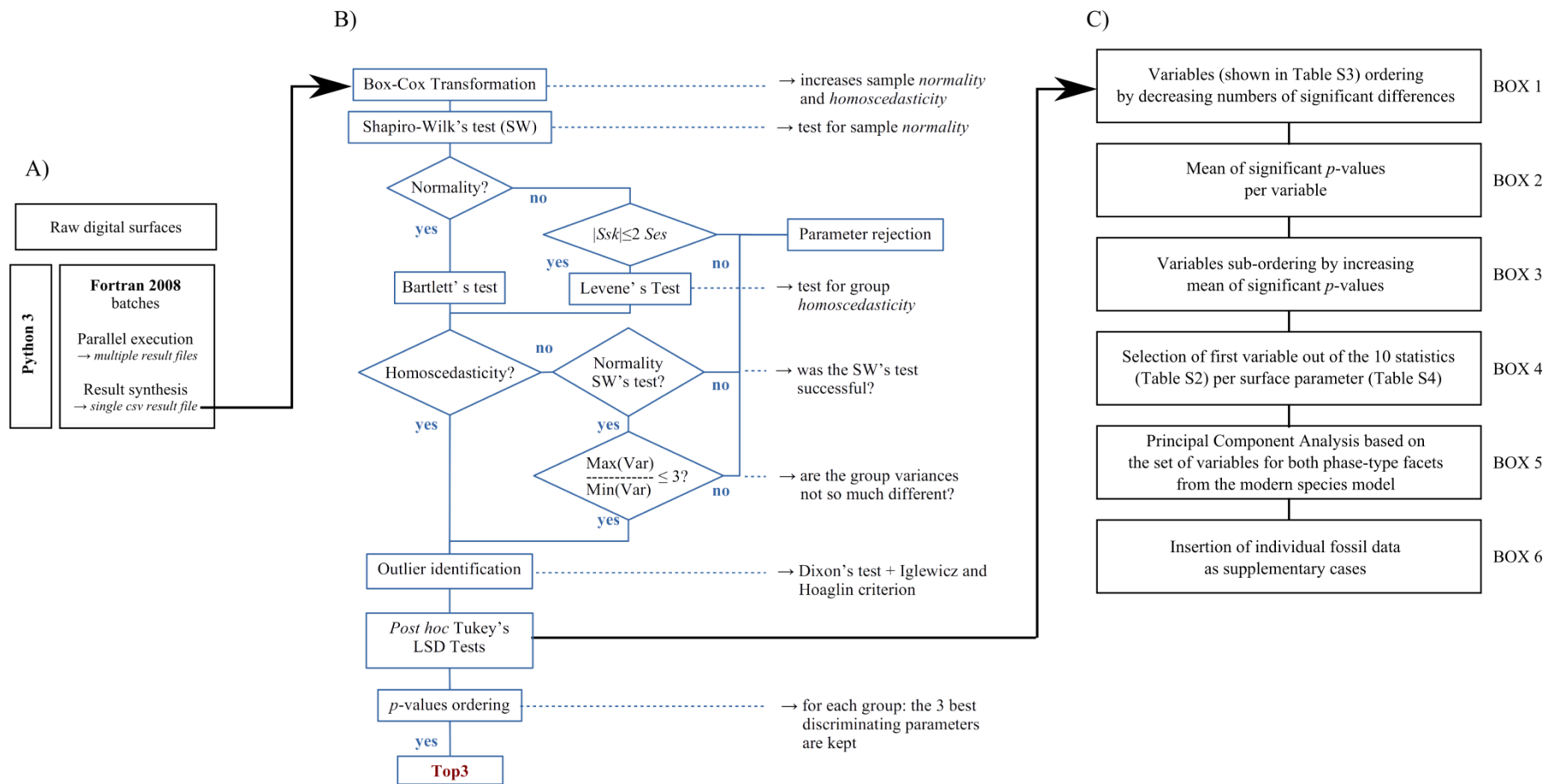


Figure 4: Workflow developed by Francisco et al. (2018b; A and B), and the implementation made in the present study (C).

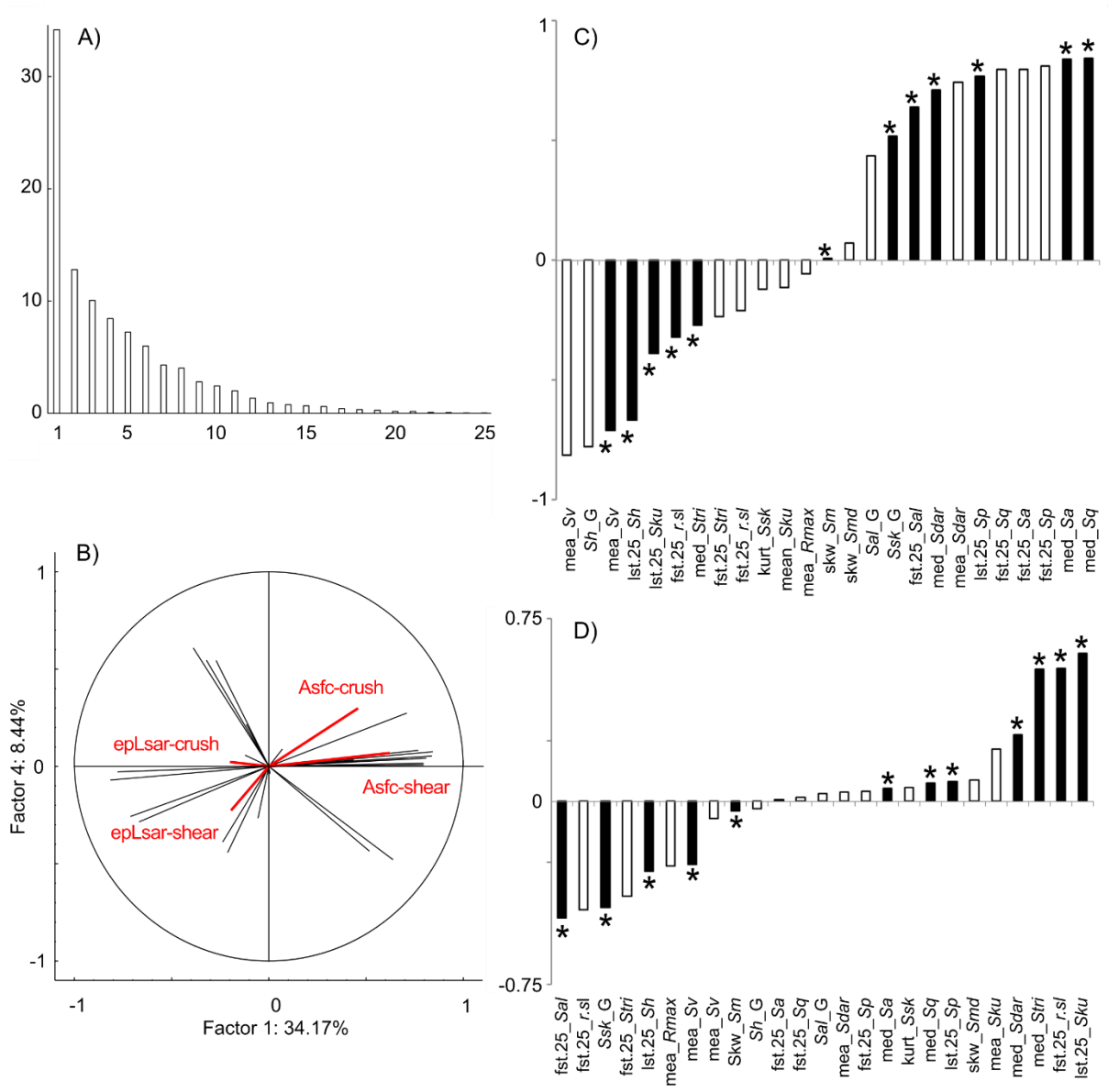


Figure 5. Principal Component Analysis based on the 25 most discriminant variables issued from both phase I and II facets of extant monkeys. Eigenvalues of the principal components (A), circle of correlation including active and supplementary variables (*Asfc* and *epLsar* on each facet) along PC1 and PC4 (B), contributions of variables on phase I (empty bars) and phase II (filled black bars with asterisk) facets along PC1 (C) and PC4 (D) with prefixes referring to statistics type whereas the suffix “G” refers to the global value calculated on the whole surface (see Table S2).

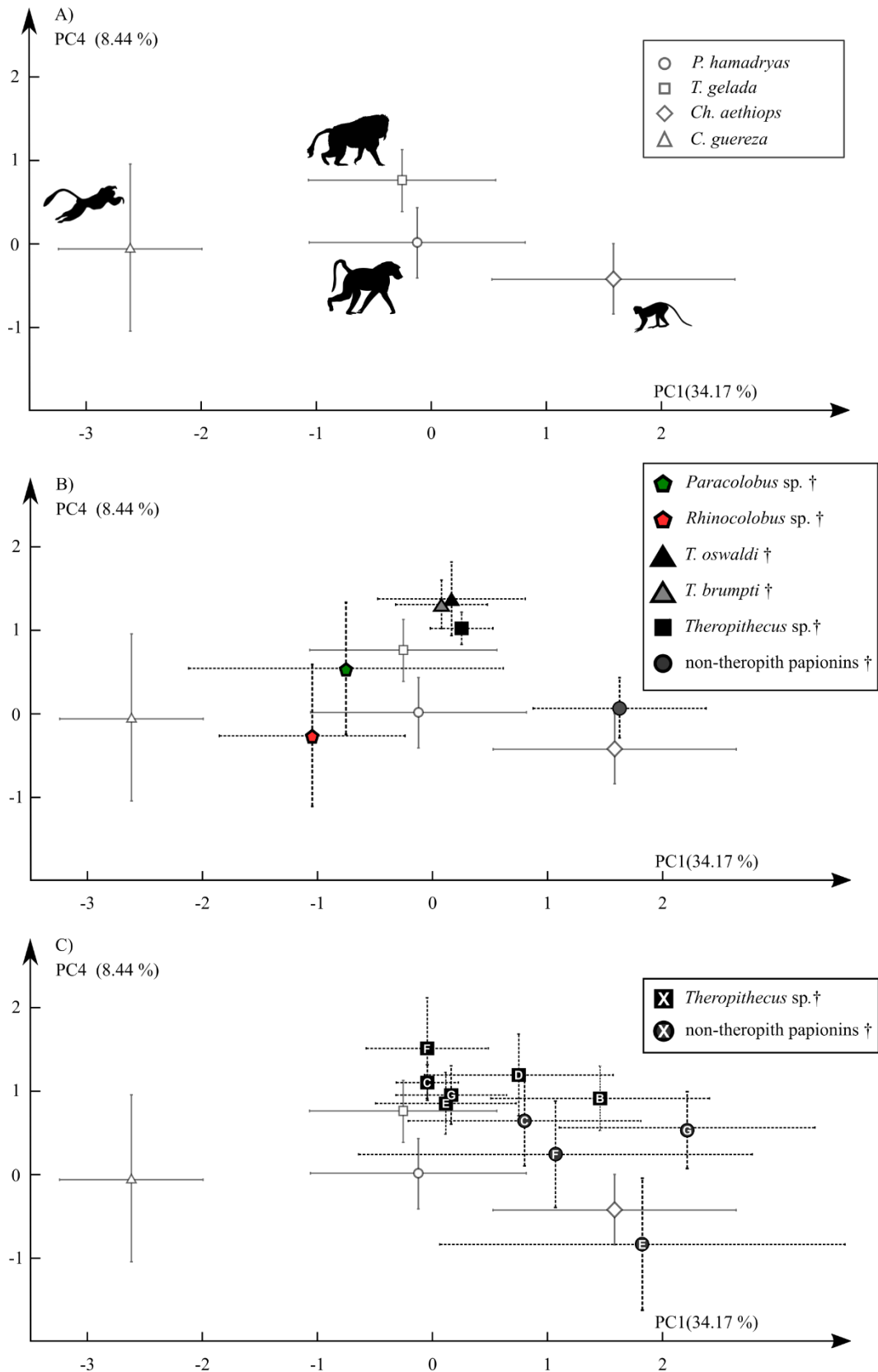


Figure 6. Distribution along PC1 and PC4 of investigated samples (mean and mean confidence interval at 95%) of extant monkeys (A) with extinct monkeys grouped as taxa (B), with extinct non-theropith papionins and *Theropithecus* (C) grouped by Member and labelled with Member capitalized letters in the symbol (see Figure for PCA details).

3.3. Insertion of extinct monkeys from the Shungura Formation into the model

The two large colobines from the Shungura Formation plot between *C. guereza* and the two extant papionins along PC1 but differ from the extant colobines in having higher coordinates along PC1 (Figure 6; Table S6). *Paracolobus* significantly differs from all extant monkeys but *T. gelada* from its coordinates along PC3 (Figure S3, Table S6), from the *Ch. aethiops* along PC4. (Figure 6, Table S6). *Rhinocolobus* significantly differs from *Ch. aethiops* and *C. guereza* in having higher coordinates along PC3, and from *T. gelada* in having lower ones along PC4. The sample of extinct non-theropith papionins strongly differs from both extant and extinct taxa along PC1 with the exception of *Ch. aethiops* and *T. oswaldi* (most likely due to its small size; Figure 6, Table S6). The extinct non-theropith papionins have also higher coordinates than *C. guereza*, *Ch. aethiops* and *P. hamadryas* along PC3. It also differs along PC4 from the extant and extinct *Theropithecus*. *Theropithecus* sp. and *T. brumpti*, significantly differ from *C. guereza* and *Ch. aethiops* in PC1, PC3 and PC4. The third theropith, *T. oswaldi*, displays the same pattern, but due to its small sample size, differences between *T. oswaldi* and *Ch. aethiops* are not significant. There is no difference between the three samples of extinct theropiths and the gelada (Figure 6, Figure S3, Table S6).

The four samples of extinct non-theropith papionins from members C, E, F, and lower part of the Member G plot on the positive ranges of coordinates along PC1 between the two extant papionins and *Ch. aethiops*, and cover the whole range from *T. gelada* and *Ch. aethiops* along PC4 (Figure 6). Variations along PC3 are smaller (Figure S3). There are significant differences, with non-theropith papionins from Member E having the lowest coordinates along PC4 and thus plotting

next to the extant *Ch. aethiops* (Figure 6, Table S6). All samples of extinct *Theropithecus* plot next to the extant gelada along PC1 except for the earliest population from Member B, which plot between the two extant papionins and *Ch. aethiops*. These early theropiths differ from the most recent ones in the sample in having significant higher values in PC1.

Between-genus variations are significant from members E to G. *Theropithecus* from member E differ from contemporaneous non-theropith papionins in having higher values in PC3 and PC4, reflecting dental microwear texture similar to that of the *T. gelada*, whereas the extinct non-theropith papionins shows strong similarities with *Ch. aethiops* (Figures 6 and S3, Table S6). Significant differences along PC4 supports the same difference between the two samples of extinct papionins from members F (Figure 6, Table S6). In Member G, the extinct non-theropith papionins differ from *Theropithecus* in having higher value in PC1 and lower ones along PC3, reflecting a pattern similar to that the one seen between the extant gelada and vervet (Figure S3, Table S6).

4. Discussion

Based on the extant monkey model, four ecospace can be defined (Figures 6 and S3). Low values along PC1 undoubtedly correspond to leaf-eating monkeys such as *C. guereza* with a small contribution of fruits or seeds and with no or at least few exogenous particles. Highest values along PC1 clearly identify opportunistic species such as *Ch. aethiops* including challenging food items. One may have expected higher coordinates along PC1 for the sample of *P. hamadryas* as its diet contains a wide spectrum of food including tough and hard items such as underground storage organs (USOs), fruits, seeds (Scott et al., 2012 and citations therein). However, from one population to

another over Africa, and from one season to another, the dietary composition of extant baboons is highly versatile, with fruit intakes varying from less than 5% to more than 60% and USOs from less than 5% up to 50% of the diet (see figure 2 in Scott et al., 2012). Such a wide spectrum of diets depending on location, season and food resources available in the habitat, is expected to produce different dental microwear textures from one sample to another, ultimately covering the whole range from the gelada to the vervet's ecospace. Besides, while the extant gelada was seen as a grass-eating specialist (Iwamoto, 1993), recent studies depict a less selective diet as this terrestrial monkey forages for dicots and even USOs at some places during some seasons (Fashing et al., 2014; Abu et al., 2017; Jarvey et al., 2018; Souron, 2018). This pictures fewer ecological contrasts between extant gelada and hamadryas baboons notably when exploiting fallback foods and explains the less contrasted than expected differences in dental microwear textures between these two samples of extant *Papio* and *Theropithecus*. PC3 and PC4 complete the picture by significantly discriminating the dental microwear textures of the two papionins, *T. gelada* being the most specialized one with very high intakes of both monocots and dicots (to a lesser extent) from the herbaceous layer. One could guess that the differences between *Theropithecus* on one hand and *Papio* and *Chlorocebus* on the other hand (as well as *Colobus* to a lesser extent) may also be driven by differences in tooth morphology and chewing mechanics. The model is here composed of four cercopithecoid monkeys sharing the same pattern of occlusal molar morphology. This strongly reduces the source of variations due to chewing mechanics, so we assume that the differences in dental microwear textures on both phase I and phase II molar facets are mainly driven by differences in diet.

The two extinct colobines, *Paracolobus* and *Rhinocolobus*, do not plot

next to *C. guereza*. This is actually not unexpected. Indeed, *C. guereza* does not cover the whole dietary range of extant Asian and African colobines, but is considered the most leaf-eating member of the subfamily (Ibrahim et al., 2017; Shumet and Yihune, 2017). Other extant colobines, notably the Asian ones include significant amount of unripe fruits and seeds in their diet (Bennett and Davies, 1994; Guo et al., 2007). Such dietary habits for extinct colobines were proposed for *Mesopithecus pentelicus* from the late Miocene of Europe based on their molar microwear textures (Merceron et al., 2009; Thiery et al., 2017). Being more than twice as large as extant colobines and having different postcranial morphologies, it is likely that *Paracolobus* and *Rhinocolobus* from the Shungura Formation had both different behavioural and feeding ecologies from the present-day *C. guereza* (Leakey, 1987; Harrison, 2011; Anderson et al., 2017; Pallas et al., 2020).

These results on extinct papionins strongly support dietary discrimination between the two genera. The extinct forms of *Theropithecus*, at least in the Omo River Valley, targeted food resources from the vegetal layers in the same way as the extant gelada does. Former studies based on dental microwear analysis and enamel carbon stable isotope composition have drawn similar conclusions (Lee-Thorp et al., 1989; Teaford, 1993; El-Zaatari et al., 2005; Cerling et al., 2013; Williams, 2014; Shapiro et al., 2016; Souron, 2018). A recent study, however, indicates that *T. oswaldi* from the Pleistocene in Spain may have included hard food items in its diet (Martínez et al., 2020). Besides, its locomotor appendicular skeleton shows that this species may have had behavioural habits similar to extant *Papio*, being able to exploit arboreal substrates (Elton, 2002). The wide distribution of the genus in and out Africa, covering various environmental contexts at different latitudes, implies that *T. oswaldi* was undoubtedly more plastic than the present-day refuge gelada in

Ethiopia. However, the present analysis attests that along the Omo Valley, *T. oswaldi* fed mostly on aerial parts of herbaceous dicots and monocots as the present-day gelada does. The differences seen between extant *Papio* and the extinct samples of non-theropith papionins are actually not unexpected. First, as said above there is no guarantee to have a taxonomic homogenous sample composed of specimens belonging to *Papio*. Besides, as said above, Scott et al. (2012) summarized the dietary composition of populations of *Papio* distributed over Africa and the southern Arabian Peninsula and found out that the proportion of fruits vary from less than 5% up to 60% whereas underground storage organs may represent half of the diet for certain populations. We may then expect great variations in dental microwear textures between extant populations of *Papio*, most likely covering the whole ecospace between extant gelada and vervets along the different PCs. There is no doubt that dental microwear textures on different populations of extant *Papio* would have overlapped with the ecospace defined by the extant *Ch. aethiops* and the different samples of extinct non-theropith papionins from the Shungura Formation.

Theropithecus from Member B incorporated more challenging foods than their relatives from upper members. It is worth noting that Negash et al. (2020) found out a significant increase of C₄ plants in the diet of extinct theropiths from Member B to upper members. Those plants being most likely terrestrial monocots. This dietary change can be regarded as a response to environmental changes. Indeed, by conducting a serial and bulk isotopic analysis on hippopotamid, suid and bovid teeth, Souron et al. (2012) and Bibi et al. (2013) detected an increase of C₄ food resources along the Omo Valley and climate seasonality from Members B to C (see also Negash et al., 2015, 2020; Blondel et al., 2018).

When focusing on ecological overlapping within members, significant differences between non-theropith papionins and *Theropithecus* were not found in Member C (partly due to the small sample of non-theropith papionins, $n = 8$), but are present for members E, F and G (Figure 6, Table S6). This suggests that *Theropithecus* were stenotopic primates, targeting food resources with less variable mechanical properties compared to those consumed by extinct non-theropith papionins, at least after 2.4 Ma. This supports previous paleo-ecological analyses (Cerling et al., 2013; Martin et al., 2018; Souron, 2018). However, while Martin et al. (2018), investigating separately the two facets through SSFA parameters, failed to detect differences between taxa in members E and F, the new approach presented here indicates low ecological overlap (in terms of dietary resources and likely in habitat use) between non-theropith papionins and *Theropithecus*. This emphasizes the benefit of the integrative analytical approach including surface sampling and phase I and II facets.

5. Conclusions

The present study aims at providing a new analytical approach to expand the usefulness of Dental Microwear Texture Analysis in primates. This includes the combination of phase I and II facets together with a surface sampling strategy aimed at measuring different statistics for a whole set of texture parameters. The results, and notably the Principal Component Analyses built with the most discriminant variables derived from the surface sampling, show that phase I facets should not be discarded as they also carry additional dietary signal as useful as the phase II facets. Our results show that the combination of the two facets makes the dietary discrimination more effective. In addition, half of the discriminant variables are not central values (mean, median) but

instead dispersion statistics of these surface texture parameters. This actually mimics the approach used by researchers using stereo-light microscopy when they quantify the frequency of large pits or wide scratches. When applied on the extant monkey model, the dietary discrimination is improved compared to former studies.

The extant species model allows us to track dietary differences between extinct monkeys of the Shungura Formation, with the baboon-like papionins with the most diverse diet including hard items. The two large colobines differ from the extant *Colobus guereza*, suggesting that they were less engaged in folivory than this African colobine. The samples of gelada-like papionins show no difference from the extant sample of geladas supporting a similar feeding ecology. The new DMTA approach found niche differences between the two extinct genera of papionins from 2.4 to 2.0 Ma. The present study provides new evidence that this dental proxy can

indeed document niche partitioning among extant species as well as in the Plio-Pleistocene fossil record from the Omo River valley.

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